RESEARCH ARTICLE

ECological Solutions and Evidence | **BRITISH ECOLOGICAL SOCIETY**

LED lighting threatens adult aquatic insects: Impact magnitude and distance thresholds

Deborah Carannante 🟢 | Claudia Sara Blumenstein | James David Hale | Raphaël Arlettaz 🟢

Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, Bern, Switzerland

Correspondence
Deborah Carannante, Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland.
Email: d.carannante@gmail.com

Deborah Carannante and Claudia Sara Blumenstein contributed equally to the study.

[Correction added on 22 June 2021, after first online publication: Conflict of Interest statement has been added.]

Abstract

1. Artificial light at night (ALAN) is increasing globally, and changing in quality due to the installation of white LED street lighting. ALAN is a threat to biodiversity and ecosystem functioning, yet important knowledge gaps exist regarding the magnitude of impacts and how these vary between habitats and levels of exposure. The disturbance of aquatic habitats by ALAN is of particular concern as human settlements and activities are often located near waterbodies, and many aquatic species are sensitive to ALAN.

2. Focusing on adult aquatic insects, an experimental approach was employed in the riparian zone of a structurally simplified river within a dark rural landscape. Two studies were used to (a) estimate the magnitude of the capture effect of white LED lamps and (b) to explore how captures at lamps vary with their distance from the river, and define any distance thresholds. Both studies sampled mayflies (Ephemeroptera), caddisflies (Trichoptera) and true flies (Diptera) repeatedly during mid-to-late summer using modified flight intercept traps positioned adjacent to portable LED lamps. In Study A, lit traps were paired with unlit controls. In Study B, lit traps were positioned at six distances up to a maximum of 80 m from the stream edge.

3. For each of the three study orders, captures were significantly higher in the lit treatment compared to the dark control, with medium to large effect sizes.

4. For all study orders, captures at lamps significantly reduced with increasing distance from the river edge. Rapid declines in captures were recorded for Trichoptera (from 10 m) and Ephemeroptera (40 m), with a more gradual decline in Diptera from 60 m that continued up to the maximum sample distance.

5. Previous research indicates that LED lighting can be less attractive to flying insects than broader spectrum alternatives. However, this study demonstrates that the effects of white LED lamps on flying adult aquatic insects should not be dismissed and can extend far from aquatic habitats. As a precautionary approach, and until finer recommendations are available, we recommend that LED lamps should be excluded from a buffer zone of ca. 40–60 m around rivers.

1 | INTRODUCTION

Light pollution is a global phenomenon (Falchi et al., 2016). Artificial lighting's varied effects on ecosystems have been known for some time (Longcore & Rich, 2004), yet it is an often-overlooked threat to biodiversity (Hölker et al., 2010). The global expansion and intensification of lighting emissions (Kyba et al., 2017), coupled with the widespread installation of white LED street lighting, has invigorated research interest in ecological light pollution (Sanders & Gaston, 2018). Artificial light at night (ALAN) can influence wildlife on the individual, population, community and ecosystem level by disrupting natural lighting cycles (Longcore & Rich, 2004) and potentially interacts with other anthropogenic pressures (Gaston et al., 2014). Including the management of ALAN within conservation and restoration initiatives is therefore justified. Research themes include impacts on rare or protected species (Stone et al., 2012), communities (Bennie et al., 2015; Hölker et al., 2015; Sanders & Gaston, 2018) and ecosystem functioning (Knop et al., 2017). Studies typically focus on lighting impacts and their variation by taxa, habitat type, lamp type and lighting dose (Longcore & Rich, 2004; Perkin et al., 2011; Stone et al., 2012; Wakefield et al., 2018). However, numerous knowledge gaps remain, including the magnitude of these impacts and their sensitivity to ecological context (Perkin et al., 2011)

The disturbance of aquatic habitats by ALAN is of particular concern because (a) human settlements are often concentrated near to water, mostly high-order rivers, particularly in temperate and cold regions (Kummu et al., 2011) and (b) many aquatic and semi-aquatic taxa show sensitivity to ALAN (Perkin et al., 2011; Rich & Longcore, 2006). Despite this threat, aquatic ecosystems are still relatively unexplored in the field of ecological light pollution (Gaston et al., 2014; Perkin et al., 2011). Rivers and riparian areas are particularly interesting from a wildlife conservation perspective as primary habitats, ecological corridors (conduits), and the interface between aquatic and terrestrial habitats. Given the close association of lighting emissions with human activity (Hale et al., 2013), key questions about the ecological consequences of ALAN within riparian habitats need to be addressed, for example, which taxa are most sensitive, what is the magnitude of any impacts and which locations should be prioritized for protection or mitigation?

More than 60% of invertebrate species are nocturnal (Hölker et al., 2010), and many react to ALAN (Eisenbeis, 2006). Profound declines in insect diversity, abundance and biomass have been reported (Forister et al., 2019; Hallmann et al., 2017; Wagner, 2019), and ALAN is assumed to be one of the many causes (Grubisic et al., 2018). Aquatic insects appear to be more affected by ALAN than their terrestrial counterparts (Perkin et al., 2014a), with many showing positive phototaxis and polarotaxis (Boda et al., 2014; Száz et al., 2015). In particular,

Ephemeroptera, Trichoptera and Diptera demonstrate disturbed behaviour due to ALAN (Perkin et al., 2014a). This is of concern, given the importance of aquatic insects as a source of food for aquatic and terrestrial predators (Perkin et al., 2011), and as bioindicators (Hodkinson & Jackson, 2005). Flying insects may suffer direct mortality at light sources due to collision with the lamp, attraction-exhaustion or predation (Eisenbeis, 2006; Perkin et al., 2011) with potential impacts on local insect populations. Furthermore, ALAN can act as an ecological trap by imitating natural environmental cues used for the detection of suitable habitats (Schlaepfer et al., 2002). Some species use horizontally polarized light reflected from the water surface to detect their oviposition sites (Horváth et al., 2009). However, oviposition can be disrupted by polarized ALAN reflecting from artificial surfaces (Száz et al., 2015), raising questions about long-term population impacts. Losses in reproductive success might scale up to substantial population declines (Perkin et al., 2011). Additionally, ALAN can inhibit night-time drift of larvae (Perkin et al., 2014b) and influence the emergence of adults from the water surface (Meyer & Sullivan, 2013).

The ecological structure and function of many waterbodies has already been damaged by stressors such as habitat degradation, chemical pollution, climate change, invasive species, and over-exploitation; ALAN poses an additional threat (Perkin et al., 2011). Estimates of impact magnitude are therefore important, enabling mitigation of artificial lighting to be prioritized in relation to other stressors.

Although the ecological impacts of artificial lighting above or along the edge of waterbodies are often conspicuous (e.g. Száz et al., 2015) and have received some research attention (Perkin et al., 2011; Tamir et al., 2017), relatively little is known about the disruption of aquatic communities by lamps positioned within the broader riparian zone. Riparian and aquatic habitats have a range of important functional connections including exchanges of organisms, energy and matter (Baxter et al., 2005; Muehlbauer et al., 2014; Schneider et al., 2002). Aquatic-terrestrial subsidies include both inputs of organic matter which are fed upon by aquatic detritivores, and the emergence of adult aquatic insects which provide food for terrestrial insectivores. The importance of riparian zones to aquatic communities is further illustrated by the presence of a terrestrial phase in the lifecycle of many aquatic insects, who use vegetated riparian areas for mating (e.g. swarming sites), moulting and as a place for resting or refuge (Erman, 1984).

Flying adult aquatic insects may be attracted to lamps located well away from a river (Manfrin et al., 2017), although it is unclear how these attraction/capture effects change with increasing perpendicular distance of lamps from the water's edge. Clarifying this proximity effect is an important step towards understanding the impact of riparian lighting on key processes such as lateral and upstream dispersal of flying aquatic insects (Bilton et al., 2001), and their predation by birds, bats, spiders, etc. (Baxter et al., 2005).

Here we test two broad hypotheses, framed to support conservation practice:

1. Operating white LED lamps in riparian areas increases the local abundance of flying adult aquatic insects.
2. As the distance between a white LED lamp and the river edge increases, a threshold is reached where its attraction effect on flying adult aquatic insects starts to decrease.

This study used an experimental approach within a dark rural landscape. We focused on three aquatic insect taxa known to be sensitive to ALAN: Ephemeroptera, Trichoptera and Diptera. Although widespread throughout Europe, Ephemeroptera and Trichoptera are often threatened at the national level (JNCC Report No. 367, 2003; Lubini et al., 2012). Thus, in this study, these taxa serve as indicators of direct threats to nature conservation. Diptera, notably Chironomidae, can be highly abundant in aquatic habitats (Ferrington, 2008) and are an important food source for many aquatic and terrestrial organisms (Baxter et al., 2005). We therefore include this group as an indicator of the broader potential impacts of artificial lighting on riparian food webs, focusing on a size range that is typically predated upon by a local bat species.

2 | MATERIALS AND METHODS

2.1 | Study area

Two studies were undertaken along the Gürbe river (46° 49' N, 7° 30' E; 500 - 600 m a.s.l.), a heavily straightened waterway flowing through intensive grassland in the lowlands of Bern, Switzerland. Lighting emission data from the satellite-mounted VIIRS sensor identify the study locations as relatively dark, with no permanent outdoor artificial lighting present within 200 m of the river edge (see Supplementary Information 1 for details). This choice of study area was intended to minimize variability between sample locations and to ensure sampling of a relatively light-naïve insect community.

2.2 | Study design

The two studies were conducted during the summer of 2017 and used the same trap design, lamp type and study site (see Supplementary Information 1 for details). White LED lamps were used in both studies, each positioned immediately adjacent to a modified flight intercept trap.

2.2.1 | Study A: Impact magnitude

This study addressed hypothesis 1, testing whether the presence of an operating white LED lamp adjacent to the river would attract more adults of our study orders compared to a non-operating lamp and also whether these capture effects would be reduced by placing lamps 40 m from the river edge. Crucially, it aimed to estimate the magnitude of any effects of ALAN (Sanders et al., 2020). This experiment was configured as a stratified random design with repeated measures. Four lit traps were each paired with an unlit control trap (referred to together as a *sample pair*) (Figure 1(a)). Treatment and control were separated from each other by 90 m. A lit treatment consisted of a modified flight intercept insect trap and a white LED lamp; the unlit control was identical, but the LED lamp remained switched off. Sample pairs were separated from each other by at least 200 m and stratified by an upstream and downstream block. Within each block, one sample pair was placed at 3 m and the other at 40 m from the river's edge (as measured along transects set perpendicular to the river axis). A total of eight traps were in operation each night (Figure 1(a)), with a total of six sampling nights. By the end of the experiment, each distance in each block had been sampled six times, resulting in a total of 48 samples (Supplementary Information 2).

2.2.2 | Study B: Distance thresholds

This study addressed hypothesis 2, testing whether the abundance of adults attracted by a white LED lamp would reduce with increasing distance of the lamp to the river edge. Crucially, it aimed to identify any distance thresholds, beyond which captures significantly reduced. The experiment was arranged in a stratified random design with repeated measures, in which a lit treatment (LED lamp + flight intercept trap) was randomly placed at six different distances (3, 10, 20, 40, 60 and 80 m) from the river edge (Figure 1(b)). These transects were spaced at least 300 m apart and again stratified by a downstream and upstream block. On the first sampling night, three lit traps were positioned in the downstream block at distances of 10, 40 and 80 m; another three lit traps were randomly allocated to the upstream block at distances of 3, 20 and 60 m. The following sampling night, distance allocations for each block were switched. Subsequent sampling nights repeated this pattern, with the caveat that no transects were sampled at the same distance more than once. The experiment was divided into two sampling sessions, each with three sampling nights (Supplementary Information 2), for a total of 36 samples.

2.3 | Lighting treatment

The lit treatment consisted of a battery-powered 20 W, 1500 lumen, white LED lamp (Apollo Light GmbH, Boizenburg, Germany; see Supplementary Information 3) fixed on a 2-m high wooden pole, facing the river and angled 45° towards the ground. By positioning the lamp at this angle, the lighting effects were more comparable to LED street lighting; surface illuminance was relatively even, the point lighting source itself was visible from the stream edge, and the lighting was directed below the horizontal plane.
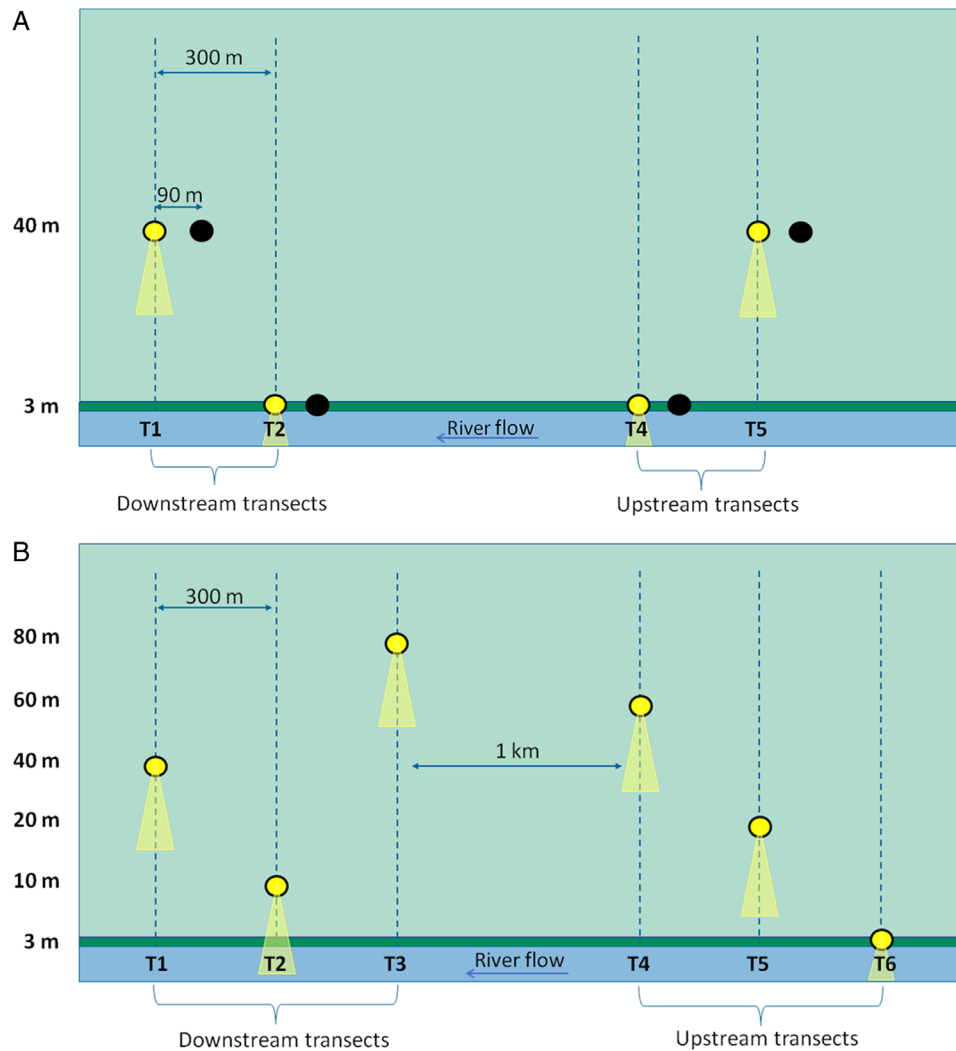
FIGURE 1 A typical sampling design for (a) Study A and (b) Study B. Yellow circles indicate traps with operating lights, and black circles indicate traps with lamps switched off (control). T1–T6 represent sampling transects set perpendicular to the river

2.4 | Insect sampling

Insects were sampled using flight intercept traps (Perkin et al., 2014a), modified with an additional sticky trap (Supplementary Information 1) to maximize the total number of individuals sampled. For the same reason, we undertook 2 min of hand collection for these groups starting 1.5 h after the beginning of the experiment. Hand collection was performed using a small paint brush to move the specimen into a plastic tube and targeted at individuals that had settled on the lamp or trap structure. The purpose of including Diptera in our analyses was to gain some indication of potential impacts on riparian food webs. The common pipistrelle *Pipistrellus pipistrellus* is highly active in this study location, and known to prey on Diptera within the body size range of 3–8 mm (Barlow, 1997). We therefore only recorded Diptera individuals within this size range. As we were interested in Diptera as a functional indicator of impacts on food availability for *P. pipistrellus*, family and sex identification were not undertaken for this group. Due to the large numbers of Diptera caught within our sticky traps, they were subsampled as in Calderone (1999).

2.5 | Sample dates and times

Sampling for both studies was undertaken between June and September 2017, to coincide with the peak in total community emergence (Baxter et al., 2005), and Ephemeroptera, Trichoptera in particular (Waringer, 1996). However, it is recognized that some Ephemeroptera, Trichoptera and Diptera species have emergence periods that fall outside of this sample window. Sample dates were separated by at least a week. Traps were set up immediately before sunset and operated for approximately 2.5 h (Supplementary Information 2), as the lamps battery life was approximately 3 h.

2.6 | Covariates

Data for the following variables were collected in the field, or from local monitoring stations: air temperature, relative humidity, wind speed, moon illuminance, grass height at the trap, width of the riparian vegetation strip, riparian tree cover, water flow and river water temperature,

sampling session, sampling night (Julian date), site number and the time gap between sunset and trap operation (time lag) (see Supplementary Information 4 for descriptions).

2.7 | Statistical analysis

Both studies used raw count data to create generalized linear mixed models (GLMMs) for each of the three orders, using the statistical software *R version 3.4.2* (R Development Core Team, 2017). We used *abundance* as the response variable, derived from the sum of the individuals in the sticky trap, the intercept trap and (for Ephemeroptera and Trichoptera) hand collection. The analyses of distance and lighting effects, assessed at order level, were performed using the *glmer* and *lmer* functions from the package *lme4* (Bates et al., 2014) or the *glmmadmb* function of the *glmmADMB* package (Skaug et al., 2018) for zero-inflated models. For highly correlated variables (Spearman's rank, /r/ >0.5), we selected the variable which correlated most strongly with the response variable and included it in the model selection process. Model selection was performed using the *dredge* function to obtain a list of possible models ranked by AIC (Akaike information criterion), and then by averaging the models within a subset of ΔAIC ≤ 2 using *model.avg* function, both from the package *MuMIn* (Bartoń, 2016). Overdispersion and zero-inflation were tested for using *testOverdispersion* and *testZeroInflation* functions from the package *DHARMa* (Hartig, 2017).

2.7.1 | Study A: Impact magnitude

For each of the study groups, the lit/unlit lighting treatment (*lighting*), the distance of the lamp from the river's edge (*distance*) and their interaction were included in the model as fixed effects. *Sample pairs* were added to each model as a random factor. When the interaction effect was not significant, the model was compared with the corresponding additive model using Akaike weights (Wagenmakers & Farrell, 2004) and the most parsimonious model was chosen. Ephemeroptera abundance was modelled using the *glmer* function assuming a Poisson distribution with an observation-level random effect to account for data over-dispersion (Harrison, 2014). Trichoptera and Diptera abundance were modelled assuming a negative binomial distribution. Effect size was calculated as Cohen's *d* (Durlak, 2009), using the function *cohen.d* from the package *effsize* (Torchiano, 2017).

2.7.2 | Study B: Distance thresholds

For all models, distance was included as a fixed effect and *transect* as a random factor. Ephemeroptera abundance was analysed using the *glmer* function assuming a Poisson distribution. Due to zero inflation, the Trichoptera abundance was analysed with the *glmmadmb* function, assuming a Poisson distribution with zero inflation. Diptera abundance was analysed with the *lmer* function assuming a normal distribution. For the post hoc analysis, a Tukey's test was performed

using the *glht* function of the *multcomp* package (Hothorn et al., 2008). Due to multiple comparisons of the six different distances from the river, the inflated false discovery rates were corrected for using the Benjamini–Hochberg method (Pike, 2011).

3 | RESULTS

3.1 | Study A: Impact magnitude

One hundred eighty-one Ephemeroptera, 2146 Trichoptera and 97,525 Diptera (body size range of 3–8 mm) were collected, for a total of 99,852 individuals (Supplementary Information 5). The average insect catch per hour per trap was approximately 412 insects in the lit treatment, and four insects in the unlit control. We identified a total of seven Ephemeroptera families and 12 Trichoptera families (Supplementary Information 6). These data exclude individuals from sticky traps, as removal of individuals inevitably damaged key diagnostic features. Of the 92 Ephemeroptera individuals captured by intercept trap and hand collection, 78 were females and 14 were males; similarly for Trichoptera, 743 females, and 67 males were captured.

Lighting significantly increased Ephemeroptera abundance at the treatment sites ($p < 0.001$) (Figure 2) with a medium Cohen's *d* effect size (Figure 3). No change in abundance between 3 and 40 m was detected ($p = 0.269$). Air temperature, tree cover and time lag had a significant negative effect on abundance (Supplementary Information 7).

Lighting significantly increased Trichoptera abundance at the treatment sites ($p < 0.001$), whilst distance reduced it ($p < 0.001$), both with a medium Cohen's *d* effect size. Water flow had a significant negative effect on abundance (Supplementary Information 7).

For Diptera, lighting significantly increased their abundance at the treatment sites ($p < 0.001$) with a large Cohen's *d* effect size, and grass height had a significant positive effect (Supplementary Information 7). No change in abundance between 3 and 40 m was detected ($p = 0.43$).

3.2 | Study B: Distance thresholds

Two hundred ten Ephemeroptera, 519 Trichoptera and 152,492 Diptera (body size range of 3 – 8 mm) were counted during this study, for a total of 153,221 individuals (Supplementary Information 8). The average catch per hour per lit trap was approximately 1702 insects. We identified a total of seven Ephemeroptera and nine Trichoptera families (Supplementary Information 6). Again, these data exclude individuals from sticky traps. Of the 210 Ephemeroptera individuals captured, 182 were female and 28 were male. For Trichoptera, 188 females and 28 males were captured in the intercept trap and hand collection.

Ephemeroptera abundance ranged from 0 to 30 individuals. Predicted mean Ephemeroptera abundance at 40 m was significantly less than at 3, 10 and 20 m, dropping rapidly by 50–60% (Figure 4(a); Supplementary Information 9). Abundance declined more gradually from 40 to 80 m, apparently reaching a plateau at 80 m. Water temperature

Fitted abundance by lighting
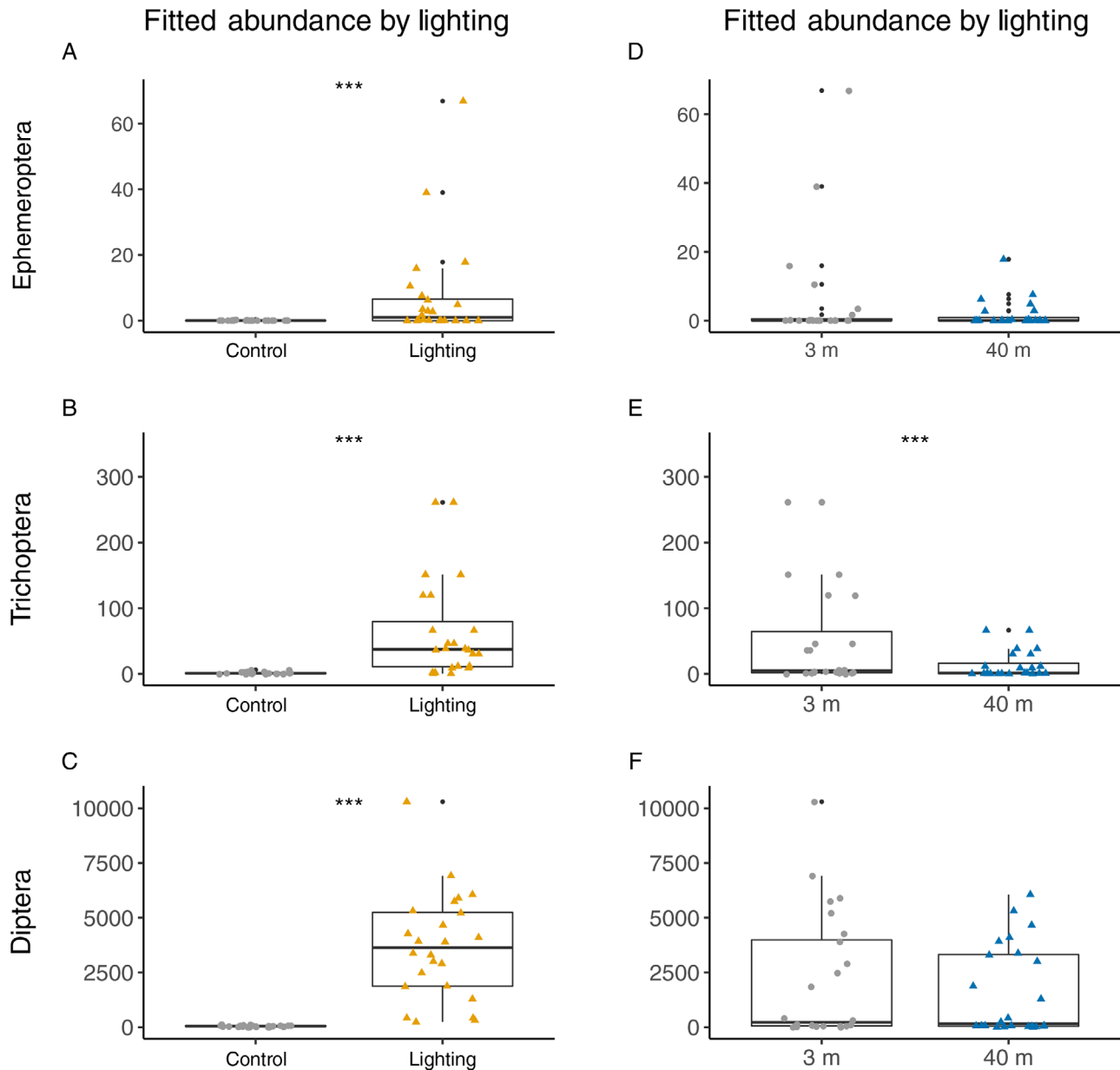
FIGURE 2 Fitted abundance of Ephemeroptera (a and d), Trichoptera (b and e) and Diptera (c and f) subjected to the lit/unlit lighting treatment (a, b and c) and to the two sampling distances (3 and 40 m) from the river's edge (d, e and f). Stars indicate a significant difference in abundance (*p < 0.05; ** p < 0.01; *** p < 0.001)

had a positive effect, whereas sampling session, grass height and time lag had a negative effect (Supplementary Information 9).

Trichoptera abundance varied from 0 to 126 individuals. Trichoptera abundance was significantly lower at 10, 20, 40, 60 and 80 m compared to 3 m, with the predicted mean falling by 75–90% (Figure 4(b); Supplementary Information 9). Air temperature and time lag had a positive effect, whereas site, sampling session, moon illuminance, and tree cover had a significant negative effect.

Diptera abundance varied between 81 and 10,508 individuals. Models revealed a gradual decrease with increasing distance from the river edge (Figure 4(c); Supplementary Information 9). The predicted mean Diptera abundance was 23% lower at 10 m compared to 3 m, but this

difference was only marginally significant. Compared to 3 m, the predicted mean Diptera abundance was significantly lower at both 60 m and 80 m. Water temperature had a significant positive effect, whereas sampling session, relative humidity, moon illuminance and grass height had significant negative effects on Diptera abundance.

4 | DISCUSSION

As ecological light pollution research reveals disturbance effects for ever more taxa, attention is turning to practical considerations around lighting dose and mitigation (Gaston et al., 2012). A key question is

Lighting effect size

Distance effect size
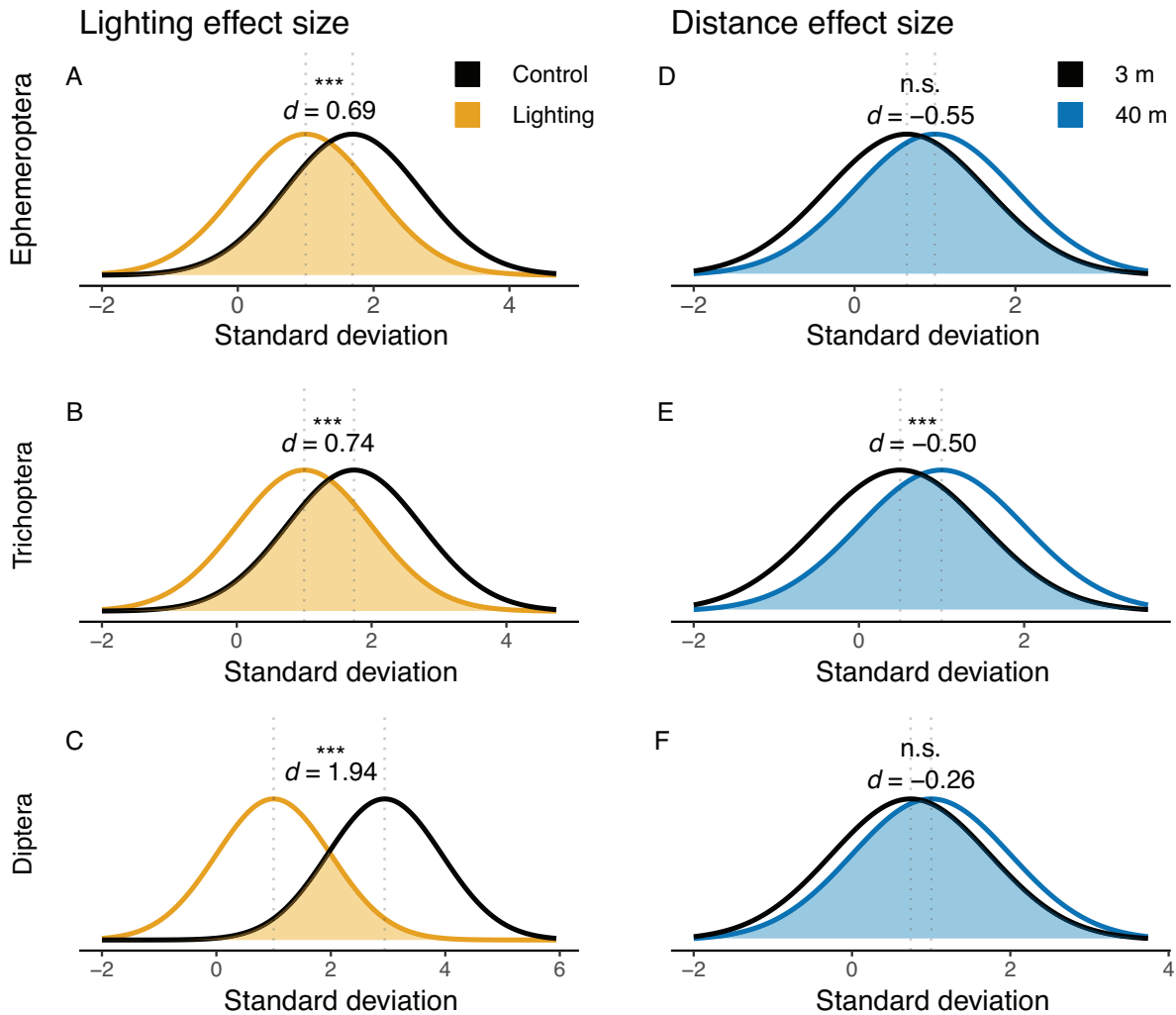
FIGURE 3 Effect sizes (ES) of lighting (a, b, c) and its distance from river edge (d, e, f) on the abundance of Ephemeroptera, Trichoptera and Diptera. ES with a value of |d| < 0.2 is "negligible", |d| < 0.5 is "small", |d| < 0.8 is "medium", |d| > 0.8 is "large"

how close does a lamp need to be to a habitat before it disturbs the resident community? Answering this question can help guide decisions on locations to target for mitigation action. Estimating the magnitude of any disturbance provides additional information, enabling the comparison of ALAN with other stressors (Grubisic et al., 2018; Perkin et al., 2011) and helping to clarify the effectiveness of mitigation measures.

This study explored the magnitude of lighting impacts on nocturnal flying insects associated with rivers, and how these change with lamp proximity to the river edge. Other studies have identified distance/proximity thresholds for taxa such as bats (Azam et al., 2018; Hale et al., 2015), but this is the first study to explore lamp-habitat proximity thresholds for adult aquatic insects. Overall, the effects were greatest for Ephemeroptera and Trichoptera when white LED lamps were placed within 40 m of the river edge. This implies that removing all lamps within 40 m of the river edge could be an effective mitigation measure for these aquatic orders, which often contain species of conservation concern. No similar drop in capture effect was observed for Diptera. Note that the spatial extent and magnitude of lighting impacts could be sensitive to historical, landscape, and technical

contexts, so it is not clear whether the finding of this research are broadly applicable.

More research is needed to explore whether lighting impacts on adult aquatic insects differ between previously dark versus lit habitats (Altermatt & Ebert, 2016), wooded versus open landscapes (Perkin et al., 2011), natural versus agricultural land covers (Grubisic et al., 2018) and between lamp types (Wakefield et al., 2018). In addition, future research should consider a broader range of aquatic invertebrate taxa and different stream types (e.g. lower order streams, with less modified stream channels).

4.1 | Study A: Impact magnitude

Study A found that white LED lighting significantly increased the local abundance of flying insects for each of the study orders. This is an important result to communicate, given that most ecological light pollution research has focused on older lighting technology. LED lamps are often portrayed as *wildlife friendly*, yet this depends on the baseline
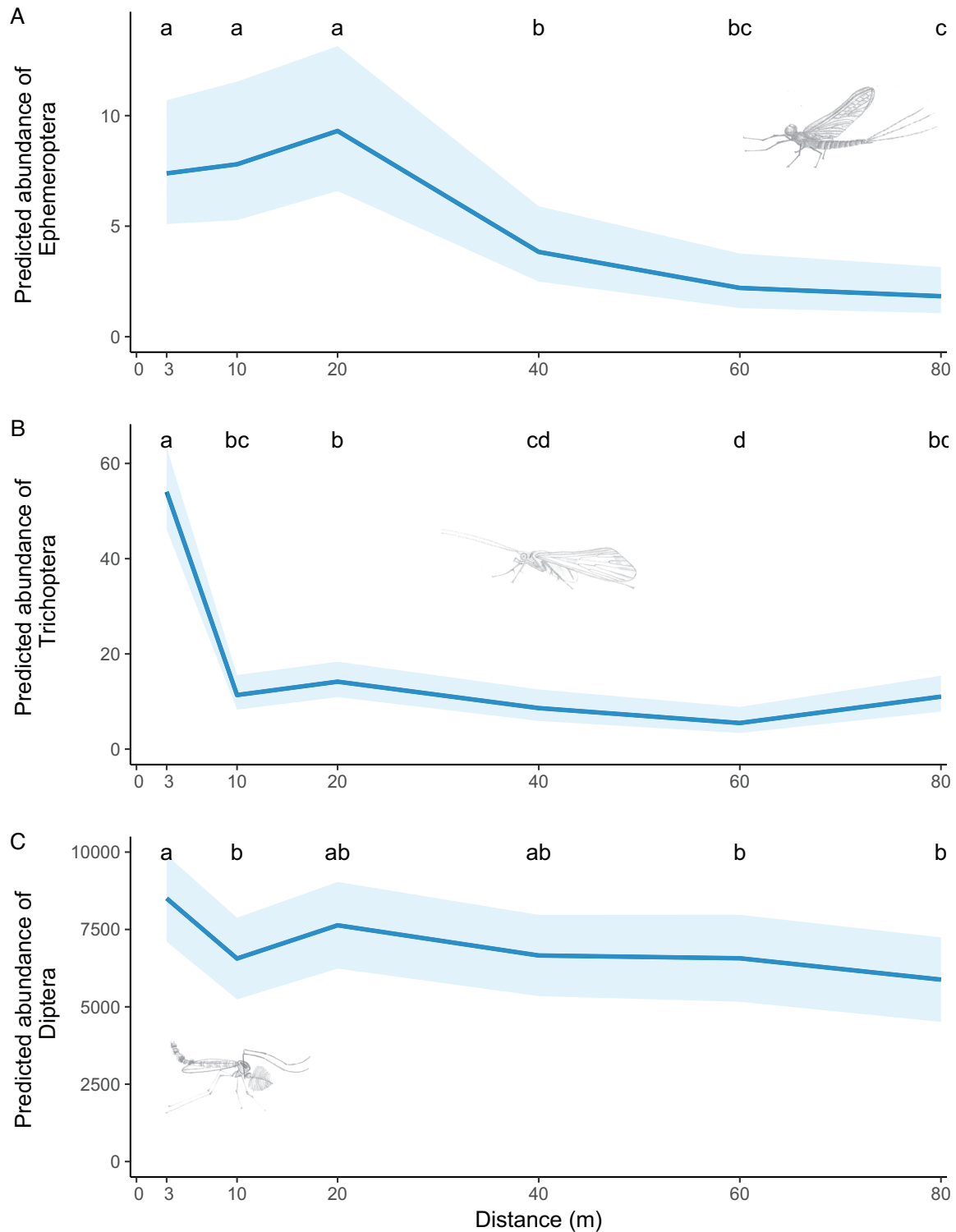
FIGURE 4 Predicted abundance (mean with confidence interval; marginal effects at the mean) of (a) Ephemeroptera, (b) Trichoptera and (c) Diptera in response to the six different sample distances from the river edge. Different letters indicate statistically significant differences between distances at an α level of 0.05

used for comparison. Wakefield et al. (2018) found that LED lamps attracted approximately the same numbers of aerial nocturnal insects as high-pressure sodium lamps, but much less than metal halide lamps. Estimating the effect magnitude provides additional useful information (Sullivan & Feinn, 2012), especially for prioritizing conservation action. We found medium/large effects of the white LED lighting treatment on our study orders, indicating that it generates a considerable increase in local insect density compared to dark background levels.

These results provide further evidence for the attractive effects of artificial lighting on our study orders (Pawson & Bader, 2014; Perkin et al., 2014a). Ephemeroptera, Trichoptera and Chironomidae (Diptera) are known to orient themselves based upon their angle to the sun or moon (Goretti et al., 2011; Malik et al., 2008; Száz et al., 2015), and the polarized signal of natural light reflecting from the water surface can be used to identify suitable oviposition sites and feeding habitats (Horváth et al., 2009). Bright LED lighting could potentially compete with natural lighting cues, leading individuals to re-orient themselves toward the artificial lighting source.

We also found that each study order reacted differently to white LED lighting, with a particularly strong effect size for Diptera abundance (Figure 3). A possible explanation is that the orders have broadly different sensitivities and responses to certain lighting intensities, wavelengths or degree of polarization (Malik et al., 2008). Insect vision has evolved photoreceptors that respond to the UV-blue-green parts of the spectrum (Briscoe & Chittka, 2001), thus artificial lights that emit radiation peaking at these wavelengths could trigger a phototactic response. This mechanism is already used to improve efficiency of light traps that target aquatic insects (Price & Baker, 2016), pests and disease vectors (Cohnstaedt et al., 2008). The magnitude of the lighting effect could therefore be linked to the sensitivity of each taxa to particular wavelengths emitted by our white LED lamps, as suggested by Grunsven et al. (2014). However, the taxonomic resolution used in this study was not sufficient to further investigate in this direction.

4.2 | Study B: Distance thresholds

For Ephemeroptera, we identified a clear distance threshold, with the number of individuals captured next to the lamps rapidly declining from a point between 20 and 40 m from the river edge (Figure 4). However, individuals were still caught at the maximum lamp/sampling distance of 80 m from the river. The ALAN impact zone for Ephemeroptera around waterbodies could therefore be relatively wide; under natural conditions individuals have been found as far as 160 m from the river edge (Muehlbauer et al., 2014). This reduction in abundance with distance could be explained by their distinct swarming behaviour. Most species are thought to swarm within 30 m from the water edge (Savolainen, 1978), so a peak in captures between 0 and 30 m would be expected. Petersen et al. (2004) and Finn and Poff (2008) also detected a rapid decline in abundance with distance, but at 15 and 10 m, respectively. However, these studies used unlit traps in uplands streams, instead of a lowland river as in our study. It is possible that the larger threshold identified in our study results from the lamps altering natural patterns

of lateral distribution, drawing swarms further from the river edge. An important caveat is that the spatial distribution of Ephemeroptera may also depend upon the swarming behaviour of the species present (Savolainen, 1978). More intensive sampling would be needed to identify the distance–response curves for particular species of conservation interest.

Trichoptera catches at lamps dropped by 80% between 3 and 10 m from the river edge. Petersen et al. (2004) demonstrated that under natural conditions Trichoptera tend to stay close to their natal habitat and drop rapidly in abundance from 0 to 15 m away from the river. In our study, Trichoptera were still captured at the maximum sampling distance of 80 m, indicating that the ALAN impact zone for this group could still be quite wide. Muehlbauer et al. (2014) found that Trichoptera dispersed laterally up to 650 m away from the river edge under natural conditions. In contrast, Finn and Poff (2008) did not record a rapid decline in Trichoptera abundance with distance. However, they studied an alpine stream harbouring mainly Limnephilidae with a large body size and thus better flight ability, whilst our study was undertaken on a lowland river dominated by Hydroptilidae that tend to be much smaller.

For Diptera, study B identified a gradual decline in captures with increasing distance from the river edge, becoming significant at 60 m. However, this trend is somewhat undermined by a marginally significant drop in abundance at 10 m, followed by a recovery at 20 m. The reduction in abundance could be an artefact of the compacted gravel road (and therefore reduced vegetation) that was adjacent to the 10-m trap. Delettre and Morvan (2000) found that under natural conditions the abundance of Chironomidae (Diptera) declined rapidly from a distance threshold of around 100 m but were still captured up to 500 m away from the river. Muehlbauer et al. (2014) demonstrated that Chironomidae can still be found up to 17 km away from waterbodies. Dispersal capability is linked to body size, wing morphology and can also vary according to different species (Delettre et al., 1992); including Diptera with a broader range of body sizes in our study could therefore have resulted in a shift in the estimated distance threshold. Even though many Diptera families are strongly associated with aquatic and riparian habitats, some species are exclusively found in terrestrial habitats (Ferrington, 2008); we therefore cannot exclude the possibility that some Diptera captures were terrestrial.

4.3 | Experimental approach

Our studies used a combined flight intercept trap adapted from the design of Perkin et al. (2014a). The main advantage of our design is its portability; trap and lamp can be transported quickly and installed off-grid without generators, and with minimal physical disturbance to the study site. This agile approach enabled simultaneous replicated sampling in relatively isolated locations, and where farming activity was incompatible with the presence of equipment in fields during the day.

Despite the flexibility of this approach, this study was limited to estimating acute impacts of artificial lighting. Sampling duration was restricted by the 3-h battery life of the LED lamp, and sampling did not

cover the full emergence/flight season for the study orders. However, given additional battery power and personnel, this approach could easily be used in future studies to estimate full-night and full-season impacts.

Our data (Supplementary Information 10 and 11) demonstrate the benefit of modifying the intercept trap, resulting in a doubling or tripling of the total catch of Ephemeroptera and Trichoptera. For Diptera, the addition of a sticky trap increased total catches by almost one order of magnitude. The numbers of Diptera for some sampling events were so high that the sticky traps almost reached capture capacity, indicating that periodic replacement of sticky traps might be required for future studies. However, there is a trade-off between the high capture rate of the sticky traps and the physical damage this trapping method causes to individual specimens. Future studies should therefore explore alternative trap designs or greater sample effort to allow a higher taxonomic resolution and exploration of any sex biases.

5 | CONCLUSION

The strong responses to white LED lighting identified here are concerning, given the conservation status of some species of Trichoptera and Ephemeroptera, orders which are often used as bioindicators for the health of aquatic ecosystems (Hodkinson & Jackson, 2005). Despite the relatively degraded river habitat, our lit traps caught at least one nationally rare species; *Oligoneuriella rhenana* (Oligoneuriidae) is the only species within its family in Switzerland and is critically endangered (Lubini et al., 2012). The high number of Diptera caught in the lit traps is particularly striking in comparison to Ephemeroptera and Trichoptera. A similar result was found in the experimental study of Russo et al. (2019) using warm LED lighting, raising concerns about population impacts for this group, and cascading ecosystem effects (Baxter et al., 2005; Manfrin et al., 2017; Meyer & Sullivan, 2013). However, it is important to note that without baseline population estimates for the species present (e.g. via benthic sampling of juveniles, or emergence trapping), we cannot speculate further on the long-term population impacts. In addition, whilst it is clear that white LED lighting can disturb the behaviour of adult aquatic insects, it is not known to what extent the lamps on their own (without the presence of traps) would have resulted in mortality, or inhibited reproduction.

Flying insects such as Diptera tend to seek shelter from wind by flying near to forest edges, hedgerows (Lewis, 1970) and riparian vegetation. Small bat species such as *P. pipistrellus* preferentially fly close to these linear landscape elements, where they can exploit the higher density of insects, are themselves protected from wind and predators and can use the structure for orientation (Verboom & Spoelstra, 1999). When our results are placed in this context, it is reasonable to conclude that white LED lamps have the potential to disrupt the typical prey of *P. pipistrellus* in riparian areas and should be excluded where possible. However, although *P. pipistrellus* is known to opportunistically forage on insects attracted to street lamps (Azam et al., 2018), acute experimental studies by Stone et al. (2012) and Russo et al. (2019) find no evidence that this species exploits the insects that aggregate around cool white LED lamps.

Although the results of this study may not be universally applicable, they are sufficient to draw attention to the risks posed by white LED lighting in riparian areas. As a precautionary approach, it makes sense for wildlife managers to implement riparian lighting exclusion zones of at least 40–60 m from the edge of rivers, with further research needed to clarify whether these distance thresholds apply to other lamp types and in different ecological contexts.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors designed the study; DC, CB and JH performed the sampling; DC and CB analysed data; JH, DC and CB lead writing the manuscript; RA provided revisions. All authors contributed to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the the University of Bern Open Repository and Information System (BORIS) https://boris.unibe.ch/151803/ (Carannante et al., 2021).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/2688-8319.12053.

ORCID

Deborah Carannante https://orcid.org/0000-0003-4268-5653
Raphaël Arlettaz https://orcid.org/0000-0001-6360-5339

REFERENCES

Altermatt, F., & Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology Letters*, *12*(4), 20160111. https://doi.org/10.1098/rsbl.2016.0111

Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., & Kerbiriou, C. (2018). Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning*, *175*, 123–135. https://doi.org/10.1016/j.landurbplan.2018.02.011

Barlow, K. E. (1997). The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *Journal of Zoology*, *243*, 597–609. https://doi.org/10.1111/j.1469-7998.1997.tb02804.x

Bartoń, K. (2016). *MuMIn: Multi-model inference*. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Baxter, C. V., Fausch, K. D., & Saunders, W. C. (2005). Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, 50, 201–220. https://doi.org/10.1111/j.1365-2427.2004.01328.x

Bennie, J., Davies, T. W., Cruse, D., Inger, R., & Gaston, K. J. (2015). Cascading effects of artificial light at night: Resource–mediated control of herbivores in a grassland ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140131. https://doi.org/10.1098/rstb.2014.0131

Bilton, D. T., Freeland, J. R., & Okamura, B. (2001). Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, 32(1), 159–181. https://doi.org/10.1146/annurev.ecolsys.32.081501.114016

Boda, P., Horvath, G., Kriska, G., Blaho, M., & Csabai, Z. (2014). Phototaxis and polarotaxis hand in hand: Night dispersal flight of aquatic insects distracted synergistically by light intensity and reflection polarization. *Naturwissenschaften*, 101, 385–395. https://doi.org/10.1007/s00114-014-1166-2

Briscoe, A. D., & Chittka, L. (2001). The evolution of color vision in insects. *Annual Review of Entomology*, 46, 471–510. https://doi.org/10.1146/annurev.ento.46.1.471

Calderone, N. W. (1999). Evaluating subsampling methods for estimating numbers of *Varroa jacobsoni* mites (Acari: Varroidae) collected on sticky–boards. *Journal of Economic Entomology*, 92, 1057–1061. https://doi.org/10.1093/jee/92.5.1057

Carannante, D., Blumenstein, C. S., Hale, J. D., & Arlettaz, R. (2021). Carannante et al. (2021) dataset. https://boris.unibe.ch/151803/

Cohnstaedt, L., Gillen, J., & Munstermann, L. (2008). Light–emitting diode technology improves insect trapping. *Journal of the American Mosquito Control Association*, 24(2), 331–334. https://doi.org/10.2987/5619.1

Delettre, Y., Tréhen, P., & Grootaert, P. (1992). Space heterogeneity, space use and short-range dispersal in Diptera: A case study. *Landscape Ecology*, 6, 175–181 https://doi.org/10.1007/BF00130029

Delettre, Y. R., & Morvan, N. (2000). Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology*, 44, 399–411. https://doi.org/10.1046/j.1365-2427.2000.00578.x

Durlak, J. A. (2009). How to select, calculate, and interpret effect sizes. *Journal of Pediatric Psychology*, 34, 917–928. https://doi.org/10.1046/j.1365-2427.2000.00578.x

Eisenbeis, G. (2006). Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. In C. Rich & T. Longcore (Eds.), *Ecological consequences of artificial night lighting* (pp. 281–304). Island Press.

Erman, N. A. (1984). The use of riparian systems by aquatic insects. In R.E. Warner & K. Hendrix (Eds.), *California riparian systems: Ecology, conservation, and productive management* (pp. 177–182). University of California Press.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., Portnov, B. A., Rybnikova, N. A., & Furgoni, R. (2016). The new world atlas of artificial night sky brightness. *Science Advances*, 2, e1600377. https://doi.org/10.1126/sciadv.1600377

Ferrington, L. C. (2008). Global diversity of non-biting midges (Chironomidae; Insecta–Diptera) in freshwater. *Hydrobiologia*, 595, 447–455. https://doi.org/10.1007/s10750-007-9130-1

Finn, D. S., & Poff, N. L. (2008). Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. *Arctic Antarctic and Alpine Research*, 40, 638–646.

Forister, M. L., Pelton, E. M., & Black, S. H. (2019). Declines in insect abundance and diversity: We know enough to act now. *Conservation Science and Practice*, 1, e80. https://doi.org/10.1111/csp2.80

Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: Options and developments. *Journal of Applied Ecology*, 49(6), 1256–1266. https://doi.org/10.1111/j.1365-2664.2012.02212.x

Gaston, K. J., Duffy, J. P., Gaston, S., Bennie, J., & Davies, T. W. (2014). Human alteration of natural light cycles: Causes and ecological consequences. *Oecologia*, 176(4), 917–931. https://doi.org/10.1007/s00442-014-3088-2

Goretti, E., Coletti, A., Di Veroli, A., Di Giulio, A. M., & Gaino, E. (2011). Artificial light device for attracting pestiferous chironomids (Diptera): A case study at Lake Trasimeno (Central Italy). *Italian Journal of Zoology*, 78, 336–342. https://doi.org/10.1080/11250003.2010.534115

Grubisic, M., Grunsven, R., Kyba, C., Manfrin, A., & Hölker, F. (2018). Insect declines and agroecosystems: Does light pollution matter? *Annals of Applied Biology*, 173, 180–189. https://doi.org/10.1111/aab.12440

Grunsven, R. H., Donners, M., Boekee, K., Tichelaar, I., Geffen, K. G., Groenendijk, D., Berendse, F., & Veenendaal, E. M. (2014). Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. *Journal of Insect Conservation*, 18, 225–231. https://doi.org/10.1007/s10841-014-9633-9

Hale, J. D., Davies, G., Fairbrass, A. J., Matthews, T. J., Rogers, C. D., & Sadler, J. P. (2013). Mapping lightscapes: Spatial patterning of artificial lighting in an urban landscape. *PloS ONE*, 8(5), e61460. https://doi.org/10.1371/journal.pone.0061460

Hale, J. D., Fairbrass, A. J., Matthews, T. J., Davies, G., & Sadler, J. P. (2015). The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats. *Global Change Biology*, 21, 2467–2478. https://doi.org/10.1111/gcb.12884

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, 12(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Harrison, X. A. (2014). Using observation–level random effects to model overdispersion in count data in ecology and evolution. *Peer J*, 2, e616. https://doi.org/10.7717/peerj.616

Hartig, F. (2017). *DHARMa: Residual diagnostics for hierarchical (multilevel/mixed) regression models*. R package version 0.1.5.

Hodkinson, I. D., & Jackson, J. K. (2005). Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. *Environmental Management*, 35, 649–666. https://doi.org/10.1007/s00267-004-0211-x

Hölker, F., Wolter, C., Perkin, E. K., & Tockner, K. (2010). Light pollution as a biodiversity threat. *Trends in Ecology & Evolution*, 25(12), 681–682. https://doi.org/10.1016/j.tree.2010.09.007

Hölker, F., Wurzbacher, C., Weißenborn, C., Monaghan, M. T., Holzhauer, S. I., & Premke, K. (2015). Microbial diversity and community respiration in freshwater sediments influenced by artificial light at night. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140130. https://doi.org/10.1098/rstb.2014.0130

Horváth, G., Kriska, G., Malik, P., & Robertson, B. (2009). Polarized light pollution: A new kind of ecological photopollution. *Frontiers in Ecology and the Environment*, 7, 317–325. https://doi.org/10.1890/080129

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50(3), 346–363. https://doi.org/10.1002/bimj.200810425

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature*, 548, 206–209. https://doi.org/10.1038/nature23288

Kummu, M., De Moel, H., Ward, P. J., & Varis, O. (2011). How close do we live to water? A global analysis of population distance to freshwater bodies. *PloS ONE*, 6(6), e20578. https://doi.org/10.1371/journal.pone.0020578

Kyba, C. C., Kuester, T., De Miguel, A. S., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C. D., Gaston, K. J., & Guanter, L. (2017). Artificially lit surface of Earth at night increasing in radiance and extent. *Science Advances*, 3(11), e1701528. https://doi.org/10.1126/sciadv.1701528

Lewis, T. (1970). Patterns of distribution of insects near a windbreak of tall trees. *Annals of Applied Biology*, 65, 213–220. https://doi.org/10.1111/j.1744-7348.1970.tb04581.x

Longcore, T., & Rich, C., (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, 2(4), 191–198.

Lubini, V., Knispel, S., Sartori, M., Vicentini, H., & Wagner, A. (2012). *Liste Rosse Efemerotteri, Plecotteri, Tricotteri. Specie minacciate in Svizzera, stato 2010. Ufficio federale dell'ambiente*, Neuchâtel: Berna, e Centro Svizzero di Cartografia della Fauna (CSCF).

Malik, P., Hegedus, R., Kriska, G., & Horvath, G. (2008). Imaging polarimetry of glass buildings: Why do vertical glass surfaces attract polarotactic insects? *Applied Optics*, 47, 4361–4374. https://doi.org/10.1364/AO.47.004361

Manfrin, A., Singer, G., Larsen, S., Weiß, N., van Grunsven, R. H., Weiß, N. S., Wohlfahrt, S., Monaghan, M. T., & Hölker, F. (2017). Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. *Frontiers in Environmental Science*, 5, 61. https://doi.org/10.3389/fenvs.2017.00061

Meyer, L. A., & Sullivan, S. M. P. (2013). Bright lights, big city: Influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. *Ecological Applications*, 23, 1322–1330. https://doi.org/10.1890/12-2007.1

Muehlbauer, J. D., Collins, S. F., Doyle, M. W., & Tockner, K. (2014). How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. *Ecology*, 95, 44–55. https://doi.org/10.1890/12-1628.1

Pawson, S. M., & Bader, M. K. F. (2014). LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications*, 24, 1561–1568. https://doi.org/10.1890/14-0468.1

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: Questions, challenges, and perspectives. *Ecosphere*, 2(11), 1–16. https://doi.org/10.1890/ES11-00241.1

Perkin, E. K., Hölker, F., & Tockner, K. (2014a). The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshwater Biology*, 59, 368–377. https://doi.org/10.1111/fwb.12270

Perkin, E. K., Hölker, F., Tockner, K., & Richardson, J. S. (2014b). Artificial light as a disturbance to light–naïve streams. *Freshwater Biology*, 59, 2235–2244. https://doi.org/10.1111/fwb.12426

Petersen, I., Masters, Z., Hildrew, A. G., & Ormerod, S. J. (2004). Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, 4, 934–950. https://doi.org/10.1111/j.0021-8901.2004.00942.x

Pike, N. (2011) Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution*, 2, 278–282. https://doi.org/10.1111/j.2041-210X.2010.00061.x

Price, B., & Baker, E. (2016). NightLife: A cheap, robust, LED based light trap for collecting aquatic insects in remote areas. *Biodiversity Data Journal*, 4, e7648. https://doi.org/10.3897/BDJ.4.e7648

Procter, D. & Harding, P. T. (2005). Proceedings of INCardiff 2003. Red Lists for Invertebrates: their application at different spatial scales – practical issues, pragmatic approaches. JNCC Report No. 367, JNCC, Peterborough, UK.

R Development Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rich, C., & Longcore, T. (2006). *Ecological consequences of artificial night lighting*. Island Press.

Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P., & Ancillotto, L. (2019). Artificial illumination near rivers may alter bat-insect trophic interactions. *Environmental Pollution*, 252, 1671–1677.

Sanders, D., & Gaston, K. J. (2018). How ecological communities respond to artificial light at night. *Journal of Experimental Zoology, Part A: Ecological and Integrative Physiology*, 329(8-9), 394–400. https://doi.org/10.1002/jez.2157

Sanders, D., Frago, E., Kehoe, R., Patterson, C., & Gaston, K. J. (2020 Nov 2). A meta-analysis of biological impacts of artificial light at night. *Nature Ecology & Evolution*. http://doi.org/10.1038/s41559-020-01322-x

Savolainen, E. (1978). Swarming in Ephemeroptera: Mechanism of swarming and effects of illumination and weather. *Annales Zoologici Fennici*, 15, 17–52.

Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17, 474–480. https://doi.org/10.1016/S0169-5347(02)02580-6

Schneider, R. L., Mills, E. L., & Josephson, D. C. (2002). *Aquatic-terrestrial linkages and implications for landscape management. Integrating landscape ecology into natural resource management* (pp. 241–262). Cambridge University Press.

Skaug, H., Fournier, D., Magnusson, A., & Bolker, B. (2018) glmmADMB: Generalized linear mixed models using AD model builder. R package version 0.8.3.4.

Stone, E. L., Jones, G., & Harris, S. (2012). Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, 18(8), 2458–2465.

Sullivan, G. M., & Feinn, R. (2012). Using effect size-or why the P value is not enough. *Journal of Graduate Medical Education*, 4, 279–282. https://doi.org/10.4300/JGME-D-12-00156.1

Száz, D., Horvath, G., Barta, A., Robertson, B. A., Farkas, A., Egri, A., Egri, A., Tarjanyi, N., Racz, G., & Kriska, G. (2015). Lamp-lit bridges as dual light–traps for the night–swarming mayfly, ephoron virgo: Interaction of polarized and unpolarized light pollution. *PLoS ONE*, 10(3), e0121194. https://doi.org/10.1371/journal.pone.0121194

Tamir, R., Lerner, A., Haspel, C., Dubinsky, Z., & Iluz, D. (2017). The spectral and spatial distribution of light pollution in the waters of the northern Gulf of Aqaba (Eilat). *Scientific Reports*, 7, 42329. https://doi.org/10.1038/srep42329

Torchiano, M. (2017). Effsize: Efficient effect size computation. R package version 0.7.1. https://CRAN.R-project.org/package=effsize

Verboom, B., & Spoelstra, K. (1999). Effects of food abundance and wind on the use of tree lines by an insectivorous bat, Pipistrellus pipistrellus. *Canadian Journal of Zoology*, 77, 1393–1401. https://doi.org/10.1139/cjz-77-9-1393

Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11(1), 192–196. https://doi.org/10.3758/BF03206482

Wagner, D. L. (2019). Insect declines in the anthropocene. *Annual Review of Entomology*, 65(1).

Wakefield, A., Broyles, M., Stone, E. L., Harris, S., & Jones, G. (2018). Quantifying the attractiveness of broad–spectrum street lights to aerial nocturnal insects. *Journal of Applied Ecology*, 55, 714–722. https://doi.org/10.1111/1365-2664.13004

Waringer, J. A. (1996). Phenology and Abundance of Ephemeroptera, Plecoptera and Trichoptera Caught by Emergence Traps at the Weidlingbach near Vienna. *Austria. Int. Revue ges. Hydrobiol. Hydrogr.*, 81, 63–77. https://doi.org/10.1002/iroh.19960810107

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.