RESEARCH ARTICLE*

Artificial light at night alters grassland vegetation species composition and phenology

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Abstract

1. Human settlements and transport networks are growing rapidly worldwide. Since the early 20th century their expansion has been accompanied by increasing illumination of the environment at night, a trend that is likely to continue over the decades to come. Consequently, a growing proportion of the world's ecosystems are exposed to artificial light at night, profoundly altering natural cycles of light and darkness. While in recent years there have been advances in our understanding of the effects of artificial light at night on the behaviour and physiology of animals in the wild, much less is known about the impacts on wild plants and natural or semi-natural vegetation composition. This is surprising, as effects of low-intensity light at night on flowering, phenology and growth form are well known in laboratory and greenhouse studies.

2. In a long-term experimental field study we exposed a semi-natural grassland to artificial light at intensities and wavelengths typical of those experienced by roadside vegetation under street lighting.

3. We found that lighting affected the trajectory of vegetation change, leading to significant differences in biomass and plant cover in the dominant species.

4. Changes in flowering phenology were variable between years, with grass species flowering between 4 days earlier and 12 days later under artificial light.

5. Policy implications. Our results demonstrate that artificial light, at levels equivalent to those in street-lit environments, can affect species composition in semi-natural vegetation. This highlights the importance of considering artificial light as a driver of vegetation change in urban, suburban and semi-natural ecosystems, and where possible, of minimising or excluding artificial light from habitats of conservation importance.

KEYWORDS
artificial light, flowering, grasslands, human-impacted environments, light pollution, phenology, photoperiodism, photopollution, plants, vegetation community

1 | INTRODUCTION

Settlements, industry and infrastructure have been associated for over a century with increasing levels of electric light at night in both the developing and developed world (Amaral, Monteiro, Camara, & Quintanilha, 2006; Bennie, Davies, Cruse, Inger, & Gaston, 2015; Bennie, Duffy, Davies, Correa-Cano, & Gaston, 2015; Jakle, 2001; Li et al., 2013). Artificial light intensity in the night time environment is estimated to be increasing globally at a rate of around 6% per year (Hölker et al., 2010), analyses of night-time satellite images show that the proportion of the world's land surface illuminated to a level that is considered light-polluted has increased to 23% (Cinzano, Falchi, &
Elvidge, 2001; Falchi et al., 2016), and a study of protected areas has revealed widespread incursion of artificial nighttime lighting into even the most protected habitats (Gaston, Duffy, & Bennie, 2015). These trends are set to continue, with urban areas predicted to triple in global extent in the coming decades (Seto, Guneralp, & Hutyra, 2012) and transport networks (road and rail) to increase in length by 60% (Dulac, 2013).

A diverse range of animal taxa are now known to be affected by night-time lighting including birds (Dominoni, Quetting, & Partecke, 2013; Kempnaers et al., 2010; Kempnaers et al., 2013), bats (Stone, Jones, & Harris, 2009, 2012), sea turtles (Witherington & Bjorndal, 1991), marine and terrestrial invertebrates (Davies, Bennie, & Gaston, 2012; Davies, Coleman, Griffith, & Jenkins, 2015; Frank, 2006), with known impacts including those on animal navigation, foraging, habitat selection and the composition of species assemblages. Habitats that are commonly illuminated at night, including road verges, hedges, rows, domestic gardens and urban ecosystems are increasingly recognised as important components of the landscape for biodiversity conservation, connectivity and maintenance of ecosystem services (Gaston et al., 2013). Yet while the impacts of artificial light on animals have become increasingly well documented, and their importance recognised, effects on natural and semi-natural vegetation are comparatively less well studied (Bennie, Davies, Cruze, & Gaston, 2016; Briggs, 2006). It has long been observed that artificial light at night has biological impacts on plants in urban settings, but such effects have rarely been quantified empirically. Street lighting, for example, can cause some urban trees to retain their leaves longer (Briggs, 2006; Matzke, 1936; Schroeder, 1945), affect flowering and yields in crops (Chen, Su, Liu, & Lee, 2009; Sinnadurai, 1981), and alter flowering and growth form in ornamental garden plants (Cathey & Campbell, 1975). Meanwhile many experimental studies have shown that light at low intensities and of short duration can have physiological effects on plants under controlled conditions (e.g. Smith, 1982). Plants utilise natural light to detect their position within the canopy, the proximity of neighbouring competitors and the length of the day, as well as a source of energy via photosynthesis (Smith, 1982). Artificial light is known to disrupt photoperiod detection systems, or trigger variation in growth form and resource allocation (Bennie et al., 2016), which could in turn produce changes in abundance, biomass and species composition. Experimental studies on grasses have shown that artificially increasing daylength can lead to an increased dry matter production and alter production of tillers (Mitchell & Lucanus, 1962), and that altering photoperiod, independently of temperature or total light flux, can affect the initiation and rate of reproductive development, and change the rate of dry matter production and leaf area expansion in many species (Adams & Langton, 2005; Hay, 1990; Hay & Heide, 1983).

The mechanisms for these effects are unclear, but it is likely that both the photoreceptor pigment phytochrome and gibberellins, the growth regulating hormones are involved (Adams & Langton, 2005). Since phytochrome is regulated by red and far-red light, bulb types which emit light at longer wavelengths (including high- and low-pressure sodium bulbs, a common technology for street lighting) may be more effective in producing a plant response than white spectrum white lighting (Bennie et al., 2016). The promotion of new leaf growth by lengthening days may lead to a feedback effect whereby increased leaf area leads to an increase in photosynthesis and hence biomass production (Hay, 1990). In so-called ‘long-day’ plants, including most temperate grasses, exposure to an extended photoperiod leads to earlier flowering under controlled conditions, again probably via the phytochrome pathway (Woods, Ream, Minevich, Hobert, & Amasino, 2014). However, under field conditions, temperature, vernalisation and photoperiod cues interact to determine flowering phenology (Körner & Basler, 2010), so it is unclear whether the effects of artificial lighting on phenology are expected to be widespread in the environment. In addition to these direct effects on plant growth and physiology, indirect effects, mediated through effects of artificial lights on the behaviour, abundance or aggregation of herbivores (Bennie, Davies, et al., 2015) or pollinators (Macgregor, Pocock, Fox, & Evans, 2015) may also play a role in impacting vegetation. It is clear that several potential physiological and ecological pathways exist via which artificial light may influence plant population dynamics and vegetation community composition. However, while physiological studies demonstrate clear direct effects of photoperiod on the growth of individual plants, and the experimental treatments used typically extend photoperiod using low intensity artificial illumination, experimental studies investigating the effects on natural plant communities under treatments designed to be comparable to the intensity and spectral composition of artificial light in the environment have not previously been undertaken. For several other anthropogenic stressors such as ozone (Barbo, Chappelka, Somers, Miller-Goodman, & Stolte, 1998) and anthropogenic nitrogen deposition (Wedin & Tilman, 1996), or climatic factors such as temperature and moisture (Grime et al., 2008), manipulative field experiments in natural plant communities have shown how physiological effects are manifested as impacts at the population and community level. However similar studies on the effects of artificial light at night on the composition of vegetation in natural systems are lacking.

Here we report the results of a long-term manipulative field experiment designed to determine the effects of artificial light at night on species composition and flowering phenology in a semi-natural grassland with composition and management similar to those of many roadside grass verges in the region. While artificial light at night increasingly encroaches into many ecosystems, we have focused here on simulating light in a roadside grassland system for two reasons. Firstly, in urban and suburban environments artificial light illuminates larger areas of low-lying vegetation, such as grassland, than forest or shrub vegetation because there is limited horizontal shading of direct light by the vegetation canopy. Secondly, while natural or semi-natural grassland has declined in many agricultural landscape (by 90% in lowland agricultural landscapes in the UK since 1945), a significant area remains along road verges which may be an increasingly significant resource for biodiversity (UK National Ecosystem Assessment 2011). The illuminance and spectral power distributions of the light treatments in this experiment were designed to simulate a light environment typical of roadside vegetation under street lights; a white LED treatment similar to broad-spectrum cool white
LED street lighting, emitting light at wavelengths between 400 and 750 nm with peak emittance in the blue portion of the spectrum, and a near-monochromatic ‘amber’ LED treatment designed to simulate low pressure sodium lighting with narrow peak emittance at around 588 nm (Figure S1). We also simulated two white lighting regimes that might have potential to mitigate any effects of street lighting on plant communities (Gaston, Davies, Bennie, & Hopkins, 2012); a low intensity regime of approximately half the intensity of the standard treatment, and a part-night lighting regime. Together the treatments were designed to investigate how recent changes in outdoor lighting technology from narrow-band sodium lighting to white LEDs, or strategies to mitigate the ecological effects of lighting such as dimming or part-night switching off may affect the impacts of artificial light at night on plant communities.

Two of the dominant grass species in the system (Agrostis tenuis and Holcus lanatus) have previously been shown to increase their dry weight production when grown as individual plants at constant temperature under a 16 hr photoperiod, compared to an 8 hr photoperiod (Mitchell & Lucanus, 1962). However, it was unclear whether comparable effects would be present when species were grown together in a natural sward under realistic ‘street lighting’ conditions. We hypothesised that artificial light treatments would significantly alter the biomass and cover and lead to an earlier flowering phenology in the three dominant grass species in the system, and alter the community composition of the vegetation.

2 | MATERIALS AND METHODS

2.1 | Field site and experimental set-up

The field experiment is located within the Lizard National Nature Reserve, Cornwall, UK (50°2′N, 5°12′W) in an unfertilised grassland on shallow, poorly drained gley soil overlaying ultrabasic serpentinite rock. Prior to the start of the experiment, the grassland was managed by grazing by sheep and ponies; in summer 2011 an experimental area, measuring 35 × 35 m was enclosed with a stock and rabbit-proof fence. This area was subsequently cut twice a year, in September and March, simulating the management regime used in many roadside verges in the UK. The vegetation within the experimental area was fairly uniform and dominated by three native grass species, A. tenuis, Anthoxanthum odoratum and H. lanatus (74% of total cover in 2011, 96% over the duration of the experiment), with forb species including Lotus pedunculatus, Trifolium repens, Cirsium palustre, Plantago lanceolate, Ranunculus acris and Prunella vulgaris locally frequent. Within this area, a grid of experimental plots was established, each plot measuring 4 × 4 m and with a 1 m margin between plots. Measurements reported in this paper are all from the central 1 m² of each plot.

30 plots were selected at random and allocated to one of the five treatments (six replicates per treatment). Lit treatments consisted of a panel of LEDs mounted 1 m above the ground on a wooden frame in the centre of the plot, with plywood shades fitted so that only the 4 × 4 m plot received direct illumination from the panel, and areas outside the plot received no direct light. The LEDs were powered by 12 V, 125 Ah vehicle batteries recharged by an array of solar panels, and controlled by a light-sensitive switch to turn on at dusk and off at dawn. Each battery had a load of approximately 0.5 A drawn from the LEDs. The treatments were (1) high intensity white (HIW) light, on which the number of individual LEDs on the panel was designed to give a surface nighttime illuminance of approximately 30 lx above ambient at ground level directly below the panel (measured values 29.6 ± 1.2 SE lx); (2) low intensity white (LIW) light, as for HIW but with fewer LEDs to give half the surface illuminance (14.6 ± 0.3 SE lx); (3) low intensity part-night lighting (LIWT), as for LIW but with an additional timer switch fitted to switch the lights off between midnight and 04.00 h (measured values 14.4 ± 0.8 lx); (4) amber light (AMB), as for HIW but with near monochromatic LEDs emitting amber light with a peak emittance at a wavelength of 588 nm and illuminance at ground level of 18.2 ± 1.3 lx; (5) an unlit control, which had a dummy wooden structure identical to the other treatments, but no lights. See Figure S1 for images of the experimental set up.

As in a previous experiment using the same lighting system (Bennie, Davies, et al., 2015), the illuminance and spectral power distributions of treatments were designed to simulate the light environment within suburban or rural roadside vegetation in the UK. The white LEDs are similar to broad-spectrum cool white LED street lighting, with peak emittance in the blue portion of the spectrum, while the amber treatment is similar in peak emittance to low pressure sodium lighting (Figure S1). The light treatments were switched on in April 2012 and regularly monitored to ensure the treatments ran continuously throughout the experiment. Light spectra of the treatments were measured using a spectrometer (Maya 2000 Pro; Ocean Optics, Dunedin FL), and illuminance was measured using a photodiometer calibrated to a CIE curve (HD2102.2, Delta Ohm, Caselle di Selvazzano, Italy). We measure and report illuminance here in lux (lx) for consistency with standards within the lighting industry and to allow direct comparisons with real-world lighting regimes, while acknowledging that measures of illuminance based on human vision alone may be poor proxies for biological effects (Bennie et al., 2016).

2.2 | Plant cover and biomass

Plant cover (frequency of pin hits from a point quadrat) and above-ground biomass were recorded to investigate both the spatial and dry mass-based composition of the vegetation. Both measures were recorded to distinguish between potential allocation-based expansion (for example leaf expansion or lateral rather than vertical growth) from changes in biomass. In late August each year from 2011 (prior to the light treatments being switched on) to 2015, plant cover was sampled along a 90 cm long transect parallel to the lighting rig in the centre portion of each experimental plot using a point-quadrat frame with 18 pins at 5 cm separation. At each pin drop, the identity of all species touching the pin were recorded.

In September of every year from 2012 onwards, prior to the mowing of the entire field, an above-ground biomass sample was taken from each plot. An area measuring 50 × 50 cm in the centre of the plot
was cut by hand to 2 cm height above ground level, air dried under ventilation in mesh bags at ambient room temperature for at least 48 hr (and until further mass loss was negligible) and sorted by species. The dry mass of each species was recorded.

2.3 Flowering and phenology

Every 2 weeks from April to September each year, the number of inflorescences of each species present was recorded. For the three dominant grass species (A. tenuis, A. odoratum and H. lanatus), inflorescences were counted in the central 1 m² of the plot only. The maturity of inflorescences were recorded on the following scale: flowering phase 1—Panicle/inflorescence/flower present but not fully emerged from sheaf or bud; flowering phase 2—panicle/inflorescence/flower fully emerged, petals not dry or fallen, fruit set not visible; flowering phase 3—petals dry or fallen, fruit set visible if applicable. In the current study, we utilise data from flowering phase 2 (fully emerged panicle) only.

2.4 Data analysis

Differences in vegetation composition (cover of all species) were assessed separately for each year by analysis of variance using permutational Multivariate Analysis of Variance (perMANOVA) with Bray–Curtis dissimilarity matrices calculated from square root transformed plant percentage cover data, as implemented in the vegan package in R.

To assess the species-specific responses, biomass and total number of inflorescences (summed throughout the season) were analysed as separate linear mixed models for each of the three dominant grass species, with plot as a random effect (to allow for repeated measures), year and light treatments as fixed (categorical) effects and interactions between year and light treatment as fixed effects. Cover values were analysed as generalised linear mixed models with a binomial link function and the same fixed and random factors as above. In cases where the fixed effect of light treatment was nonsignificant but interaction terms were significant (indicating that there was no consistent effect of light treatment across years but that effects varied between years), the main effect was removed and the interaction term retained.

To test for differences in flowering date, weighted mean flowering dates were calculated for each plot for each species in each year as the mean value of the Julian day of the year of each survey multiplied by the number of inflorescences observed, divided by the total number of inflorescences observed for that year. As above, differences in flowering date were tested using linear models with year as a categorical fixed effect interacting with light treatments, and plot as a random effect, and the fixed effect of light was dropped from the model if nonsignificant. Models were implemented using the nlme package in R (version 3.0.1). In all linear mixed models normality of residuals was checked visually using Q–Q plots and homogeneity of variance confirmed using Levene’s tests.

3 RESULTS

3.1 Vegetation composition

No significant differences in species composition between plots allocated to different light treatments were detected prior to the start of the experiment in 2011, or for the first 2 years of the experiment, 2012 and 2013 (F = 0.94, p = 0.56; F = 0.71, p = 0.81; F = 1.34, p = 0.20).

![Figure 1](image-url) Cover, measured by point quadrat hits (max = 18) for three dominant grass species in each year. Experimental treatments: C = unlit control, A = amber light, H = higher intensity white light, L = lower intensity white light, P = low intensity white part-night light. Stars represent annual significant differences between light treatments and the unlit control. *p < .05, **p < .01, ***p < .001
In both 2014 and 2015, however, there were significant effects of the artificial light treatments on species composition ($F = 0.24, p = .034$; $F = 2.48, p = .007$).

Significant differences in cover (frequency) values between light treatments and the control plots were most marked in *H. lanatus* (Figure 1, Table S3). For this species we detected significantly greater cover in plots lit by amber light in 2013, 2014 and 2015, greater cover in HIW plots in 2013 and 2014, and greater cover in LIW plots in 2015. These differences appear to be associated with a long-term decline in cover of this species in the control plots following the exclusion of grazing, while cover was fairly constant in lit plots, rather any increases over time in the lit plots. *Anthoxanthum odoratum* also had significantly greater cover in amber and LIW plots in 2014 and 2015 (Figure 1, Table S2). *Agrostis tenuis*, by contrast, had significantly lower cover values under amber light in both 2012 and 2015 (Figure 1, Table S1).

Significant differences in biomass of the three dominant grass species between light treatments also emerged during the study, although there was no significant effect of any treatment detected on overall biomass in any year (Figure 2, Table S4). *Agrostis tenuis* had significantly lower biomass in the LIW treatment in 2014, and in the amber, LIW and LIWT treatments in 2015. *Anthoxanthum odoratum* had significant higher biomass under amber light in 2015, and *H. lanatus* had significantly higher biomass under the HIW treatment in 2013, and under both the amber and HIW treatments in 2014. These results are broadly consistent with those recorded in cover/frequency, although the significance of effects varies between measures, suggesting linked patterns in spatial and dry mass composition.

### 3.2 Flower density and phenology

No significant differences in total annual flower density were detected under any treatment in any year for any of the three dominant grass species (Tables S8–S10).

Significant differences in mean flowering date occurred between years in all species; in 2013, flowering was 8 days later than in 2012 in *H. lanatus*, 9 days later in *A. tenuis* and 15 days later in *A. odoratum* (Tables S11–S13, Figure 3). In this year the late-flowering *A. tenuis* flowered on average 4 days earlier in both amber and HIW treatments ($p = .022$ and $p = .024$ respectively; Figure S11). In 2015, *A. odoratum* flowered on average 12 days later than in 2012 ($p < .001$), and a further 7 days later under amber lights ($p = .014$) and *A. tenuis* flowered 4 days later under the LIWT treatment.

### 4 DISCUSSION

This study demonstrates that artificial light, at illuminance levels and spectral power distributions equivalent to typical street lighting, can alter species composition, and the balance of cover and biomass between plant species in a natural vegetation community. This has important implications for biodiversity conservation not only in urban and suburban areas, but also in the increasing proportion of natural, semi-natural and agricultural ecosystems in the vicinity of settlements, industry or transport networks illuminated at night.

The mechanism behind the observed effects on composition is unclear. Some changes, such as the decline in *H. lanatus* cover and...
biomass in control plots but not in lit treatments and reverse trend in A. tenuis (Figures 1 and 2), seem to represent a resistance to changes in composition in lit treatments following successional changes after the cessation of grazing, rather than changes in vegetation structure induced by light. Plant growth form, resource allocation and phenol- ogy are all directly affected by artificial light in many species (Bennie et al., 2016), and in some temperate grasses artificially extended daylength can lead to increased or decreased production of tillers, and increased leaf area expansion and dry matter production (Adams & Langton, 2005; Hay, 1990; Hay & Heide, 1983; Mitchell & Lucanus, 1962). Differential effects between species are one explanation for the observed divergence between lit and dark plots in both biomass and cover. The particularly marked effects of the amber light treatment are consistent with previous observations that sodium lighting (or LEDs with similar spectral power distributions dominated by longer wavelengths) often have marked effects on flowering (Bennie, Davies, et al., 2015; Cathey & Campbell, 1975) and suggests a link to the phytochrome pathway in plants; phytochrome is sensitive to the ratio between red and far red light and the peak emissions of sodium lighting fall within its region of sensitivity (Bennie et al., 2016). Further experimental work is needed to establish if phytochrome-mediated processes are indeed altering the competitive balance between species. While direct effects on plant physiology are a plausible explanation for the observed effects on species composition, cover and biomass, we cannot rule out indirect effects, for example mediated through the effects of the light treatments on herbivory. Ecological effects of artificial light can cascade through trophic levels (Bennie, Davies, et al., 2015) and street lighting is known to change the composition of communities of grassland invertebrates (Davies et al., 2012, 2017); it is possible, although perhaps unlikely, that light-mediated changes in the abundance of invertebrate herbivores impacted the vegetation. While large vertebrate herbivores were excluded from the site, following the cessation of grazing field voles (Microtus agrestis) became abundant in the tall grass. Microtus voles can have marked effects on species composition in grasslands (Howe, Zorn-Arnold, Sullivan, & Brown, 2006), and their nocturnal activity may be modified by the presence of artificial light as a predator avoidance strategy.

**FIGURE 3** Mean flowering dates of three dominant grass species in each year. Experimental treatments: C = unlit control, A = amber light, H = higher intensity white light, L = lower intensity white light, P = low intensity white part-night light. Bar plots represent show median values (thick line), inter-quartile range (coloured bar) and 95% range with outliers [Colour figure can be viewed at wileyonlinelibrary.com]
While artificial light treatments did not consistently cause earlier flowering, we did detect some limited significant effects of light on flowering phenology on the grasses in the experimental plots. It is notable that in 2013, which was an unusually cold spring in the UK (reportedly the coldest for over 50 years; UK Met Office, 2013), all three species flowered significantly later than in other years, but the late-flowering species *A. tenuis* flowered significantly earlier in both the amber and HIW plots than in control plots in this year. It is known that temperature and photoperiod co-limit spring phenological processes in many plant species (e.g. Basler & Körner, 2012), and the lack of direct effects of light for most species/year combinations in this experiment may reflect the dominant role of temperature in this system. Photoperiod (and hence the disruptive effect of artificial light) may assume a more prominent role in determining flowering phenology under unusual temperature conditions (Körner & Basler, 2010); either when temperature requirements for flowering are fulfilled later than usual (as in 2013), and so lengthening days are a more reliable cue for the advancing season, or when cues are fulfilled earlier, so short daylength can act as a check on early phenology in unusually warm winter conditions. If temperature cues are dominant, it suggests that the spring phenological effects of artificial light in natural systems, being mediated by the ambient spring temperature, may be rarer than might be expected by the abundance of evidence of daylength-cues for flowering in experimental studies. In such studies plants are typically maintained under temperature conditions suitable for flowering and artificial light treatments are employed to extend perceived daylength. However, it also raises the potential for interacting effects between climate change and artificial light disrupting phenological responses by masking daylength as a cue, given that in such a scenario, two major signals for seasonal phenology are altered. With continuing climate change, the effects of artificial light on phenology may become more apparent as temperature becomes a less reliable cue for the onset of spring.

If the observed compositional effects of artificial light on this system are typical of grassland ecosystems, and of vegetation communities as a whole, then it is likely that such effects are widespread in the environment, and that globally artificial light at night is a driver of species composition in a considerable area of urban, suburban and roadside vegetation. The precise extent of the effect will depend on the intensity thresholds for ecological responses. The illuminance of the treatments used here were comparable to road verges in the vicinity of streetlights, and the lower intensity treatments (~15 lux) had significant effects in many cases; if the threshold for effects is lower than this, compositional effects may extend tens to hundreds of metres away from light sources. In the extreme case, detectable levels of artificial light can extend tens to hundreds of kilometres from cities, reflected within the atmosphere as ‘skyglow’ (Kyba, Ruhtz, Fischer, & Hölker, 2011) albeit at orders of magnitude lower than the levels used in this study. Further work is needed to establish dose–response relationships and wavelength-specific thresholds of light intensity at which light impacts on vegetation community structure and phenology. Research is also needed to identify the species (based on phylogeny, plant functional type or geographical origin) and communities most sensitive to artificial light at night, as at present there is little basis to predict to where and when impacts on vegetation will be most severe. Given the development of cover and biomass responses over several years, and the context-dependent effects of artificial light on phenology varying between years, this study demonstrates the need for manipulative, long term field experiments to elucidate the nature, extent and magnitude of impacts of artificial light in the environment.

In terms of the differences between lighting treatments, we found that amber lighting, simulating low-pressure sodium street lighting, generally had an effect of greater or equal significance and/or magnitude than white light treatments. It has been suggested that a recent shift from narrow-spectrum sodium lighting to broader spectrum white light sources may increase the ecological impacts on animal species (Gaston et al., 2012); however, the results of this study suggest that fitting or retaining sodium bulbs is not sufficient to prevent potential effects on plants and vegetation. The limited effects of the low intensity and low-intensity part-night treatments in most cases suggest that dimming and part-night lighting, by contrast, may help to limit the extent and severity of artificial light on natural vegetation. However, in some cases our low intensity light treatment appeared to have a larger effect than the high intensity treatment, so more experimental
work is clearly needed to establish dose-response or threshold relationships. The experimental design used here imposed an abrupt sharp edge to the illuminated plot using plywood shielding (see Figure 4); real street lighting is often characterised by more gradual gradients of light along which gradients of ecological effects may be observed. However, efficient lighting designs may impose sharp edges by shielding unnecessary illumination (particularly paths with a strong horizontal component) and focusing light where it is required.

In the light of the findings of this study, and in the absence of a clear understanding of the scope, spectral sensitivity and intensity thresholds of impacts of artificial light on vegetation communities, it seems sensible to adopt a precautionary approach and to seek to avoid night-time illumination of natural and semi-natural habitats except where there is a clear proven need for artificial light. Where there is such a need, light should be focused on where it is needed (for example footpaths and pavements), and unnecessary illumination of vegetation avoided (Gaston et al., 2012). This applies particularly for areas of particular interest for biodiversity or species conservation, or those providing key ecosystem services. Frequently illuminated habitats including roadside verges, hedgerows, parks and domestic gardens are increasingly valued for their potential for biodiversity conservation and for their role in connecting fragmented habitat patches and providing resources for pollinators (Cousins, 2006; Davies et al., 2009; Goddard, Dougill, & Benton, 2010; Hanley & Wilkins, 2015; Hovd & Skogen, 2005; Le Viol et al., 2008; Tikka, Högmander, & Koski, 2001). Such habitats are sometimes managed specifically for wildlife, as in the case of road-side nature reserves (Parr & Way, 1988). Opportunities to reduce the ecological consequences of artificial light at night range from novel adaptive lighting dimming technologies, to switching lighting off for all or part of the night or simple shielding to direct light only where it is most needed (Gaston et al., 2012). To minimise the effects of artificial light on natural and semi-natural ecosystems such opportunities should be taken wherever possible.

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AUTHORS’ CONTRIBUTIONS

K.J.G. conceived the idea for this study and secured funding. K.J.G., J.B., T.W.D. and D.C. designed the experiment. D.C., J.B. and T.W.D. built and maintained the experiment and J.B., D.C., T.W.D. and F.B. collected data. J.B., T.W.D. and F.B. analysed the data. J.B. wrote the initial manuscript and all authors contributed to subsequent revisions.

DATA ACCESSIBILITY

The data used in this manuscript are archived in the Open Research Exeter archive: http://hdl.handle.net/10871/27138.

REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.