Aquatic Sciences (2025) 87:38
https://doi.org/10.1007/s00027-025-01161-7

Aquatic Sciences

RESEARCH ARTICLE

Artificial light at night reduces emergence and attracts flying adults of aquatic Diptera

A. Manfrin[1] · F. Hölker[2,3] · S. Teurlincx[4] · V. Baranov[5] · R. H. A. van Grunsven[6] · M. Bundschuh[1,7] · M. T. Monaghan[2,3]

Received: 17 October 2024 / Accepted: 8 January 2025

Abstract
Artificial light at night (ALAN) is a widespread, human-induced alteration of the landscape that affects insect dispersal and potentially contributes to insect decline. We used an experimental area with streetlights installed adjacent to an agricultural drainage ditch to experimentally assess the abundance and diversity of emerging and flying aquatic Diptera over a period of six months in summer and autumn. Emergence was two-fold lower in the lit site, while flying adults were eight-fold more abundant at traps under lights. Results were taxon- and sex-specific. Males of nine taxa were less abundant in lit emergence traps, and females of most taxa were more abundant in lit air-eclector traps than in controls. We developed an empirical model based on emergence and capture rates and used this model to estimate that the majority of the 54 flying Diptera taxa we identified were attracted to light from the adjacent water body, and that a few taxa were attracted from a distance of up to 1800 m. This work provides evidence that artificial light in riparian areas can reduce emergence in aquatic Diptera and hinder dispersal, with effects that vary depending on the taxon. Because many riparian predators rely on adult aquatic insects as prey, these changes can cascade across aquatic-terrestrial ecosystem boundaries. Given the large number of streetlights that are installed along freshwater shorelines, the observed effects are likely to be of relevance to freshwater bodies around the globe.

Keywords Light pollution · Cross-ecosystem · Insects · Aquatic subsidies · Chironomidae · Non-biting midges

Introduction

Ecosystems are connected through reciprocal fluxes of material, energy and organisms (Polis et al. 1997; Loreau et al. 2003; Baxter et al. 2005). The ecological relevance of such fluxes for receiving ecosystems are a function of their quantity and quality (Marcarelli et al. 2011). In riparian areas, emerging aquatic insects provide a food resource for a wide range of terrestrial consumers (e.g. Nakano and Murakami 2001; Sanzone et al. 2003; Paetzold et al. 2005; Marczak and Richardson 2007; Bartels et al. 2012). Despite the ecological significance of this subsidy, most studies of how anthropogenic stressors may impact emergence have focused on chemical and hydromorphological alterations of the water (e.g., Whiles and Goldowitz 2001; Larsen et al. 2016; Schulz et al. 2015, 2024; Kennedy et al. 2016; Kraus et al. 2021; Ohler et al. 2023; Pietz et al. 2023). Consequently, there is less understanding of the impact of landscape stressors.

Artificial light at night (ALAN) is one of the most widespread human-induced alterations of the landscape (Hölker et al. 2010; Linares Arroyo et al. 2024), but to date only a few studies have examined its ecological impact on aquatic insect emergence (Meyer and Sullivan 2013; Manfrin et al. 2017; Sullivan et al. 2019). This lack of knowledge is particularly concerning in light of the worldwide decline of insect populations (e.g. Leather 2017; Hallmann et al. 2017, 2021; Sánchez-Bayo and Wyckhuys 2019; Baranov et al.

✉ A. Manfrin
a.manfrin@rptu.de; alessandro.manfrin@hotmail.com

[1] iES Landau, Institute for Environmental Sciences, RPTU Kaiserslautern-Landau, Landau, Germany

[2] Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

[3] Institut für Biologie, Freie Universität Berlin, Berlin, Germany

[4] Department of Aquatic Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands

[5] Estación Biológica de Doñana CSIC, Seville, Spain

[6] Dutch Butterfly Conservation, Wageningen, The Netherlands

[7] Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

2020; Jähnig et al. 2021), with ALAN being proposed as one of the drivers of their decline (Grubisic et al. 2018; Owens et al. 2020). Commonly used artificial light sources such as street lamps can function as ecological traps (van Langevelde et al. 2011; Degen et al. 2016; van Grunsven et al. 2020; Spoelstra et al. 2023), and massive numbers of insects can be affected during swarming events (e.g. Száz et al. 2015). Insects may become exhausted, leading to reduced dispersal and reproduction (Perkin et al. 2011; Degen et al. 2016; van Geffen et al. 2015a, b). Urban and suburban areas, together with their outdoor light sources, are often located near rivers, streams and lakes (Kummu et al. 2011). The projected worldwide expansion of urbanised land (Chen et al. 2020) suggests that any impact of ALAN on freshwater ecosystems (Hölker et al. 2023) may be widespread.

The effect of ALAN may be relevant for the early life stages of aquatic insects because photoperiod is known to regulate emergence in some taxa (Corbet 1964; Brittain 1982; Kühne et al. 2021). ALAN may also disrupt diel behaviour patterns (Hölker et al. 2010; Perkin et al. 2011, 2014) and attract or repulse insects directly (Ali et al. 1984; 1986; 1994; Boda et al. 2014; Száz et al. 2015; but see Donners et al. 2018). Manfrin et al. (2017) reported a three-fold increase in aquatic insect emergence dominated by mayflies after one year of experimental exposure to street lamps with a light intensity of approximately 15 lx on the water surface (high-pressure sodium lamps), a light intensity comparable to values often found in urban and suburban freshwaters (up to 20 lx; Jechow and Hölker 2019). Meyer and Sullivan (2013) reported reductions in mean body size (76%) and taxonomic richness (16%) in emerging aquatic insects exposed to similar levels of ALAN (10–12 lx on the water surface, LED lamps) potentially reducing the availability of essential fatty acids derived from aquatic organisms, which are key nutrients for terrestrial predators (Martin-Creuzburg et al. 2017). Dietary shifts in terrestrial insect consumers were also reported in both studies (Manfrin et al. 2018; Sullivan et al. 2019).

Diptera are the most diverse group of insects with aquatic representatives, making up nearly half (approx. 45,000) of all aquatic insect species on Earth (Dijkstra et al. 2014). The Chironomidae are the most abundant and diverse Dipteran family in many freshwater habitats, and many of these species are known to depend on light cues. It has been observed that eclosion and emergence are regulated by lunar periodicity (Corbet 1958; Kaiser et al. 2016; Andreatta and Tessmar-Raible 2020). Females locate oviposition sites using horizontally polarised light, and larvae choose habitats based on light intensity and wavelength (Horváth et al. 2011; Kühne et al. 2021). As gatherers, filter-feeders, scrapers and predators, but also as a food resource for many aquatic predators, Chironomidae larvae are an important component of aquatic food webs (Armitage et al. 2012). Also, they play an important role in the carbon and nitrogen cycles of shallow aquatic systems (Hölker et al. 2015a; Baranov et al. 2016; McGinnis et al. 2017). After emergence, flying Chironomids typically disperse up to 500 m from their aquatic habitat (Delettre and Morvan 2000), but they have been found up to 17,000 m away from a waterbody (Muehlbauer et al. 2014). Due to the abundance and ecological importance of dipterans, any response of this order to ALAN may have far-reaching consequences. While evidence of ALAN being attractive to dipterans (up to 80 m) has been reported (Carannante et al. 2021), information on the taxa- and sex-related impacts of ALAN over larger distances is still lacking, even though such data are relevant to our understanding of the full dimension of potential impacts (Carannante et al. 2021).

In the study reported here, we predicted that ALAN would change the abundance and taxonomic composition of emerging and flying Diptera, and that these changes would be sex- and taxon-dependent. We employed a large-scale field experiment to manipulate ALAN over a period of six months in the summer and autumn of 2014 and quantified Diptera using emergence traps and air-eclector flight traps. We also developed an empirical model that combined emergence and flight capture data to estimate the taxon-specific and sex-specific mean and maximum distance at which Diptera were attracted by ALAN.

Methods

Study area and experimental design

The experimental study area was established in 2012 and is described in detail elsewhere (Holzhauer et al. 2015; Manfrin et al. 2017). The study area included two sites located in a 750-km^2 International Dark-Sky Reserve (International Dark Sky Association 2015), within the Westhavelland Nature Park (Germany). At each site, three parallel rows of four conventional street lamps, each 4.75 m high and located 20 m apart from each other, were installed in the riparian grass at 3, 23 and 43 m from an agricultural drainage ditch (see Fig. 1a, c). During the study, street lamps at the lit site were equipped with a high-pressure sodium lamp (70 W, VIALOX NAV-T Super 4Y, yellow 2000 K; Osram, Munich, Germany), with the lamps reaching a maximum illuminance of approximately 50 lx at ground level. Minimum illuminance was approximately 10 lx between adjacent lamps in the same row, and approximately 1 lx between rows (see Holzhauer et al. 2015 for details of light distribution and spectral composition). Nocturnal illuminance ranged from 13.3 to 16.5 lx at the water surface and from 6.8 to 8.5 lx at the sediment surface (water depth of approx. 50 cm; Hölker et al. 2015b). Since July 2012, all 12 street lamps at the lit site have been on at night between civil twilight at dusk

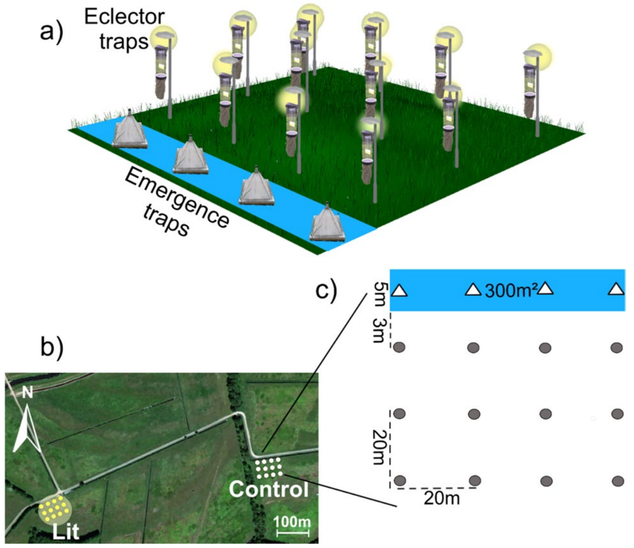

Fig. 1 Study area in the Westhavelland Nature Park (Germany). **a** Depiction of the lit site (60 × 48 m, including the ditch) with 12 street lamps, 4 emergence traps and 12 air-eclector traps (not drawn to scale). Each emergence trap was adjacent to a street lamp. **b** Plan of experimental sites showing location of lit (Lit) and dark (Control) sites. The dark site was located along the same agricultural drainage ditch as the lit site, and had the same structural design, but lamps were not equipped with functioning bulbs. **c** Plan view depicting lamps as filled circles and emergence traps as triangles. The shaded (blue) rectangle delineates the water surface (300 m^2) adjacent to each site. Map data (**b**) are by Google Earth Pro 7.3.0.3832 (32-bit) (5 Mar 5 2011), Lochow, Germany (52°41′29.81″ N, 12°27′37.54″ E; eye altitude 1.09 km; DigitalGlobe 2017). Color figure online

and dawn. The control site has the same infrastructure of 16 street lights but has remained dark. The sites are separated by approximately 600 m (800 m along the drainage ditch) and a row of trees, and are very similar in other environmental characteristics (e.g. water physical and chemical parameters, hydromorphology and riparian vegetation) (Holzhauer et al. 2015).

Insect sampling

Insects were collected from both the lit and dark sites from May to October 2014. Newly emerged aquatic insects were sampled using four pyramid-shaped floating emergence traps (base dimensions 0.85 × 0.85 m, mesh size 300 µm) at each site. These were placed in the drainage ditch at a distance of approximately 1 m from the bank, directly adjacent to each street lamp (Fig. 1a, c), and anchored to the shoreline from both sides with rope. Insects were collected in a plastic container filled with 70 % ethanol, placed at the top of each emergence trap. Emergence traps were deployed twice each month except in May when the sampling was conducted only once, and in July when the sampling was conducted three times, for a total of 12 sampling events. Traps were deployed for varying periods of time ranging from 1 day to 1 week (range 24 to 185 h). Flying adult insects were collected using 12 air-eclector traps at each site. Traps consisted of two perpendicular acrylic panels (each 0.2 × 0.5 × 0.003 m) mounted above a collecting funnel, placed 0.5 m below each streetlamp (Fig. 1a) and fitted with collecting containers prefilled with 70% ethanol for preservation (for more details, see Manfrin et al. 2017, 2018). Air-eclector traps were active for one rainless 24-h sampling event every month, during either a first- or third-quarter moon. An exception was in July when sampling was conducted twice, leading to seven sampling events in total.

Taxonomic identification

Aquatic Diptera caught in emergence and air-eclector traps were identified to the lowest taxonomic level possible (species level when possible, otherwise to genus, tribe or family), resulting in a total of 93 identified taxa (Electronic Supplementary Material [ESM] Table S1). All specimens were also sexed and counted. Chironomidae were first sorted into morphotypes under a stereo microscope (150× magnification), after which three to five specimens of each sex were randomly selected, mounted in glycerol and identified under a light microscope using the taxonomic keys of Langton and Pinder (2007), Wiederholm (1989), Makarchenko and Makarchenko (2006) and Ferrington and Saether (2011). In total, 73 chironomid species were identified, of which 55 were identified using DNA barcoding; these voucher specimens are stored in ethanol at the Zoological Research Museum Alexander Koenig (Zoologisches Forschungsmuseum Alexander Koenig [ZFMK]), Bonn, Germany. Details and accession numbers available as Supplement 2 in Chimeno et al. (2023).

Statistical analysis

The number of emerging Diptera was standardised to catch per unit of effort (CPUE) by dividing the total number of individuals caught in each trap by the hours of deployment and then dividing the product by the water surface area covered by the trap (0.7225 m^2). This value was then multiplied by 24 to obtain values of CPUE as number of individuals per square meter per day. The CPUE of flying Diptera was calculated as the number of individuals caught per 24 h of trap operation. We considered both emergence and air-eclector traps to be spatially dependent and therefore summed the CPUE of all traps in each site for each trap type and sampling event. From these CPUE values, diversity was expressed as the exponential Shannon diversity index (Jost 2006), and richness as the number of taxa present at each site.

The multiple sampling events (i.e. temporal observations) at each site were considered (pseudo) replicates for the statistical analysis. Linear models as implemented in the "stats" package in R (version 4.3.1; R Core Team 2023) were used to test for differences in CPUE between lit and dark sites. Analyses were performed separately for emerging (12 sampling events) and flying Diptera (seven sampling events), and for total CPUE (sum of CPUE from all taxa) and for each taxon. Linear models included the factors "site" (lit, dark), "sex" (male, female) and their interaction.

When serial autocorrelation was detected in the residuals, a correction for temporal autocorrelation structure was included in the linear model. We used the auto.arima function in the "forecast" package (version 8.21.1; Hyndman et al. 2023) for R to identify the best temporal autocorrelation structure based on the Akaike information criterion (AIC). When "site" or "site:sex" factors were significant, we performed contrast analysis using pairwise comparisons (different site, same sex–different site, different sex–same site) using least-squares means with the "lsmeans" package (version 2.30–0; Lenth 2016) for R. The distribution of residuals was assessed using quantile-plots (Wilk and Gnanadesikan 1968) using the graphics package for R, ensuring that the results aligned with model residual assumptions (Zuur and Ieno 2016).

Model-based estimates of attraction to ALAN

We built an empirical model combining taxon-specific CPUE data with spatial data on water surface around the study site to make an estimate of the mean and maximum distance from which Diptera were attracted to the centre of the lit site. The estimation was applied to taxa that showed a significant "site" or "site:sex" effect (see section Results). Our model of Diptera attraction was based on a first-order estimate of the minimum water surface area needed to supply the number of individuals (24 h^{-1} m^{-2}) captured during light in air-eclector traps. The model was developed with the following basic assumptions: (1) ALAN effects of reduced emergence (see section Results) extend only to the adjacent water surface (300 m^2; see Fig. 1c) and water beyond this is assumed to function identically to the control site in terms of emergence; (2) the impact is non-directional (i.e. spherical) due to the propagation properties of light; and (3) emerging insect densities are homogeneous in either lit or unlit ditches (i.e. not affected by habitat patchiness). Other factors that might impact the attraction of insects, such as wind, rainfall, predation and competition, were not considered in the model.

To calculate an attraction distance, we first calculated the relative capture rate of each species for the light and dark sites as:

$$RC = \frac{A^{i}_{ECL} + C_{ECL}}{A^{I}_{EMR} + C_{EMR}} \tag{1}$$

where the relative capture (RC) is a function of the CPUE (A) of species i captured in the air-eclector trap (ECL) divided by the CPUE (A) of species i captured in the emergence trap (EMR) recalculated to square meters (m^2) of adjacent water area (in 300 m^2 of water directly adjacent to the lit field; see Fig. 1c). To avoid zero values on either side of the relative capture formula (1), we centred all values around the minimal number of individuals being captured (c, CPUE as individuals per m^2 per day), which is calculated using formula 2 and 3.

$$C_{EMR} = {}^{1}\Big/ \frac{d\max_{EMR}}{area_{EMRtrap}} \Big/ area_{water} \tag{2}$$

$$C_{ECL} = \frac{1}{d\max_{ECL}} \tag{3}$$

where c_{EMR} is a correction factor based on a single individual being caught in the trap (1) corrected for the maximum deployment duration of sampling of the emergence traps ($dmax_{EMR}$; 185/24 h = 7.7 days), the area of the emergence traps ($area_{EMR\ trap}$; 2.89 m^2) and the total water area ($area_{water}$; 300 m^2). c_{ECL} is a similar correction factor based on a single individual being caught in the air-eclector trap corrected for the maximum deployment duration of said traps ($dmax_{ECL}$; 16.5/24 h = 0.69 days).

Using the relative capture for both light and dark sites we calculated the attraction factor (AF) as:

$$AF = \frac{RC_{lit}}{RC_{dark}} \tag{4}$$

The attraction distance was estimated by multiplying AF by the area of water from which insects could originate, beginning with the water adjacent to the dark site (28 m from the centre of the field, corresponding to 300 m^2; Fig. 1c) and increasing to include water within a radius of 28–5000 m from the centre of the field in 0.5-m increments. The amount of water was estimated using a spatial GIS analysis of the lit site using the "rgeos" package (Bivand et al. 2023) for R. Spatial information was extracted from municipal maps of water bodies and supplemented using satellite imagery (Google Earth) for smaller ditches that were not included in the maps. The water surface area in each 0.5-m iteration was compared to the water surface area required to supply the number of individuals captured, resulting in an approximation of attraction distance. This was repeated for all taxa that showed a significant "site" or "site:sex" effect.

Results

Diptera abundance and dominant taxa

A total of 2424 Diptera were collected in emergence traps, 1272 females and 1152 males, belonging to 74 taxa (ESM Table S1). Most were chironomids belonging to the tribes Chironomini and Tanytarsini, including the most abundant species *Parachironomus monochromes*, *Paratanytarsus inopertus* and *Cladopelma edwardsi*. In total, 2143 individuals were collected in the air-eclector traps, 1833 females and 310 males, belonging to 54 taxa (Table S1). The most abundant species belonged to the tribes Chironomini, namely *Cricotopus* sp., *Procladius crassinervis* and *Glyptotendipes glaucus*.

CPUE, taxa richness and diversity

Total Diptera emergence was two-fold lower at the lit site (mean ± standard deviation [SD] CPUE 3.72 ± 3.29) than at the dark site (7.84 ± 6.99) (Table 1; Fig. 2a), independent of sex. The taxonomic richness and diversity of emerging Diptera did not differ between sites or among sites and sexes (Fig. 2b, c). Differently from the analysis of the total emergence community, when taxa were examined individually, we found that 13 emerging taxa exhibited a significant site or site:sex interaction, namely: *Chaoborus* sp., 11 species of Chironomidae and individuals assigned to the Chironomidae tribe Pentaneurini (Table 1). Ten species had lower emergence CPUE at the lit site (indicated by a negative delta CPUE value in Table 1) than at the dark site, while the Pentaneurini individuals and *Monopelopia tenuicalcar* had higher emergence at the lit site (Table 1). Nine species had lower male emergence CPUE at the lit site compared to the dark site, while Pentaneurini showed higher female CPUE in the lit site (Table 1). Emergence at the dark site appeared to be more variable among the temporal replicates compared with that at the lit site (Fig. 2a).

The number of flying Diptera captured in the air-eclector traps was approximately eight-fold higher at the lit site (mean ± SD CPUE 416.48 ± 592.23) than at the dark control site (52.17 ± 146.72) (Table 1; Fig. 3a). Overall, females were six-fold more abundant at the lit site (717.67 ± 733.47) than males (115.28 ± 101.40) (Table 1, Fig. 3a). The analysis of individual taxa revealed significantly higher female than male abundance at the lit site for four taxa, namely *Chironomus dorsalis*, *Chironomini*, *G. glaucus* and Orthocladiinae (Table 1). Diversity and richness of flying Diptera were 2.8-fold and 4.2-fold higher in the lit site (Table 1, Fig. 3b, c), with no sex-specific effect of ALAN.

Estimation of aquatic Diptera attraction to ALAN

Examined individually, most taxa for which we observed a significant effect of site or a site:sex interaction (CPUE model) in emergence or air-eclector traps were attracted from the water body directly adjacent to the lit field (Fig. 4; ESM Table S2). Females were attracted from farther distances than males in the Chironomini (mean ± SD 157.1 ± 242.9 m for females; 1.6 ± 4.3 m for males), *P. nubeculosum* (354.9 ± 633.2 m; 42.9 ± 52.8 m) and *P. crassinervis* (215.6 ± 331.5 m; 32.1 ± 33.6 m). Males were attracted from farther away in *C. edwardsi* (132.5 ± 154.6 m males; 24.8 ± 63.8 m females) and *E. tendens* (133.3 ± 142.9 m; 45.8 ± 69.2) (Fig. 4). Females and males of *G. glaucus* were equally attracted (105.9 ± 110.8 m; 107.1 ± 127.0 m).

Discussion

In this study, we observed taxon-specific and sex-specific changes in the abundance of emerging and flying aquatic Diptera in response to ALAN. The two-fold lower total emergence of Diptera into the lit riparian area was driven by significant reductions for 13 taxa, nine of which had lower emergence of males but not of females. The eight-fold higher abundance of flying Diptera at the lit site was driven by a higher number of females of four taxa, which may have consequences for female–male encounter rates and reproduction (Degen et al. 2017). According to our empirical model developed to estimate attraction distance, most individuals were attracted to light from the adjacent water body, although males of 15 taxa and females of six taxa were attracted from greater distances, with maximum distances of attraction observed in *P. nubeculosum* (approx. 1800 m), *P. crassinervis* (900 m) and Chironomini sp. females (670 m).

Emergence

The lower emergence rates of Diptera at the lit site contrasted with the increased total emergence of aquatic insects under ALAN observed at the same site 1 year earlier (Manfrin et al. 2017). In that study, the mayfly *Cloeon dipterum* (Linnaeus, 1761) was the most abundant insect taxon, which may have obscured the opposite patterns in Diptera. ALAN may have reduced the survival of Diptera larvae by impacting ontogeny (Armitage 1995; Nabity et al. 2007; Kaiser et al. 2016) although we did not measure benthic densities. Increased light intensity (either ALAN or natural) can increase predation by other invertebrates and fish (see Czarnecka et al. 2019; Kühne et al. 2021), which may reduce larval and pupal densities (Cerri and Fraser 1983; Lee et al. 2013). ALAN may also interfere with larval development

Table 1 F-statistics for the significant differences in catch per unit effort, taxa richness and exponential of Shannon diversity of emerging and aquatic adult flying (in air-eclector traps) Diptera between sites (lit, dark), and their interaction with sex (site:sex)

Trap type	Taxa	Terms	F[a]	Contrasts	delta CPUE[b]	p[c]
Emergence trap	Total	Site	$F_{1,24}=4.52$*	Lit—dark	− 3.56	0.044
	Chaoborus sp.	Site:sex interaction	$F_{1,24}=43.19$***	Lit—dark	− 4.75E-03	<0.001
				Female dark—male dark	− 9.51E-03	<0.001
				Male lit—male dark	− 9.51E-03	<0.001
	Cladopelma edwardsi	Site	$F_{1,24}=5.27$*	Lit—dark	− 0.71	0.031
	Corynoneura celeripes	Site:sex interaction	$F_{1,24}=43.19$***	Lit—dark	− 4.75E-03	<0.001
				Female dark—male dark	− 9.51E-03	<0.001
				male lit—male dark	− 9.51E-03	<0.001
	Endochironomus tendens	Site:sex interaction	$F_{1,24}=5.90$*	Lit—dark	− 0.13	0.029
				Female dark—male dark	− 0.29	0.005
				Male lit—male dark	− 0.27	0.005
	Microtendipes chloris	Site:sex interaction	$F_{1,24}=20.60$***	Lit—dark	− 0.02	<0.001
				Female dark—male dark	− 0.04	<0.001
				Male lit—male dark	− 0.04	<0.001
	Monopelopia tenuicalcar	Site	$F_{1,24}=8.21$**	Lit—dark	0.29	0.008
	Parachironomus digitalis	Site:sex interaction	$F_{1,24}=18.76$***	Lit—dark	− 0.05	<0.001
				Female dark—male dark	− 0.11	<0.001
				Male lit—male dark	− 0.10	<0.001
	Paratanytarsus tenellulus	Site:sex interaction	$F_{1,24}=3.94$#	Female dark—male dark	− 0.10	0.033
				Male lit—male dark	− 0.08	0.033
	Pentaneurini	Site:sex interaction	$F_{1,24}=43.19$***	Lit—dark	4.75E-03	<0.001
				Female lit—female dark	0.01	<0.001
				Female lit—male lit	0.01	<0.001
	Polypedilum tritum	Site:sex interaction	$F_{1,24}=6.57$*	Lit—dark	− 0.03	0.017
				Female dark—male dark	− 0.07	0.001
				Male lit—male dark	− 0.06	0.003
	Robackia demeijerei	Site:sex interaction	$F_{1,24}=43.19$***	Lit—dark	− 0.01	<0.001
				Female dark—male dark	− 0.03	<0.001
				Male lit—male dark	− 0.03	<0.001
	Tanypus punctipennis	Site	$F_{1,24}=9.14$**	Lit—dark	− 0.61	0.006
	Tanytarsus cf dispar	Site:sex	$F_{1,24}=20.60$***	Lit—dark	− 0.03	<0.001
				Female dark—male dark	− 0.05	<0.001
				Male lit—male dark	− 0.05	<0.001

Table 1 (continued)

Trap type	Taxa	Terms	F^a	Contrasts	delta CPUE[b]	p^c
Air-eclector trap	Total	Site:sex	$F_{1,24} = 5.81$*	Lit—dark	422.3	0.004
				Female lit—female dark	741.94	0.002
				Female lit—male lit	718.39	0.002
	Taxa richness	Site	$F_{1,24} = 15.89$***	Lit—dark	10.93	< 0.001
	exp (Shannon)	Site	$F_{1,24} = 8.69$**	Lit—dark	5.21	0.007
	Chironomus dorsalis	Site:sex interaction	$F_{1,24} = 27.14$***	Lit—dark	0.55	< 0.001
				Female lit—female dark	0.92	< 0.001
				Female lit—male lit	0.76	< 0.001
	Chironomini	Site:sex interaction	$F_{1,24} = 3.84$#	Lit—dark	98.19	0.062
				Female lit—female dark	196.37	0.021
				Female lit—male lit	225.45	0.012
	Chironomus plumosus	Site	$F_{1,24} = 6.28$*	Lit—dark	6.24	0.019
	Chironomus sp.	Site	$F_{1,24} = 4.72$*	Lit—dark	2.81	0.04
	Cladopelma edwardsi	Site:sex interaction	$F_{1,24} = 4.19$#	Lit—dark	0.96	0.014
				Female lit—male lit	− 1.49	0.016
				Male lit—male dark	1.70	0.009
	Cladopelma virescens	Site	$F_{1,24} = 3.96$#	Lit—dark	2.68	0.058
	Glyptotendipes glaucus	Site:sex interaction	$F_{1,24} = 7.85$**	Lit—dark	53.12	< 0.001
				Female lit—female dark	85.07	< 0.001
				Female lit—male lit	65.00	< 0.001
	Orthocladiinae	Site:sex interaction	$F_{1,24} = 5.37$*	Lit—dark	2.79	0.029
				Female lit—female dark	5.58	0.006
				Female lit—male lit	8.61	< 0.001
	Parachironomus monochromus	Site	$F_{1,24} = 4.40$*	Lit—dark	3.73	0.047
	Polypedilum nubeculosum	Site	$F_{1,24} = 7.27$*	Lit—dark	33.75	0.013
	Procladius crassinervis	Site	$F_{1,24} = 4.35$*	Lit—dark	38.40	0.048

CPUE Catch per unit effort

[a] Asterisks and hashtag indicate significant main effect at: *** = < 0.001; ** = < 0.01; * = < 0.05; # = < 0.07

[b] Delta CPUE is the estimation of difference between the first and second factor (e.g. lit—dark)

[c] Significance (p) of the pairwise contrast analysis

by disrupting the photoperiod, which regulates development (Corbet 1964; Brittain 1982).

Temperature and light are important cues in ontogenesis, particularly for Chironomidae in temperate regions (Pinder 1986). While the peak in emergence in late Spring and early Autumn at the control site reflected natural dynamics (Manfrin et al. 2017; Kolbenschlag et al. 2023), these patterns were not observed under ALAN, which suggests that ALAN may interfere with seasonal cues such as temperature and natural photoperiod, resulting in a loss or alteration of temporal structure (Hölker et al. 2021).

An exception to the pattern of a reduced emergence at the lit site was that *Monopelopia tenuicalcar* and other Pentaneurini emerged at higher rates in the lit site. This might be explained by the predatory diet of *M. tenuicalcar* larvae (Syrovátka 2018) profiting from favourable visual conditions for predation in lit areas, as has been observed in piscivorous fishes (Nelson et al. 2021). This, in turn, may have led to higher survival and rates of emergence observed at the lit site; however, other taxa with predatory larvae, such as. *Procladius* spp., did not exhibit different emergence rates in lit and unlit sites. Since males tend to emerge earlier

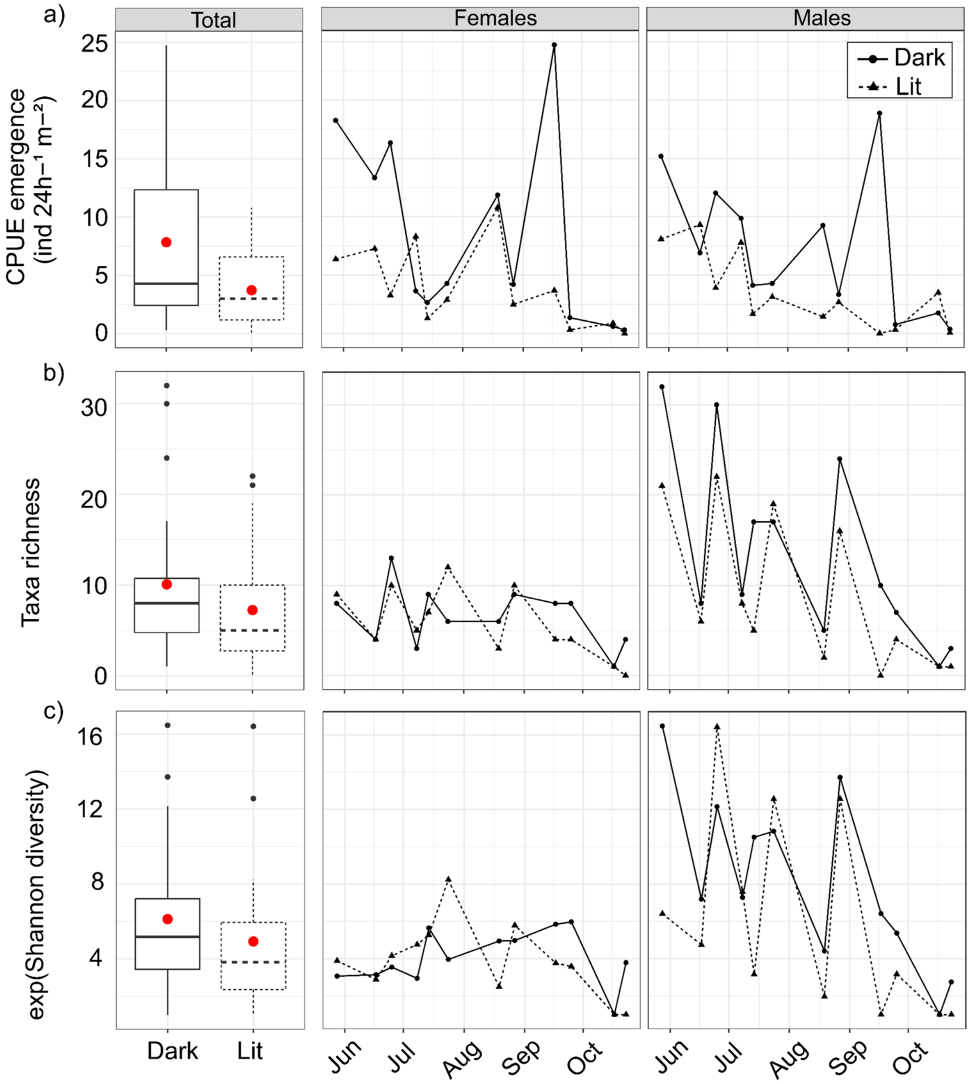

Fig. 2 Aquatic Diptera emergence as total catch (left panels) and sex-specific catch (middle and right panels) per sampling event as catch per unit effort (*CPUE*) (**a**), taxa richness (**b**) and the exponential of Shannon diversity (**c**) at dark (= control) (solid line) and lit (broken line) sites. CPUE was calculated as the sum of the CPUE of all traps for each site and sampling event. In boxplots shown in left panel, the box box = interquartile range, whiskers = minimum and maximum values, mid-line = median and filled red circle = mean

than females and start to swarm, waiting for the females to emerge (McLachlan 1986), the reduced emergence of the males and the overall increase in the number of females (i.e. no reduction in emergence, but clear attraction to ALAN) observed for the majority of taxa at the lit site may decrease the encounter rates and ultimately reproductive success (e.g. Degen et al. 2017). It is interesting to note that variation across sampling events (the replicates in our study) suggests that most taxa peaked in abundance in the Spring and Summer while some (e.g. *C. edwardsi, E. tendens*, *G. glaucus*) were similarly attracted throughout the study period (Figs. 1, 2; ESM Fig. S1).

Sex-specific flight response

ALAN attracted flying aquatic Diptera to the lit site, locally increasing their densities in the lit riparian area. While such aggregation may increase the chances of mating success, it may also cause an increase in intra- and inter-specific competition for space and resources. The attraction of females by ALAN for many of the taxa, could theoretically be explained by different sensory abilities and impact mechanisms. The more pronounced phototactic behaviour in female chironomids compared to males is attributed to the female's use of reflected horizontally polarised light on the water surface as a signal indicating suitable oviposition sites (Lerner et al. 2008); this makes females, but not males, more sensitive to light at night. When ALAN reflects off the water surface, it can become polarised and possible mask natural polarisation cues, which is likely to become an ecological hazard for flying polarotactic aquatic insects (Pérez Vega et al. 2024). We observed that females were captured more frequently than males, while for comparison an opposite pattern was observed in moths which are not dependent on aquatic oviposition sites (Altermatt et al. 2009). However, in several aquatic caddisfly species, males and females are attracted to artificial light to different degrees (Waringer et al. 1986). In addition, Honnen et al. (2019) and Fyie et al.

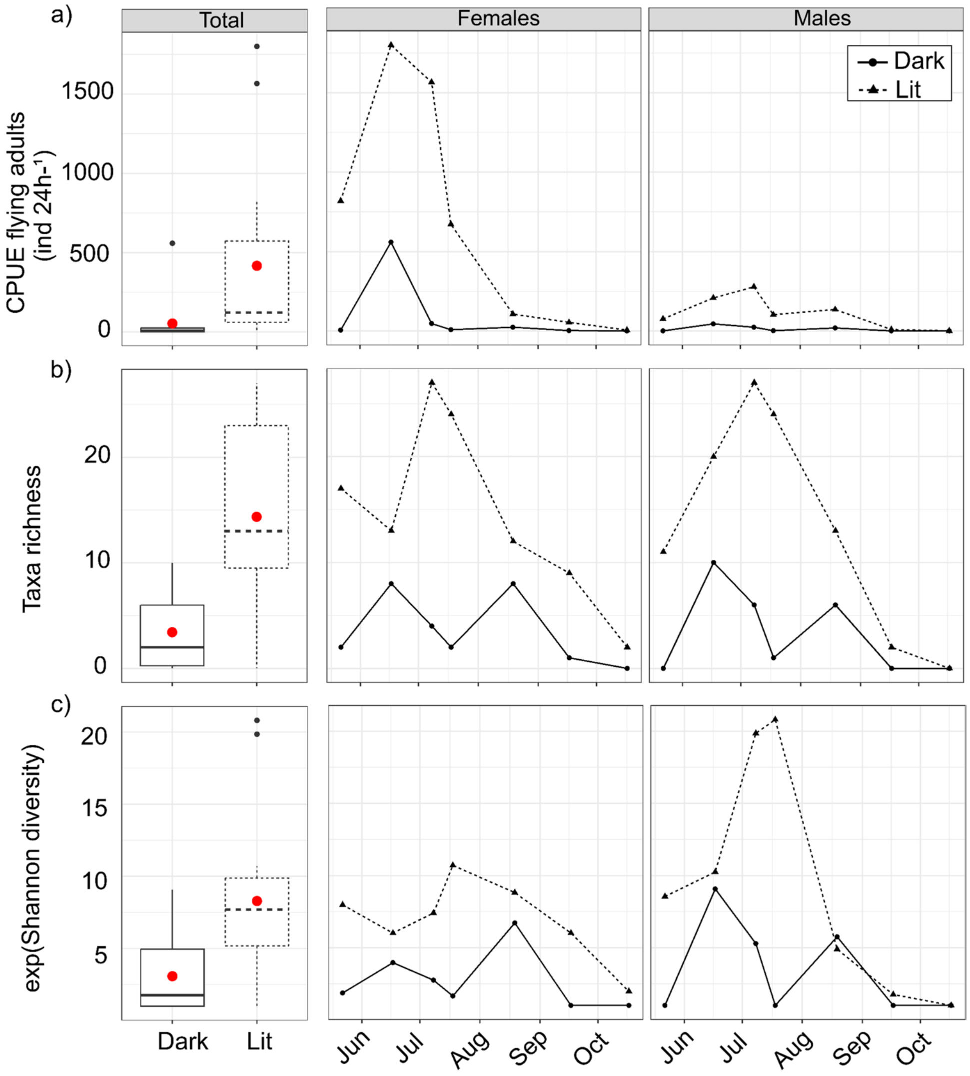

Fig. 3 Aquatic adult flying Diptera caught at air-eclector traps as total catch (left panels) and sex-specific catch per sampling event (middle and right panels) as catch per unit effort (*CPUE*) (**a**), taxa richness (**b**) and the exponential of Shannon diversity (**c**). In boxplots shown in left panel, the box box = interquartile range, whiskers = minimum and maximum values, mid-line = median and filled red circle = mean

(2024) found that ALAN can affect the expression of clock-genes in *Culex* mosquitoes in a sex-specific manner, with ALAN-exposed female *Culex pipiens f. molestus* being more active than males once lights were switched off. Thus, sex-specific sensory abilities and impact mechanisms may well explain the differences in sex-specific flight responses.

Attraction to ALAN

For the majority of taxa, and consistent with the findings of previous studies (Delettre and Morvan 2000; but see Muehlbauer et al. 2014), our model found that Chironomidae tend not to disperse far from the stream from which they emerge. Our model estimated a greater attraction distance for only a few taxa, and slightly greater distances for males of these taxa. In contrast, females of three taxa, *P. nubeculosum*, *P. crassinervis* and Chironomini sp., were attracted from much greater distances than males and females of other taxa, suggesting that these females may exhibit stronger phototactic behaviour, possibly related to oviposition flights (McLachlan 1986; Delettre and Morvan 2000). The attracting effect of ALAN over large distances, as estimated here, may significantly increase the distance these insects move away from the water and thereby change the biological signature of the river in a wider landscape context (Muehlbauer et al. 2014; Gurnell et al. 2016), a factor that has rarely been considered in conservation efforts.

Our model was based on assumptions that may not always be valid. First, we assumed that all emerging individuals are collected in air-eclector traps. Although light elicits positive phototaxis, the lamps used in the present study are unlikely to be such a strong attractor that all the emerging insects are drawn into the trap. The result is an underestimation of attracted/emerging individuals used to calculate the factor of attraction and, subsequently, an underestimation of the attraction distance. Recent findings in moths suggest that artificial lights trap passing insects rather than attract them from a long distance, but little is known about the flight to

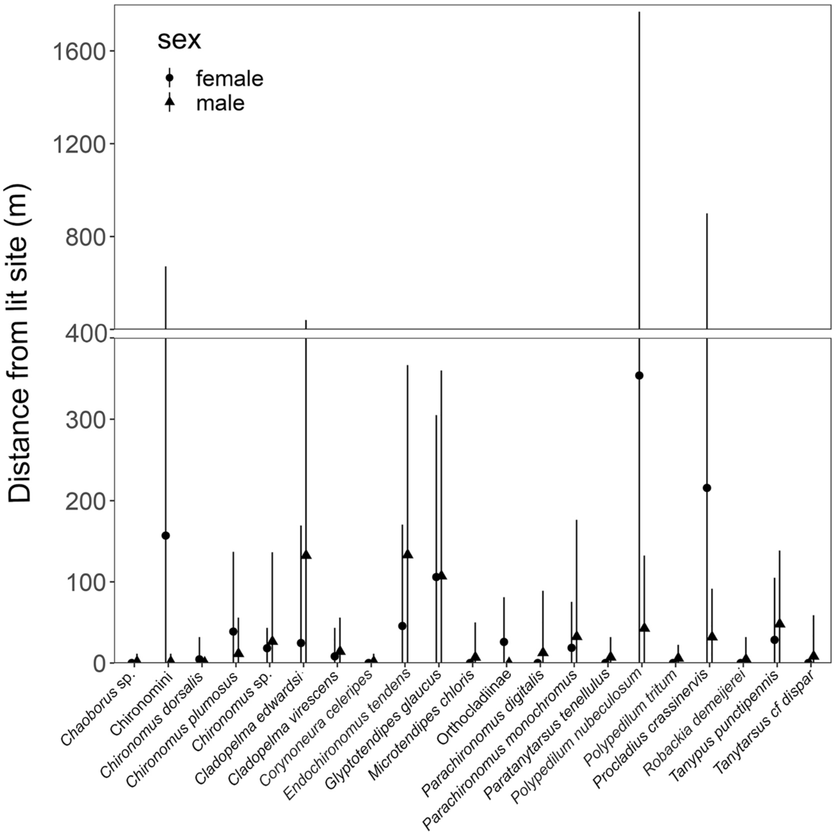

Fig. 4 Estimated attraction distance (filled shapes = mean; bars = minimum and maximum when > 0) for taxa for which "site" or the "site:sex" interaction was significant based on a linear model (Table 1) for adult Diptera either emerging or flying for which the mean distance was > 0 (i.e. attraction factor > 1; Table S2) for males, females or both. Note that the scaling of bottom and top panels are different to highlight taxa differences

light over long distances (Degen et al. 2024; Fabian et al. 2024). Second, we assumed that the density of Diptera larvae was homogeneous, which could inflate attraction distance. This assumption is likely to be wrong, with species being patchily distributed. Both simplifications were applied across all taxa and independent of sex; thus the general patterns are likely to reflect real phenomena, even if the exact numbers are uncertain. Finally, it is important to recognise that our results are likely applicable to open landscapes, such as the agricultural area where the experiment was conducted. In densely vegetated areas, estimates of attraction distance to ALAN may differ significantly due to the filtering effects of the landscape structure on insect dispersal (Delettre and Morvan 2000) and the attenuation of ALAN through vegetation over greater distances.

In conclusion, we found a two-fold reduction in total emergence of aquatic Diptera at an ALAN-lit site, and an eight-fold increase in the number of adults flying at light. In both cases, patterns varied widely among taxa and between sexes. While our model estimations indicate that most Diptera at lights were attracted from the water body adjacent to the lit site, some were attracted from up to 1800 m away. This long-range attraction would have been overlooked with common coarser taxonomic approaches, underscoring the value of high-resolution, species-specific assessments. Consequently, this study highlights the risk of ALAN disrupting key processes in aquatic-terrestrial meta-ecosystems. Given the large number of streetlights present along freshwater bodies (Hölker et al. 2023), and the ongoing global increase in lighting emissions (Kyba et al. 2017, 2023), the effects observed in this study may help explain insect decline and inform conservation efforts. In this context, the correct positioning and shielding of luminaires near water may be particularly important order to reduce the ecological impact of ALAN across habitat boundaries (Dietenberger et al. 2024).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00027-025-01161-7.

Acknowledgements This work was carried out within the Erasmus Mundus Joint Doctorate Program SMART, funded by the Education, Audiovisual and Culture Executive Agency of the European Commission. Funding was also provided by the Federal Ministry of Education and Research, Germany (BMBF-033L038A) and the Federal Agency for Nature Conservation, Germany (FKZ 3514821700). Alessandro Manfrin was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; 326210499/GRK2360). Sven Teurlincx was funded by a Netherlands Organisation for Scientific Research (NWO-Talent program) VENI TTW Grant (no. 20285). Viktor Baranov´s work was funded by the Spanish State Research agency Ramon y Cajal fellowship (RyC2021-032144I). We thank Stefan Heller and Nina-Sophie Weiß for help during the experiment. We also thank Stephen Osakpolor for helping with the quality check of the R script and Stefano Larsen for giving suggestions on an earlier draft of the manuscript.

Author contributions AM, FH, ST and MTM contributed to the study conceptualisation. AM and ST contributed to the data analysis and wrote the first draft of the manuscript. All authors contributed to the writing and review of the previous versions of the manuscript and approved the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability Datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

References

Ali A, Stafford SR, Fowler RC, Stanley BH (1984) Attraction of adult Chironomidae (Diptera) to incandescent light under laboratory conditions. Environ Entomol 13(4):1004–1009

Ali A, Stanley BH, Chaudhuri PK (1986) Attraction of some adult midges (Diptera: Chironomidae) of Florida to artificial light in the field. Fla Entomol 69:644–650

Ali A, Ceretti G, Barbato L, Marchese G, Andrea D, F, Stanley B, (1994) Attraction of *Chironomus salinarius* (Diptera: Chironomidae) to artificial light on an island in the saltwater lagoon of Venice, Italy. J Am Mosq Control Assoc 10(1):35–41

Altermatt F, Baumeyer A, Ebert D (2009) Experimental evidence for male biased flight-to-light behavior in two moth species. Entomol Exp Appl 130(3):259–265

Andreatta G, Tessmar-Raible K (2020) The still dark side of the moon: molecular mechanisms of lunar-controlled rhythms and clocks. J Mol Biol 432(12):3525–3546

Armitage PD (1995) Behaviour and ecology of adults. Springer Netherlands, Dordrecht, pp 194–224

Armitage PD, Pinder LC, Cranston PS (eds) (2012) The Chironomidae:biology and ecology of non-biting midges. Springer

Baranov V, Lewandowski J, Romeijn P, Singer G, Krause S (2016) Effects of bioirrigation of non-biting midges (Diptera: Chironomidae) on lake sediment respiration. Sci Rep 6(1):27329

Baranov V, Jourdan J, Pilotto F, Wagner R, Haase P (2020) Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. Conserv Biol 34(5):1241–1251

Bartels P, Cucherousset J, Steger K, Eklöv P, Tranvik LJ, Hillebrand H (2012) Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology 93(5):1173–1182

Baxter CV, Fausch KD, Carl Saunders W (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw Biol 50(2):201–220

Bivand R, Rundel C (2023) rgeos: Interface to Geometry Engine - Open Source ('GEOS'). https://r-forge.r-project.org/projects/rgeos/; https://libgeos.org; http://rgeos.r-forge.r-project.org/index.html. Accessed 15 Sept 2024

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

Brittain JE (1982) Biology of mayflies. Annu Rev Entomol 27:119–395

Carannante D, Blumenstein CS, Hale JD, Arlettaz R (2021) LED lighting threatens adult aquatic insects: impact magnitude and distance thresholds. Ecol Solut Evid 2(2):e12053

Cerri RD, Fraser DF (1983) Predation and risk in foraging minnows: balancing conflicting demands. Am Nat 121:552–561

Chen G, Li X, Liu X, Chen Y, Liang X, Leng J, Xu X, Liao W, Qiu YA, Wu Q, Huang K (2020) Global projections of future urban land expansion under shared socioeconomic pathways. Nat Commun 11(1):537

Chimeno C, Rulik B, Manfrin A, Kalinkat G, Hölker F, Baranov V (2023) Facing the infinity: tackling large samples of challenging Chironomidae (Diptera) with an integrative approach. PeerJ 11:e15336

Corbet PS (1958) Lunar periodicity of aquatic insects in Lake Victoria. Nature 182(4631):330–331

Corbet PS (1964) Temporal patterns of emergence in aquatic insects. Can Entomol 96:264–279

Czarnecka M, Kakareko T, Jermacz Ł, Pawlak R, Kobak J (2019) Combined effects of nocturnal exposure to artificial light and habitat complexity on fish foraging. Sci Total Environ 684:14–22

Degen T, Mitesser O, Perkin EK, Weiß NS, Oehlert M, Mattig E, Hölker F (2016) Street lighting: sex-independent impacts on moth movement. J Anim Ecol 85(5):1352–1360

Degen T, Hovestadt T, Mitesser O, Hölker F (2017) Altered sex-specific mortality and female mating success: ecological effects and evolutionary responses. Ecosphere 8(5):e01820

Degen J, Storms M, Lee CB, Jechow A, Stoeckl AL, Hölker F, Jakhar A, Walter T, Walter S, Mitesser O, Hovestadt T (2024) Shedding light with harmonic radar: unveiling the hidden impacts of streetlights on moth flight behavior. Proc Natl Acad Sci USA 121(42):e2401215121

Delettre YR, Morvan N (2000) Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshw Biol 44(3):399–411

Dietenberger M, Jechow A, Kalinkat G, Schroer S, Saathoff B, Hölker F (2024) Reducing the fatal attraction of nocturnal insects using tailored and shielded road lights. Commun Biol 7(1):671

Dijkstra KDB, Monaghan MT, Pauls SU (2014) Freshwater biodiversity and aquatic insect diversification. Annu Rev Entomol 59:143–163

Donners M, van Grunsven RH, Groenendijk D, van Langevelde F, Bikker JW, Longcore T, Veenendaal E (2018) Colors of attraction: modeling insect flight to light behavior. J Exp Zool A Ecol Integr Physiol 329(8–9):434–440

Fabian ST, Sondhi Y, Allen PE, Theobald JC, Lin HT (2024) Why flying insects gather at artificial light. Nat Commun 15(1):689

Ferrington JRLC, Saether OA (2011) A revision of the genera *Pseudosmittia* Edwards, 1932, *Allocladius* Kieffer, 1913, and *Hydrosmittia* gen. n. (Diptera: Chironomidae, Orthocladiinae). Zootaxa 2849(1):1–314

Fyie LR, Westby KM, Meuti ME (2024) Light pollution disrupts circadian clock gene expression in two mosquito vectors during their overwintering dormancy. Sci Rep 14(1):2398

Grubisic M, van Grunsven RHA, Kyba CC, Manfrin A, Hölker F (2018) Insect declines and agroecosystems: does light pollution matter? Ann Appl Biol 173(2):180–189

Gurnell AM, Bertoldi W, Tockner K, Wharton G, Zolezzi G (2016) How large is a river? Conceptualizing river landscape signatures and envelopes in four dimensions. Wiley Interdiscip Rev Water 3(3):313–325

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12(10):e0185809

Hallmann CA, Ssymank A, Sorg M, de Kroon H, Jongejans E (2021) Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. Proc Natl Acad Sci USA 118(2):e2002554117

Hölker F, Wolter C, Perkin EK, Tockner K (2010) Light pollution as a biodiversity threat. Trends Ecol Evol 25(12):681–682

Hölker F, Vanni MJ, Kuiper JJ, Meile C, Grossart HP, Stief P, Adrian R, Lorke A, Dellwig O, Brand A, Hupfer M (2015a) Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems. Ecol Monogr 85(3):333–351

Hölker F, Wurzbacher C, Weißenborn C, Monaghan MT, Holzhauer SI, Premke K (2015b) Microbial diversity and community respiration in freshwater sediments influenced by artificial light at night. Philos Trans R Soc Lond B Biol Sci 370(1667):20140130

Hölker F, Bolliger J, Davies TW, Giavi S, Jechow A, Kalinkat G, Longcore T, Spoelstra K, Tidau S, Visser ME, Knop E (2021) 11 pressing research questions on how light pollution affects biodiversity. Front Ecol Evol 9:767177

Hölker F, Jechow A, Schroer S, Tockner K, Gessner MO (2023) Light pollution of freshwater ecosystems: principles, ecological impacts and remedies. Philos Trans R Soc Lond B Biol Sci 378(1892):20220360

Holzhauer SIJ, Franke S, Kyba CC, Manfrin A, Klenke R, Voigt CC, Lewanzik D, Oehlert M, Monaghan MT, Schneider S, Heller S, Kuechly H, Brüning A, Honnen AC, Hölker F (2015) Out of the dark: establishing a large-scale field experiment to assess the effects of artificial light at night on species and food webs. Sustainability 7(11):15593–15616

Honnen AC, Kypke JL, Hölker F, Monaghan MT (2019) Artificial light at night influences clock-gene expression activity and fecundity in the mosquito *Culex pipiens* f. *molestus*. Sustainability 11(22):6220

Horváth G, Móra A, Bernáth B, Kriska G (2011) Polarotaxis in non-biting midges: female chironomids are attracted to horizontally polarized light. Physiol Behav 104(5):1010–1015

Hyndman R, Athanasopoulos G, Bergmeir C, Caceres G, Chhay L, O'Hara-Wild M, Petropoulos F, Razbash S, Wang E and Yasmeen F (2023) forecast: forecasting functions for time series and linear models. R package version 8.21.1. https://pkg.robjhyndman.com/forecast/. Accessed 10 Oct 2024

International Dark Sky Association (IDA) (2015) International Dark Sky Reserves: Westhavelland (Germany). Available online at: https://www.darksky.org/our-work/conservation/idsp/reserves/westhavelland/. Accessed 5 May 2023

Jähnig SC, Baranov V, Altermatt F, Cranston P, Friedrichs-Manthey M, Geist J, He F, Heino J, Hering D, Hölker F, Jourdan J, Kalinkat G, Kiesel J, Leese F, Maasri A, Monaghan MT, Schäfer RB, Tockner K, Tonkin JD, Domisch S (2021) Revisiting global trends in freshwater insect biodiversity. WIREs Water 8(2):e1506

Jechow A, Hölker F (2019) How dark is a river? Artificial light at night in aquatic systems and the need for comprehensive night-time light measurements. WIREs Water 6(6):e1388

Jost L (2006) Entropy and diversity. Oikos 113(2):363–375

Kaiser TS, Poehn B, Szkiba D, Preussner M, Sedlazeck FJ, Zrim A, Neumann T, Nguyen LT, Betancourt AJ, Hummel T, Vogel H (2016) The genomic basis of circadian and circalunar timing adaptations in a midge. Nature 540(7631):69–73

Kennedy TA, Muehlbauer JD, Yackulic CB, Lytle DA, Miller SW, Dibble KL, Kortenhoeven EW, Metcalfe AN, Baxter CV (2016) Flow management for hydropower extirpates aquatic insects, undermining river food webs. Bioscience 66(7):561–575

Kolbenschlag S, Gerstle V, Eberhardt J, Bollinger E, Schulz R, Bruehl CA, Bundschuh M (2023) A temporal perspective on aquatic subsidy: Bti affects emergence of Chironomidae. Ecotoxicol Environ Saf 250:114503

Kraus JM, Kuivila KM, Hladik ML, Shook N, Mushet DM, Dowdy K, Harrington R (2021) Cross-ecosystem fluxes of pesticides from prairie wetlands mediated by aquatic insect emergence: implications for terrestrial insectivores. Environ Toxicol Chem 40(8):2282–2296

Kühne JL, van Grunsven RH, Jechow A, Hölker F (2021) Impact of different wavelengths of artificial light at night on phototaxis in aquatic insects. Integr Comp Biol 61(3):1182–1190

Kummu M, De Moel H, Ward PJ, Varis O (2011) How close do we live to water? A global analysis of population distance to freshwater bodies. PLoS ONE 6(6):e20578

Kyba CC, Kuester T, De Miguel AS, Baugh K, Jechow A, Hölker F, Bennie J, Elvidge CD, Gaston KJ, Guanter L (2017) Artificially lit surface of Earth at night increasing in radiance and extent. Sci Adv 3(11):e1701528

Kyba CC, Altıntaş YÖ, Walker CE, Newhouse M (2023) Citizen scientists report global rapid reductions in the visibility of stars from 2011 to 2022. Science 379(6629):265–268

Langton PH, Pinder LCV (editors) (2007). Keys to the adult male Chironomidae of Britain and Ireland, vol 1 and 2. Freshwater Biological Association (FBA), Lakeside, Newby Bridge.

Larsen S, Muehlbauer JD, Marti E (2016) Resource subsidies between stream and terrestrial ecosystems under global change. Glob Change Biol 22(7):2489–2504

Leather SR (2017) "Ecological Armageddon"—more evidence for the drastic decline in insect numbers. Ann Appl Biol 172(1):1–3

Lee CY, Kim DG, Baek MJ, Choe LJ, Bae YJ (2013) Life history and emergence pattern of *Cloeon dipterum* (Ephemeroptera: Baetidae) in Korea. Environ Entomol 42(6):1149–1156

Lenth RV (2016) Least-squares means: the R package lsmeans. J Stat Softw 69:1–33

Lerner A, Meltser N, Sapir N, Erlick C, Shashar N, Broza M (2008) Reflected polarization guides chironomid females to oviposition sites. J Exp Biol 211(22):3536–3543

Linares Arroyo H, Abascal A, Degen T, Aubé M, Espey BR, Gyuk G, Hölker F, Jechow A, Kuffer M, Sánchez de Miguel A, Simoneau A, Walczak K, Kyba CCM (2024) Monitoring, trends and impacts of light pollution. Nat Rev Earth Environ 5:417–430

Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol Lett 6(8):673–679

Makarchenko EA, Makarchenko MA (2006) Chironomids of the genus *Bryophaenocladius* Thienemann, 1934 (Diptera, Chironomidae, Orthocladiinae) from the Russian Far East. Far Eastern Entomol 158:1–24

Manfrin A, Singer G, Larsen S, Weiß N, Van Grunsven RH, Weiß NS, Wohlfahrt S, Monaghan MT, Hölker F (2017) Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. Front Environ Sci 5:61

Manfrin A, Lehmann D, van Grunsven RHA, Larsen S, Syväranta J, Wharton G, Voigt CC, Monaghan MT, Hölker F (2018) Dietary changes in predators and scavengers in a nocturnally illuminated riparian ecosystem. Oikos 127(7):960–969

Marcarelli AM, Baxter CV, Mineau MM, Hall JR, R. O. (2011) Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92(6):1215–1225

Marczak LB, Richardson JS (2007) Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. J Anim Ecol 76(4):687–694

Martin-Creuzburg D, Kowarik C, Straile D (2017) Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. Science of the Total Environment 577:174–182

McGinnis DF, Flury S, Tang KW, Grossart HP (2017) Porewater methane transport within the gas vesicles of diurnally migrating *Chaoborus* spp.: an energetic advantage. Sci Rep 7(1):1–7

McLachlan AJ (1986) Sexual dimorphism in midges: strategies for flight in the rain-pool dweller *Chironomus imicola* (Diptera: Chironomidae). J Anim Ecol.

Meyer LA, Sullivan SMP (2013) Bright lights, big city: influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. Ecol Appl 23(6):1322–1330

Muehlbauer JD, Collins SF, Doyle MW, Tockner K (2014) How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. Ecology 95(1):44–55

Nabity PD, Higley LG, Heng-Moss TM (2007) Light-induced variability in development of forensically important blow fly *Phormia regina* (Diptera: Calliphoridae). J Med Entomol 44(2):351–358

Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc Natl Acad Sci USA 98(1):166–170

Nelson TR, Michel CJ, Gary MP, Lehman BM, Demetras NJ, Hammen JJ, Horn MJ (2021) Effects of artificial lighting at night on predator density and salmonid predation. Trans Am Fish Soc 150(2):147–159

Ohler K, Schreiner VC, Link M, Liess M, Schäfer RB (2023) Land use changes biomass and temporal patterns of insect cross-ecosystem flows. Glob Change Biol 29(1):81–96

Owens AC, Cochard P, Durrant J, Farnworth B, Perkin EK, Seymoure B (2020) Light pollution is a driver of insect declines. Biol Conserv 241:108259

Paetzold A, Schubert CJ, Tockner K (2005) Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. Ecosystems 8(7):748–759

Perkin EK, Hölker F, Richardson JS, Sadler JP, Wolter C, Tockner K (2011) The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. Ecosphere 2(11):1–16

Perkin EK, Hölker F, Tockner K, Richardson JS (2014) Artificial light as a disturbance to light-naïve streams. Freshw Biol 59(11):2235–2244

Pérez Vega C, Hölker F, Zielinska-Dabkowska KM, Jechow A (2024) Polarised light pollution on river water surfaces caused by artificial light at night from illuminated bridges and surroundings. J Limnol 83:2173

Pietz S, Kolbenschlag S, Roeder N, Roodt AP, Steinmetz Z, Manfrin A, Schwenk K, Schulz R, Schaefer RB, Zubrod JP, Bundschuh M (2023) Subsidy quality affects common riparian web-building spiders: consequences of aquatic contamination and food resource. Environ Toxicol Chem 42(6):1346–1358

Pinder LCV (1986) Biology of freshwater Chironomidae. Annu Rev Entomol 31(1):1–23

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28(1):289–316

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 10 Oct 2024

Sánchez-Bayo F, Wyckhuys KA (2019) Worldwide decline of the entomofauna: a review of its drivers. Biol Conserv 232:8–27

Sanzone DM, Meyer JL, Martí E, Gardiner EP, Tank JL, Grimm NB (2003) Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134:238–250

Schulz R, Bundschuh M, Gergs R, Brühl CA, Diehl D, Entling MH, Fahse L, Frör O, Jungkunst HF, Lorke A, Schäfer RB (2015) Review on environmental alterations propagating from aquatic to terrestrial ecosystems. Sci Total Environ 538:246–261

Schulz R, Bundschuh M, Entling MH, Jungkunst HF, Lorke A, Schwenk K, Schäfer RB (2024) A synthesis of anthropogenic stress effects on emergence-mediated aquatic-terrestrial linkages and riparian food webs. Sci Total Environ 908:168186

Spoelstra K, Teurlincx S, Courbois M, Hopkins ZM, Visser ME, Jones TM, Hopkins GR (2023) Long-term exposure to experimental light affects the ground-dwelling invertebrate community, independent of light spectra. Philos Trans R Soc Lond B Biol Sci 378(1892):20220364

Sullivan SMP, Hossler K, Meyer LA (2019) Artificial lighting at night alters aquatic-riparian invertebrate food webs. Ecol Appl 29(1):e01821

Syrovátka V (2018) The predatory behaviour of Monopelopia tenuicalcar (Kieffer, 1918) larvae in a laboratory experiment. J Limnol 77(s1):88–94

Száz D, Horvath G, Barta A, Robertson BA, 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

van Geffen KG, van Eck E, de Boer RA, van Grunsven RHA, Salis L, Berendse F, Veenendaal EM (2015a) Artificial light at night inhibits mating in a Geometrid moth. Insect Conserv Diversity 8(3):282–287

van Grunsven RHA, van Deijk JR, Donners M, Berendse F, Visser ME, Veenendaal E, Spoelstra K (2020) Experimental light at night has a negative long-term impact on macro-moth populations. Curr Biol 30(12):694–695

van Langevelde F, Ettema JA, Donners M, WallisDeVries MF, Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. Biol Conserv 144(9):2274–2281

Van Geffen KG, Groot AT, Van Grunsven RHA, Donners M, Berendse F, Veenendaal EM (2015b) Artificial night lighting disrupts sex pheromone in a noctuid moth. Ecol Entomol 40(4):401–408

Waringer JA (1986) The abundance and distribution of caddisflies (Insecta: Trichoptera) caught by emergence traps in the 'Ritrodat' research area of the Lunzer Seebach (Lower Austria) from 1980 to 1982. Freshw Biol 16(1):49–59

Whiles MR, Goldowitz BS (2001) Hydrologic influences on insect emergence production from central Platte River wetlands. Ecol Applic 11(6):1829–1842

Wiederholm T (1989) The adult males of Chironomidae (Diptera) of the Holarctic region-keys and diagnoses. Entomol Scand Suppl 34:1–532

Wilk MB, Gnanadesikan R (1968) Probability plotting methods for the analysis for the analysis of data. Biometrika 55(1):1–17

Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. Methods Ecol Evol 7(6):636–645