University of Basel

Master’s Degree in
Sustainable Development

msd

Effects of luminaire shape, light level, and LED color temperature on nocturnal insect abundance

Author	Sina Sohneg 15-056-468
Focal Area	Natural Sciences
Submission Date	22 December 2021
First Reviewer	Prof. Dr. rer. nat. Patricia Burkhardt-Holm
Institution	University of Basel, Department of Environmental Sciences, Program Man-Society-Environment
Second Reviewer	PD Dr. Janine Bolliger
Institution	Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Research Unit Land Change Science, Land-use Systems

WSL

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ABSTRACT

Artificial light at night (ALAN) is an important driver of insect decline. Nocturnal insects are particularly vulnerable to ALAN because of its fatal attraction and are suffering from increasing light pollution worldwide. Insects act as a primary food source for many organisms and are providers of crucial ecosystem services such as pollination. Thus, insects are vital for healthy ecosystems that are imperative for sustainable development. The aim of this study was to provide an ecological assessment of the impacts of combined LED luminaire characteristics (luminaire shape, light level, LED color temperature) on nocturnal insect abundance. To contribute to the development of sustainable outdoor lighting, this study aimed to determine which luminaire characteristic affects nocturnal insect abundance the most and to find the combination of luminaire characteristics that attracts the lowest number of nocturnal insects. For this purpose, field experiments at three forest sites were carried out. The results indicate that luminaire shape had the strongest impact on nocturnal insect abundance, with 225.5% more insects caught at diffused luminaires. The least insect-attracting combination of luminaire characteristics consisted of flat luminaire shape, low light level (50% dimming), and warm LED color temperature (2200K).

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STATEMENT OF PLAGIARISM

I hereby declare that this submission is my own work and that I have fully acknowledged the assistance received in completing this work and that it contains no material that has not been formally acknowledged. I have mentioned all source materials used and have cited these in accordance with recognized scientific rules.

Full name/student number: Sina Sohneg 15-056-468

Date of issue: 22 December 2021

Signature:

S. Sohneg

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INTRODUCTION

1.1 Artificial light at night and insect decline

Well-known anthropogenic drivers of rapid changes in the environment, such as climate change, air pollution, and habitat loss, are threatening living organisms (Desouhant et al. 2019). Light pollution is increasingly recognized as another key driver of environmental changes (Bolliger et al. 2020b; Horton et al. 2019; Kyba et al. 2017). Light pollution can be caused by excessive and poorly planned artificial light at night (ALAN), of which a substantial part originates from street lights (Bolliger et al. 2021; Rowse et al. 2018). The extent of ALAN is still globally increasing by around 6 % per year (Hölker et al. 2010), leading to a steady decrease in areas in which dark nights can be found.

The widespread "loss of the night" caused by ALAN goes hand in hand with several detrimental impacts on the environment, including flora and fauna, but also on human health and well-being (Kyba et al. 2017). In humans, physiological disorders and diseases resulting from hormonal deregulation are suspected consequences of ALAN (Lunn et al. 2017). With respect to plants and animals, ALAN interferes negatively with organisms' fitness, and thus with the survival of populations (Desouhant et al. 2019). Further, ALAN reinforces the homogenization of species communities, as light tolerant species become even more common, while more sensitive species become even rarer (SWILD 2011).

Especially nocturnal organisms, which make up for 30 % of present biodiversity in vertebrates and more than 60 % in invertebrates (Hölker et al. 2010), are disturbed by ALAN due to their physical adaptions to living in dark environments. Their senses, such as their vision, are often sharpened (Hölker et al. 2010). As a consequence, they react sensitively to changes in light conditions within their environment. The life cycles of nocturnal insects are immensely influenced by ALAN which is increasingly acknowledged to contribute to insect decline (Kalinkat et al. 2021; Owens et al. 2020; Grubisic et al. 2018; Owens & Lewis 2018; van Langevelde et al. 2018). ALAN does not only act as a fatal attraction trap by causing flight-to-light behavior which in turn leads to insects circling around the light source until they die of exhaustion or predation, it also causes temporal- (desynchronization of insects from their normal biorhythms) and spatial (disruption in the insects' ability to navigate in three-dimensional space) disorientation, alters foraging activities and species interactions (Owens & Lewis 2018), and impairs insects mating success (van Geffen et al. 2015).

Insects are an important food source for many organisms. Hence, negative impacts on insects' fitness, resulting in reduced biomass and population sizes, may cascade to higher organizational levels in the food chain (Hölker et al. 2010). Furthermore, decreasing numbers of insects can threaten important regulating and supporting ecosystem services provided by insect communities especially in agroecosystems (e.g. pollination, natural pest control, decomposition of organic material, nutrient cycling), having direct impacts on human health and well-being (Grubisic et al. 2018; Knop et al. 2017; Altermatt & Ebert 2016; Hölker et al. 2010). Therefore, continuous global insect decline is a serious threat to whole ecosystems and entire ecological communities (Sanders & Gaston 2018).

1.2 Ecological impact research of ALAN

Due to higher luminous efficacy and efficiency of light-emitting diodes (LED), older light sources (e.g. HPS) in outdoor lighting are being replaced (Kyba et al. 2017). LED luminaires can differ in various characteristics: spectral composition defining color temperature of LED light, total amount of emitted light, and spatial distribution of light into the environment determined by luminaire housing designs. In LED luminaires, light levels can be dynamically adjusted to real-time demands by making use of smart lighting technologies (dimming; Rowse et al. 2018). Furthermore, a broad range of white LED color temperatures, and also an increasing diversity of housing designs are available. Most LED streetlights emit light vertically down on the road (focused/flat luminaire shapes). But horizontally emitting luminaire-housing shapes are also commercially available (diffused luminaire shapes; Bolliger et al. 2021).

These luminaire characteristics induce effects with varying severities on the environment and wildlife (Owens & Lewis 2018). A general trend in scientific literature concerning ALAN is that cold white LED color temperatures with a greater proportion of emitted blue light have more harmful impacts on the ecological environment, in particular on nocturnal insects, than warmer LED color temperatures with lower intensity blue spectral emissions (Bolliger et al. 2021; Somers-Yeates et al. 2013; van Langevelde et al. 2011). Lower light levels tend to be less harmful and might contribute to the mitigation of ALAN's detrimental effects on nocturnal species (Bolliger et al. 2020c; Rowse et al. 2018). A recent study highlighted the potentially amplified negative impact of luminaires with enhanced horizontal light emissions into the surroundings from diffused luminaire shapes on nocturnal insect abundance (Bolliger et al. 2021).

However, the effects of luminaire shape on nocturnal insects are poorly researched. Likewise, there is a lack of scientific ecological assessments and direct experimental evidence of the combined impact of the full set of luminaire characteristics (luminaire shape, light level, LED color temperature) on nocturnal insect abundance.

1.3 Contribution to sustainable outdoor lighting

The mitigation of ALAN is an interdisciplinary topic, evoking a conflict between environmental aspects and social needs. From the perspective of the environment and wildlife, it would be best to simply switch off all light sources at night. Contrarily, from the point of view of humans, ALAN represents an important aspect of safety, both technical (road and air traffic), as well as societal and psychological ("feeling safe"; Horton et al. 2019). Thus, it will be of utmost importance to strive for a compromise by making outdoor light sources less harmful for wildlife (e.g. by reducing the triggering of flight-to-light behavior) while at the same time accounting for human needs. Outdoor lighting at night fosters human development by providing people the opportunity to extend their days into the night in a self-selected manner. Still, the extent and characteristics of outdoor lighting need to stay within safe and sustainable boundaries that prevent the triggering of interferences with fundamental environmental processes and conditions. For defining these boundaries and framework conditions for sustainable outdoor lighting that meets the needs of the environment, animals, and humans, a scientific basis for ecological assessments has to be created first.

This study aims to contribute to this basis in terms of nocturnal insects by analysing the effects of combined characteristics of LED luminaires (luminaire shape, light level, LED color temperature) on nocturnal insect abundance. Finding combinations of light characteristics that attract fewer insects will contribute to the preservation of insect populations, and thus ecosystem services which are preconditions for sustainable development. In the long run, the results of this study should be used to formulate ecological recommendations for sustainable streetlight management, that are backed by light technicians, contributing to the development and application of sustainable outdoor lighting (Fig. 1). The recommendations are meant to support local, cantonal, and federal agencies in the formation of light pollution mitigation options, and hence more sustainable ALAN.

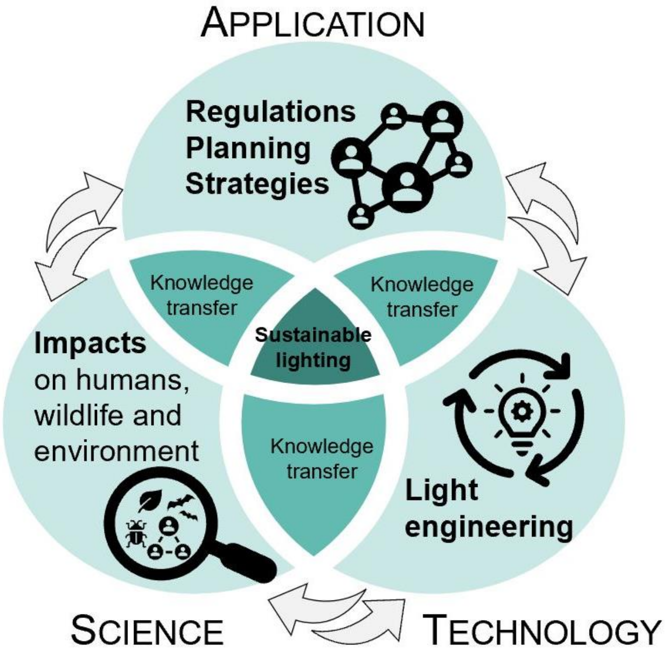

Figure 1: Interplay between scientific research, technological development and application strategies heading towards sustainable lighting.

The following research questions are aimed to be answered: (1) Which luminaire characteristic affects the nocturnal insect abundance the most? (2) Which combination of luminaire characteristics results in the lowest nocturnal insect abundance?

First, based on a previous study (Bolliger et al. 2021), the expectation is that the characteristic luminaire shape is affecting the nocturnal insect abundance the most. Second, it is expected that the combination of flat luminaire shape, low light level, and warm LED color temperature results in the lowest nocturnal insect abundance.

2. MATERIALS AND METHODS

2.1 Study sites

The field experiments were executed at three long-term forest observations sites (LWF[1]) of the Swiss Federal Institute for Forest, Snow, and Landscape Research (WSL). The forested study

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[1] LWF: Langfristige Waldökosystemforschung (Long-term Forest Ecosystem Research). https://www.wsl.ch/en/forest/forest-development-and-monitoring/long-term-forest-ecosystem-research-lwf.html

sites are supplied with electricity, equipped with meteorological stations, and were not under the direct influence of artificial light at night prior to the field experiments. The sites were located in Birmensdorf in the canton of Zurich, Lägern in the canton of Aargau, and Alpthal in the canton of Schwyz (Fig. 2).

The study site in Birmensdorf is in the Swiss Lowlands (518m a.s.l.). The forest, in which the field experiment took place, is a temperate mixed deciduous forest. The mean height of the vegetation in the sampling area is 8.44m (sd: 10.82m; min: 0m; max: 36m). The distance from the study site to the closest settled areas (Birmensdorf Sternen, Uitikon Waldegg) is approximately 400m. During the field season, a severe thunderstorm in the night of 12 July 2021 changed the forest structure in Birmensdorf. While the majority of the experiment remained unaffected, trees around one luminaire (BD02) were toppled during the storm (Fig. 2). The study site at Lägern is located at 866m a.s.l. at the eastern fringe of the Jura mountains. The study site forest can be categorized as a temperate mixed deciduous forest. The mean height of the vegetation in the sampling area is 25.93m (sd: 13.42m; min: 0m; max: 45m). The distance from the study site to the closest settled areas (Wettingen, Otelfingen) is approximately 2km. The study site at Alpthal is a pre-alpine location (996m a.s.l.). The forest is a temperate mixed conifer forest. The mean height of the vegetation in the sampling area is 13.08m (sd: 11.11m; min: 0m; max: 37m). The distance from the study site to the closest settled area (Alpthal Brunni) is approximately 500m.

2.2 Experimental setup

The effects of the combined LED luminaire characteristics on nocturnal insect abundance were investigated at the three study sites and catches were analysed for 28 nights per site (16 June – 1 July 2021 and 21 July – 5 August 2021).

At each study site, 12 LED streetlights (Schréder IZYLUM) were installed. Aluminum poles were erected and fixed with 60cm long ground screws. The streetlights were attached to these poles at a height of 2.5m. The following light treatments were considered: three LED color temperatures (amber 2200K, warm white 3000K, neutral white 4000K), two light levels (permanent dimming to 50% of the full light level, full light level (100%)), and two luminaire shapes (with standard vertical light distribution (flat), with increased horizontal light distribution into the surroundings (diffused)). As a control to the light treatments, there were two dark plots (insect traps without light exposure) at each study site (Fig. 2).

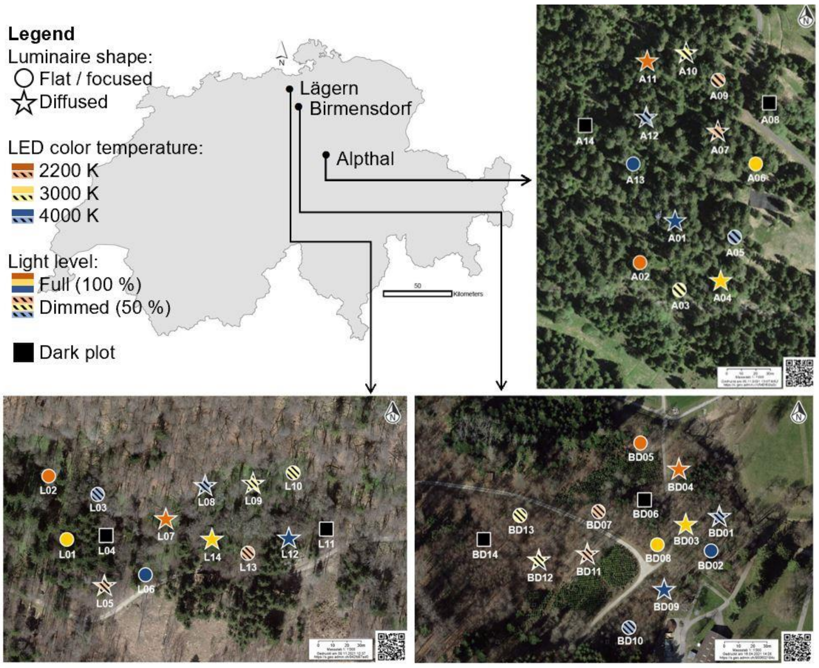

Figure 2: Location of the three study sites and experimental setup at each study site (© CNES, Spot Image, swisstopo, NPOC, public.geo.admin.ch).

Figure 3: Diffusor mounted on streetlight (Picture: Martin Obrist, WSL).

The selected LED color temperatures were set in the streetlights, and the treatment light level was programmed by the staff of the electricity works of the canton of Zurich (EKZ) beforehand. To mimic diffused luminaire shapes with enhanced horizontal light emission in the environment compared to standard, vertically emitting LED luminaire shapes, white plexiglass tubes were mounted to the LED streetlights (diffusors; Fig. 3). The diffusors have a diameter of 150mm and a length of 245mm. The diffusors' transmittance of light is 44%.

Random assignments of luminaires and dark plots on each study site prevented selection biases. A minimum buffer distance of 30m between all the luminaires and dark plots was maintained to avoid interferences. 30 meters were a trade-off between scientific considerations to avoid interferences and technical considerations related to the electrical infrastructure.

Before starting the field experiments, the luminaires needed to be calibrated regarding luminous flux to assure comparability. The calibration was performed at the Swiss Metrological Institute METAS in Bern. The calibration included the following standard measurements: (1) EN 13032-1:2004 measurement and graphical display of photometric data of lamps and luminaires – part 1: measurements and data format; (2) EN 13032-4:2015 measurement and graphical display of photometric data of lamps and luminaires – part 4: LED lamps, LED modules and LED luminaires; (3) CIE 84-1989 measurement of luminous flux; (4) CIE S025:2015 test method for LED lamps, LED luminaires and LED modules. Despite a loss of luminous flux by 23% for diffusor-carrying luminaires, diffused and flat-emitting luminaires remained comparable in luminous flux (Appendix Table A1).

In Figure 4, the spectral distribution of the three examined LED color temperatures can be seen. The figures show typical curves for the selected LED color temperatures: 4000K with a clear peak in the blue spectrum (short wavelengths), and 3000K and 2200K with reduced peaks in the blue spectrum. Nowadays, especially LED color temperatures around 3000K and 4000K are used for outdoor lighting installations.

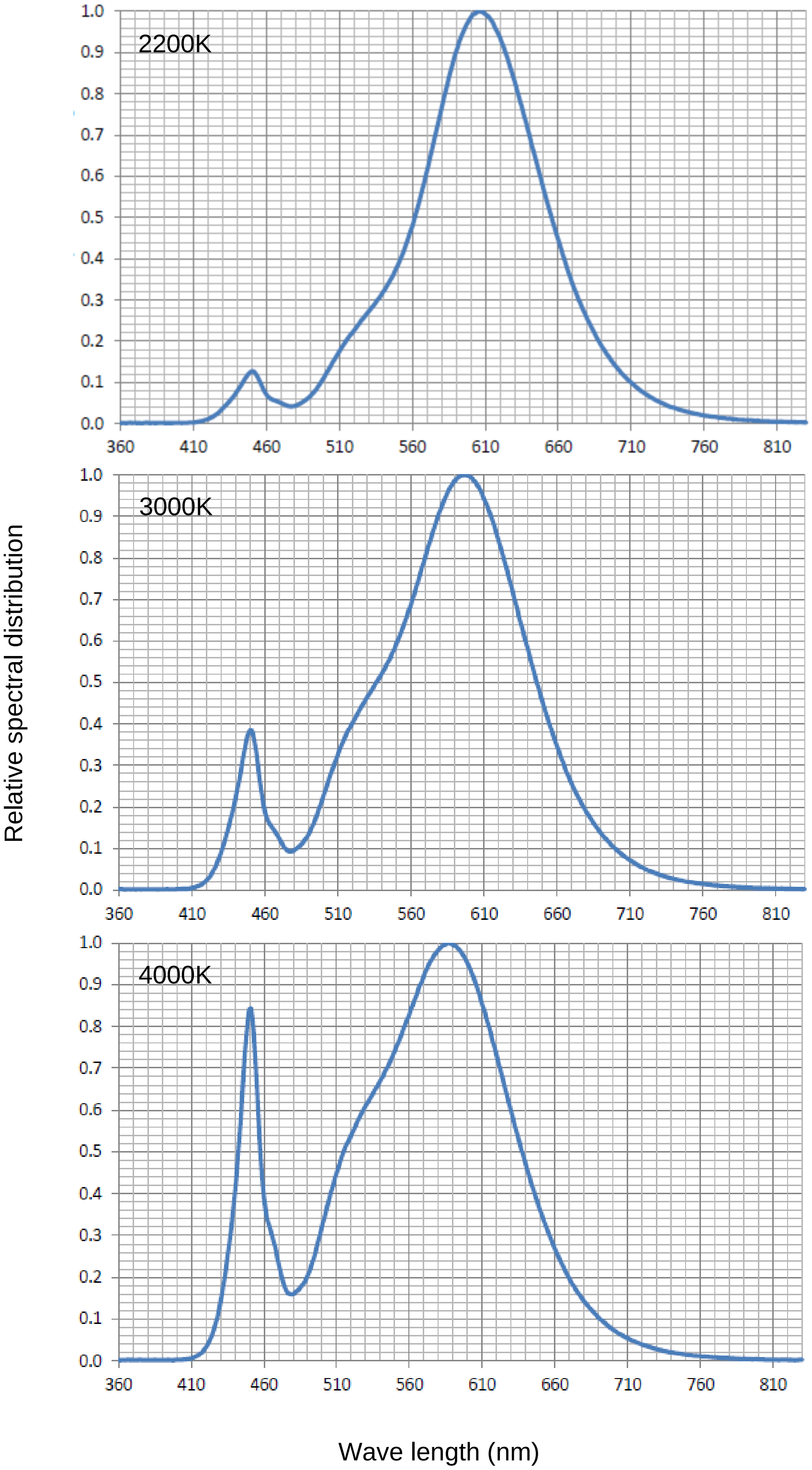

Figure 4: Spectral distribution of the LED luminaires: 2200K, 3000K, 4000K (EKZ).

2.3 Nocturnal insect abundance

To sample nocturnal insects, an automated flight-interception trap (Bolliger et al. 2020a) was mounted to each luminaire and dark plot at a height of about 1m at each study site (42 traps in total).

The automated flight-interception trap consists of a commercial flight interception-trap (Polytrap®) and a platform, that can be rotated by a stepper motor, holding seven cups that contain water with low concentrations of a biocide (Rocima™), and a passage hole (Bolliger et al. 2020a; Fig. 5). This composition allows collecting insects during seven user-defined time intervals, and therefore, the traps need to be emptied and refilled only once every seven intervals. During intervals where no insect trapping is planned, the passage hole is in the funnel position (Bolliger et al. 2020a; Fig. 5).

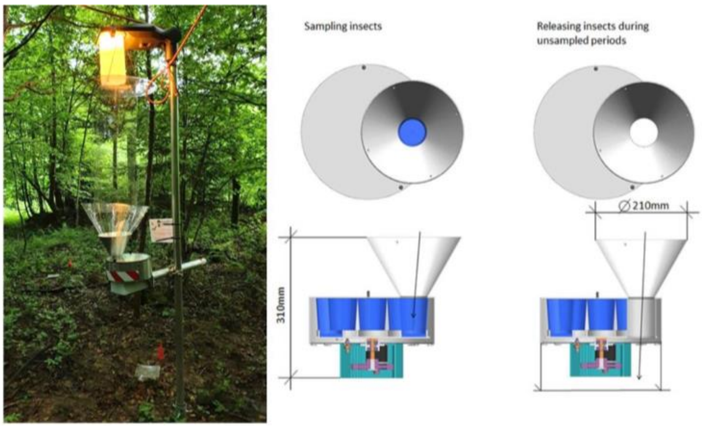

Figure 5: Automated flight-interception trap consisting of an unmodified commercial flight-interception trap (transparent plastic construction) and a rotating platform with seven cups and one passage hole (adapted from Bolliger et al. 20202a).

For these field experiments, the traps were active at night with a sampling period from sunset to sunrise. The samples were collected once a week. When arriving at the site, it was checked whether the traps had worked properly, or any failures had occurred via an application (BGX Commander Version 2.3.10) installed on the mobile phone. Failures were noted and the affected samples were excluded. Afterwards, the traps were reset for the next seven nights of sampling. Overall, 28 nights per site were sampled.

In the entomology lab, the sampled insects (stored in 70% alcohol) were counted and sorted into the following groups: Aranea, Crustacea/Myriapoda, Coleoptera, Heteroptera, Homoptera, Hym-Symphyta, Hym-Apocrita, Hym-Formicidae, Neuropterida, Diptera, Saltatoria, Lepidoptera, Trichoptera, Ephemeroptera, Plecoptera, Rest_2, Rest_3, Gastropoda, amphibians, reptiles, and mice. Some of the groups were further separated into several families. The sorting protocol is shown in Appendix Table A2. For this study, the ten most prevalent taxonomic insect groups were used for further analyses: Coleoptera, Diptera, Ephemeroptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, Neuropterida, Plecoptera, and Trichoptera. For insect identification, stereo microscopes (Leica Wild M10, Leica M80) were used.

2.4 Environmental data

Assessing combined effects of luminaire variables on nocturnal insect abundance relative to environmental variables, such as precipitation, temperature, and vegetation height, is important to consider when concluding on the effects of the tested light treatments on nocturnal insect abundance.

Thus, mean nightly temperatures and nightly precipitation sums were measured by the meteorological stations at the three study sites. Mean nightly temperatures were measured by smart weather sensors (Lufft WS300), nightly precipitation sums by pluviometers (OTT Pluvio^2 L). The meteorological variables were measured at a height of 2.5m on meadows near the study sites. Mean vegetation heights of the sampling areas and of every luminaire and dark plot in a radius of 3m were determined by the vegetation height model VHM (Ginzler & Hobi 2015).

2.5 Statistical analysis

To assess the effects of the light treatments and environmental variables on the sampled nocturnal insect abundance, generalized linear mixed-effect models (GLMM) were fitted in R (RStudio Version 2021.09.1 Build 372) using the Ime4 package (Bates et al. 2015).

The GLMM were fitted by using a negative binomial error distribution to account for over-dispersed count data (Zuur et al. 2010). The variable insect abundance (total and per insect group) was defined as the dependent variable. The light treatments and environmental variables were set as fixed factors. By the inclusion of night IDs and luminaire IDs (BD01-14; L01-14; A01-14; Fig. 2), which account for intrinsic variation, random effects could be considered.

To check for multicollinearities of the explanatory variables, variance inflation factors (VIF) were estimated (R package car).

For the assessment of model performances, R^2 and the Akaike information criterion (AIC) were used.

3. RESULTS

3.1 Nocturnal insect abundance

3.1.1 Nocturnal insect abundance per taxonomic group

During the four weeks of sampling, a total of 63'293 insects were caught. With 51'129 individuals, Diptera was the most frequently sampled insect group, followed by Coleoptera with 5'412 individuals, Lepidoptera with 2'830 individuals, and Hymenoptera with 2'689 individuals (Fig. 6). Lower numbers of individuals ranging between 421 and 51 were caught in the insect groups Heteroptera, Homoptera, Trichoptera, Neuropterida, Ephemeroptera, and Plecoptera (Fig. 6).

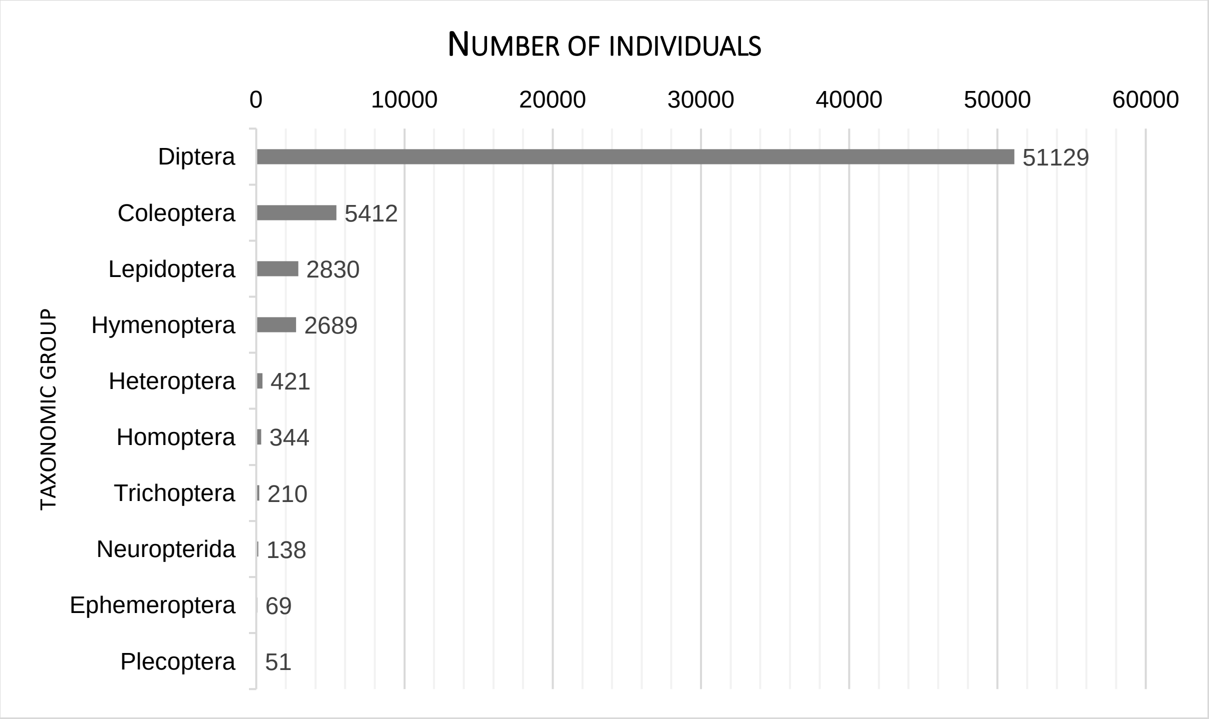

Figure 6: Number of insect individuals caught over all three study sites (Birmensdorf, Lägern, Alpthal) assigned to ten taxonomic insect groups.

Of the 63'293 insects in total, 16'309 were sampled in Birmensdorf, 21'545 in Lägern, and 25'439 in Alpthal. The distributions of sampled insect individuals into taxonomic insect groups per site are shown in the Appendix Figures A1-A3.

3.1.2 Nocturnal insect abundance per night and light treatment

The mean numbers of insects caught per night at luminaires, regardless of the light treatments, were higher than the mean number of insects caught at dark plots (Table 1). When comparing the light treatments, the combination of diffused luminaire shape, 100% light level, and LED color temperature of 2200K resulted in the highest mean abundance with 133 insects. This is followed by the combination of diffused luminaire shape, 100% light level, and LED color temperature of 3000K. The lowest mean abundance caught, with 22 individuals, was achieved by the light treatment combining flat luminaire shape with light level dimmed to 50%, and LED color temperature of 2200K (Table 1).

Table 1: Mean number of insects caught per night and light treatment (all three study sites).

Luminaire shape	Light level	LED color temperature	Number of samples	Mean abundance	Standard error
Dark	Dark	Dark	139	1.0360	0.1120
Diffused	100%	2200	77	132.6883	24.8661
Diffused	100%	3000	84	122.4524	16.7783
Diffused	100%	4000	82	92.7317	9.9714
Diffused	50%	2200	82	86.0244	9.9591
Diffused	50%	3000	70	77.8571	9.8591
Diffused	50%	4000	84	70.8333	9.2322
Flat	100%	2200	81	38.2716	3.9994
Flat	100%	3000	82	25.5610	3.1602
Flat	100%	4000	84	33.5238	3.6335
Flat	50%	2200	82	22.0976	2.6620
Flat	50%	3000	84	33.7143	4.0547
Flat	50%	4000	82	30.8415	3.5659

3.2 Effects of luminaire and environmental variables on nocturnal insect abundance

The tables of the regression results are shown in Appendix Tables A3-A4. With VIF values of around 1, it can be assumed that the predictors (light treatments, environmental variables) were independent (Zuur et al 2010; Appendix Table A5).

3.2.1 Light treatments

The regression assessments showed that luminaire shape was the most determining variable for the total nocturnal insect abundance sampled at all study sites, per study site, and the abundance of most taxonomic insect groups (Fig. 7, 8; Appendix Tables A3, A4).

Table 2 shows the increase of mean nocturnal insect abundance from luminaires with a flat luminaire shape to luminaires with a diffused luminaire shape. On average, 225.5% more insects were caught at luminaires with diffused luminaire shape compared to luminaires with a flat luminaire shape (Table 2). This effect was statistically significant for the total insect abundance, as well as for the abundances of the following taxonomic insect groups: Diptera (+263.2%), Coleoptera (+127.8%), Lepidoptera (+217.5%), Hymenoptera (+48.2%), Heteroptera (+186.5%), Homoptera (+65.7%), Trichoptera (+107%), Neuropterida (+523.7%), and Plecoptera (+40.7%; Table 2; Figs. 7, 8; Appendix Table A3). This effect was not statistically significant for the abundance of Ephemeroptera, although a trend towards a higher number of individuals caught at luminaires with diffusors can be seen (+257.5%; Table 2; Fig. 8; Appendix Table A3).

Table 2: Increase of mean nocturnal insect abundance from luminaires with flat luminaire shape to luminaires with diffused luminaire shape in percentage for three LED color temperatures (2200K, 3000K, 4000K) and two light levels (50%, 100%; all study sites).

	Increase of mean nocturnal insect abundance from luminaires with flat to diffused luminaire shape (%)						
Insect group	**2200K 50%**	**2200K 100%**	**3000K 50%**	**3000K 100%**	**4000K 50%**	**4000K 100%**	**Mean**
All insects	+289	+247	+131	+379	+130	+177	+225.5
Diptera	+324	+296	+181	+430	+149	+199	+263.2
Coleoptera	+165	+136	+107	+197	+90	+75	+127.8
Lepidoptera	+482	+169	+129	+290	+81	+154	+217.5
Hymenoptera	+33	+30	-72	+231	-9	+76	+48.2
Heteroptera	+250	+378	+157	+166	+31	+137	+186.5
Homoptera	+41	+33	+170	+66	-29	+113	+65.7
Trichoptera	+67	-42	+42	+175	+193	+207	+107

Neuropterida	+2200	-11	+100	+550	+79	+224	+523.7
Ephemeroptera	+333	+137	+420	+95	+583	-23	+257.5
Plecoptera	NA (no catch for flat shape)	+122	NA (no catch for flat shape)	NA (no catch for flat shape)	-2	+2	+40.7

Light level was another determining variable in the regression assessments (Figs. 7, 8; Appendix Table A3). On average, 33.3% less insects were caught at luminaires with light level dimmed to 50% compared to luminaires with fully lit light (100%; Table 3). The effect was statistically significant for the total insect abundance (+33.3%), as well as for the abundances of the following groups: Diptera (+35.3%), Hymenoptera (+114%), and Plecoptera (+193%). The response of the remaining taxonomic insect groups (Coleoptera, Lepidoptera, Heteroptera, Homoptera, Trichoptera, Neuropterida, and Ephemeroptera) to light levels was not statistically significant (Fig. 8; Appendix Table A3). Nonetheless, there was a general trend towards fewer insects caught with dimmed light levels compared to full light levels (Table 3; Figs. 7, 8; Appendix Table A3).

Table 3: Increase of mean nocturnal insect abundance from 50% dimmed luminaires to fully lit luminaires in percentage for three LED color temperatures (2200K, 3000K, 4000K) and two luminaire shapes (flat, diffused; all study sites).

	Increase of mean nocturnal insect abundance from 50% dimmed luminaires to fully lit luminaires (%)						
Insect group	**2200K Flat**	**2200K Diffused**	**3000K Flat**	**3000K Diffused**	**4000K Flat**	**4000K Diffused**	**Mean**
All insects	+73	+54	-24	+57	+9	+31	+33.3
Diptera	+72	+60	-15	+60	+7	+28	+35.3
Coleoptera	+54	+38	-18	+18	+44	+33	+28.2
Lepidoptera	+88	-13	-35	+11	+8	+51	+18.3
Hymenoptera	+108	+283	-69	+269	0	+93	+114
Heteroptera	-7	+27	+61	+67	-26	+34	+26
Homoptera	-14	-19	+195	+81	-42	+73	+45.7

Trichoptera	+221	+12	+2	+99	+14	+20	+61.3
Neuropterida	+1216	-49	-66	+11	-2	+77	+197.8
Ephemer-optera	+35	-26	+2	-62	+290	-56	+30.5
Plecoptera	NA (no catch for 50%)	+305	NA (no catch)	+67	+193	+207	+193

For LED color temperature, only the regression models for Coleoptera and Plecoptera showed statistically significant effects (Fig. 8; Appendix Table A3). More Coleoptera individuals were caught at luminaires with 2200K compared to 4000K (+26.7%). More Plecoptera individuals were caught at luminaires with 2200K compared to 3000K and 4000K (+143.9% resp. +394.3%; Fig. 8; Appendix Table A3). For the abundances of the remaining insect groups (Diptera, Lepidoptera, Hymenoptera, Heteroptera, Homoptera, Trichoptera, Neuropterida, and Ephemeroptera) and the total insect abundance, there were no statistically significant effects (Figs. 7, 8; Appendix Table A3). No general trend could be detected.

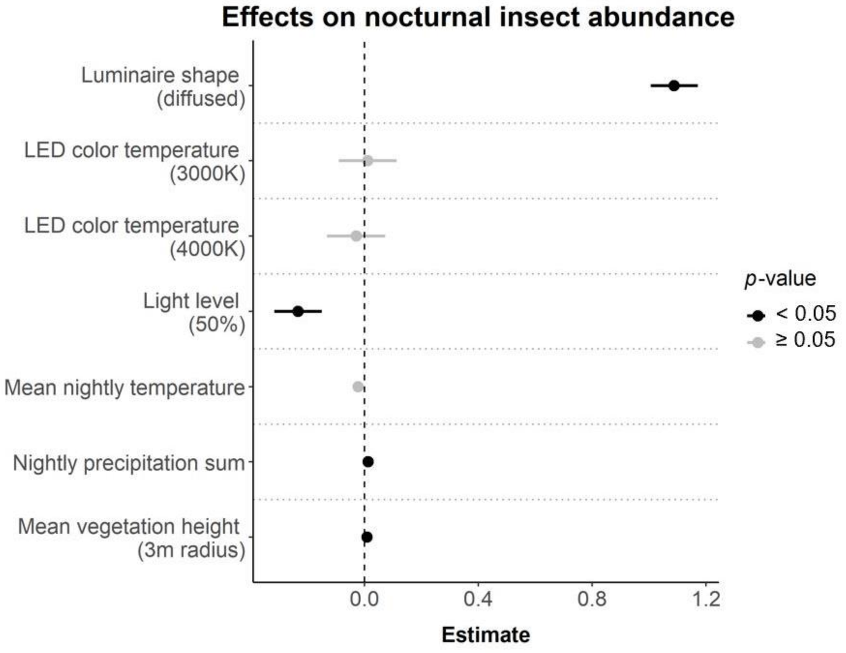

Figure 7: Effects of the tested luminaire and environmental variables on nocturnal insect abundance. The dots represent regression parameter estimates and the bars +/- standard errors. For some estimates, the standard error is too small to be visualized. Statistical significance (*p*-value < 0.05) is shown by black dots, whereas statistically insignificant estimates (*p*-value ≥ 0.05) are represented by grey dots. Regression tables are reported in Appendix Table A3.

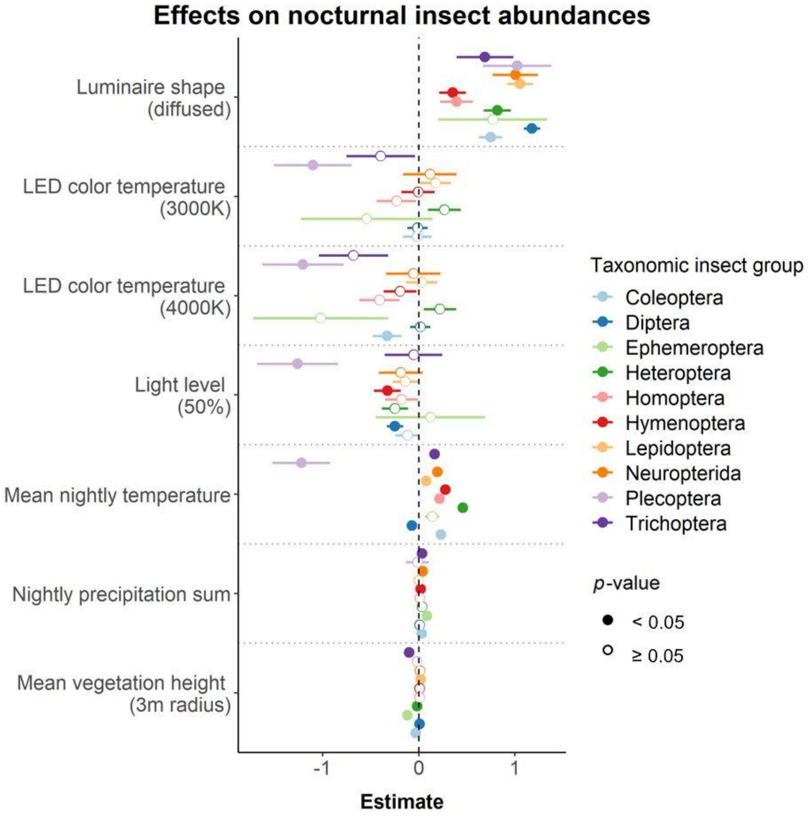

Figure 8: Effects of the tested luminaire and environmental variables on nocturnal insect abundances of the ten taxonomic insect groups (represented by different colors). The dots represent regression parameter estimates and the bars +/- standard errors. For some estimates, the standard error is too small to be visualized. Statistical significance (*p*-value < 0.05) is shown by filled dots, whereas statistically insignificant estimates (*p*-value ≥ 0.05) are represented by hollow dots. Regression tables are reported in Appendix Table A3.

3.2.2 Environmental variables

The effect of mean nightly temperature was statistically significant for Diptera, Coleoptera, Lepidoptera, Hymenoptera, Heteroptera, Homoptera, Trichoptera, Neuropterida, and Plecoptera, but not for Ephemeroptera and the total insect abundance (Figs. 7, 8; Appendix Table A3). Although the effect was negative for Diptera and Plecoptera, meaning the higher the mean nightly temperature the fewer specimens from these groups were caught, a positive trend towards more insects caught at higher mean nightly temperatures could be detected in the following groups: Coleoptera, Lepidoptera, Hymenoptera, Heteroptera, Homoptera, Trichoptera, and Neuropterida (Fig. 8; Appendix Table A3).

For nightly precipitation sum, statistically significant effects were shown for the total insect abundance, as well as for the abundances of the taxonomic groups Coleoptera, Hymenoptera, Trichoptera, Neuropterida, and Ephemeroptera (Figs. 7, 8; Appendix Table A3). The small, but statistically significant effect was positive, meaning that the higher the nightly precipitation sum the higher the mean nocturnal insect abundances.

The regression assessments showed statistically significant effects of mean vegetation heights (considered for a 3m radius at each luminaire) for the total insect abundance, and the abundance of Diptera, Coleoptera, Lepidoptera, Heteroptera, Trichoptera, and Ephemeroptera (Figs. 7, 8; Appendix Table A3). These effects were inconsistent among the groups. For the total insect abundance, Diptera and Lepidoptera the effect was positive: the higher the woody vegetation canopy around the luminaire the more insects were caught (Figs. 7, 8; Appendix Table A3). The statistically significant regressions results of Coleoptera, Heteroptera, Trichoptera, and Ephemeroptera showed the reverse effect: the higher the woody vegetation canopy around the luminaire the fewer insects were caught (Fig. 8; Appendix Table A3). Thus, no general trend could be detected.

3.3 Model performance

With R^2 values around 0.5 to 0.8 the model performance was appropriate except for Trichoptera (0.3972), Homoptera (0.2379), Neuropterida (0.1979) and Ephemeroptera (0.0242; Appendix Table A3).

4. DISCUSSION

4.1 Light treatments

This study provided an ecological assessment of the combined impacts of three LED color temperatures (2200K, 3000K, 4000K), two light levels (50%, 100%), and two luminaire shapes (flat, diffused) on nocturnal insect abundance. It was aimed to answer the following research questions: (1) Which luminaire characteristic affects the nocturnal insect abundance the most? (2) Which combination of luminaire characteristics results in the lowest nocturnal insect abundance?

Based on the results of a previous study by Bolliger et al. (2021), it was expected that the luminaire characteristic luminaire shape affects the nocturnal insect abundance the most. The results of this study confirmed this expectation. Luminaires with increased horizontal light distribution into the surroundings (diffused luminaire shape), independent of light level and LED color temperature, attracted significantly more (on average +225.5%) insects than luminaires with vertical light distribution (flat luminaire shape). Luminaire housing shapes determine the spatial distribution of light into the environment and therefore, how bright the emitted light is perceived (Bolliger et al. 2021). Luminaires with horizontally scattered light are perceived brighter by humans and are visible over a greater distance than luminaires with vertical light distribution. It is possible that nocturnal insects share this perception and are more attracted to horizontally scattered, unfocused light due to greater visibility. Thus, well-focused luminaire shapes could reduce the negative impacts of ALAN on nocturnal insects.

The luminaire characteristic light level appears to be more important for some taxonomic insect groups than for others. Nonetheless, a general trend towards fewer insects captured at luminaires with low light levels compared to luminaires with fully lit light could be detected (on average -33.3%). This finding is in line with another similar study by Bolliger et al. (2020c) and is profound as most nocturnal insects are positively phototactic and are likely attracted by brighter light (Owens et al. 2020, van Langevelde et al. 2018). As only two light levels were included in the field experiments, it is possible that testing further dimming levels would result in a stronger effect and reveal an optimal light level for the protection of nocturnal insects from the negative effects of light.

In this study, LED color temperature was of minor importance. This result is not in line with common findings of studies reporting especially harmful effects of cooler LED color temperatures on insects (Bolliger et al. 2021, Somers-Yeates et al. 2013, van Langevelde et al. 2011). Yet, a number of studies (Bolliger et al. 2020b, Justice & Justice 2016, Pawson & Bader 2014) concur that no significant differences between the effects of warmer and cooler LED color temperatures were detected. These contrary results might be due to the fact, that warmer LED color temperatures still emit a proportion of the blue spectra which is attractive for most insects (Fig. 4; Pawson & Bader 2014). The exact spectral composition might be more decisive for the attraction of nocturnal insects than the LED color temperature by itself. Longcore et al. (2015) stated that LEDs emitting the same color temperatures can result in different insect attraction levels resulting from adjusted spectral compositions. By using longpass optical filters or monochromatic LEDs with narrow spectral wavelengths avoiding the blue-green spectra, detrimental effects of LED light on nocturnal insects could be mitigated (Pawson & Bader 2014). Gaston et al. (2012) suggest the creation of white LED light by combining colored, monochromatic LED light sources. This way the emitted wavelengths can be controlled and critical regions of the spectrum could be avoided. Further studies are needed to assess this possibility.

As expected, the luminaires with the combination of flat luminaire shape, low light level (dimmed to 50%), and the warmest LED color temperature (2200K) attracted the lowest nocturnal insect abundance (22 individuals per night on average). Thus, this combination was the least harmful to insects. The decisive factor was the flat luminaire shape. The luminaires with this specific combination of characteristics showed statistically significant differences for all luminaires with diffused luminaire shape, regardless of LED color temperature and light level, but for no luminaires without a diffusor (Appendix Table A6; Appendix Fig. A4). This means that the definition of the least insect-attracting combination of luminaire characteristics depends primarily and, in this study, solely on the luminaire shape.

It can be concluded that luminaire shape is the stronger and more consistent driver for nocturnal insect abundances compared to the here considered light levels and LED color temperatures.

4.2 Environmental variables

Contrary to results from previous comparable studies (Bolliger et al. 2020b, Bolliger et al. 2020), the meteorological variables (mean nightly temperature, nightly precipitation sum) were not strong drivers of the number of caught insects. Still, a trend towards higher nocturnal insect abundances with warmer air temperatures at night could be detected, remaining consistent with other findings (Bolliger et al. 2020b, Bolliger et al. 2020c). As for the nightly precipitation sum, it only weakly explains the nocturnal insect abundance. Contrary to expectations, the detected statistically significant effects were slightly positive, meaning more insects were caught when higher precipitation occurred. The field experiments took place in a particularly rainy summer. Consequently, one potential explanation is that insects, or at least insects of certain taxonomic groups, sought shelter under the luminaires and eventually fell into the traps, resulting in slightly higher abundances during rainy nights.

The mean vegetation height in a radius of 3m around each luminaire contributed very little to the explanation of the results. Higher vegetation increased abundances for some insect groups but reduced the abundances of other groups. Therefore, one cannot make an overarching conclusion for all groups based on these results. Possible mechanisms to explain these outcomes are that high vegetation may promote habitat opportunities for some insects, resulting in high abundances of insects at the site, which can be attracted to the luminaires. On the other hand, high vegetation can possibly shield surroundings from scattered light. Therefore, some insects may not have had a view of the luminaires, resulting in the lower numbers of these insects caught.

4.3 Recommendations and outlook

This study shows that luminaire shape is an important driver for the fatal attraction of high numbers of insects. Thus, well-focused luminaire designs need to be considered in the development of sustainable outdoor lighting. Additionally, the results of this study are in favor of dimmed light levels. Further studies should seek to investigate the effects of a wider range of light levels to identify optimal mitigation possibilities by dimming.

Although LED color temperatures played an insignificant part in this particular study, other studies (Bolliger et al. 2020b, Justice & Justice 2016, Gaston et al. 2012) made reasonable arguments to use warm white LED color temperatures to mitigate the harmful effects of ALAN. Avoiding blue spectrum light emissions will likely result in reduced insect attraction and reduce light pollution in form of skyglow (Justice & Justice 2016, Somers-Yeates et al. 2013, Gaston et al. 2012). Further studies should be directed towards the identification of critical spectral compositions (wavelengths) rather than color temperatures, that cause detrimental effects. This will aid in the installation of lighting which avoids these harmful spectra.

The results of this study provide a base for further research to build upon. Studies refining the levels of luminaire characteristics are needed to deepen the understanding of insect-friendlier light sources. In particular, long-term experiments are required to gain a better understanding of the adverse effects of ALAN on insects and how these can be reduced (Kalinkat et al. 2021).

4.4 Conclusion

The aim of this study was to determine which examined light characteristic has a particularly negative impact on nocturnal insect abundance and which combination of light characteristics attracts the least number of insects. The results of this study contributed to the knowledge of important factors that need to be considered when striving for light sources with less detrimental effects on nocturnal insects and thus, to the basis of assessment for more sustainable outdoor lighting.

Results of this study in combination with further research concerning the effects of ALAN on nocturnal insects should be used to formulate ecological recommendations for sustainable street light management and light pollution mitigation options, contributing to the application of streetlights with less harmful luminaire properties for nocturnal insects and hence, more sustainable ALAN.

It must be taken into account that this study investigated the effects of light on nocturnal insect abundances in forests that did not experience prior effects of ALAN. Insect communities of peri-urban and urban areas that have previously been under the influence of ALAN may have already undergone a selective process favoring less light-sensitive species resulting in altered, less diverse communities when compared to communities experiencing naturally dark nights (Altermatt & Ebert 2016). These communities, which have not been exposed to ALAN, need to be preserved and prevented from light-induced, long-term evolutionary changes to secure the biodiversity of nocturnal insects which are of crucial importance, not only as a food source of higher organizational levels but also as ecosystem service providers (Altermatt & Ebert 2016).

Expanding the perspective, it can be expected that anthropogenic interferences into the natural light environment are affecting organisms that have evolved within a natural, ALAN-free, light setting, which includes almost all life on this planet (Owens 2020). Reducing the impact of ALAN should thus be in the interest of all inhabitants of earth. Although preserving and increasing unlit areas may be the most effective path to mitigate the negative effects ALAN has on the environment, wildlife, and humans, simply switching off lights can not be the solution as it counters social and economic needs (Gaston et al. 2012). ALAN is needed by humans to guarantee technical safety and also the psychological feeling of safety (Horton et al. 2019). A compromise between reducing light emissions where they are not needed, making the light sources less detrimental for wildlife, while also accounting for human needs, is important to be strived for. Therefore, studies researching social and economic aspects of ALAN are just as important to complete the basis of assessment for effective and sustainable light pollution mitigation strategies that meet the needs of the environment, animals, and humans.

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WSL EKZ

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APPENDIX

Table A1: Standardization of the luminous flux (lm) for the tested LED color temperatures. Lumen (lm) is a measure of the total quantity of visible light emitted per unit of time by a source.

LED color temperature	**Luminous flux (METAS)**	**Standardized luminous flux**
Amber (2155 K)	2231 lm	1500 lm
Warm white (2889 K)	1935 lm	1500 lm
Neutral white (3699 K)	1938 lm	1500 lm

Table A2: Sorting protocol.

Sorting protocol - Polytrap Sorter: Collection date: Site: Plot:								
Gläschencode	**Date**							
	Taxon	**pos_1**	**pos_2**	**pos_3**	**pos_4**	**pos_5**	**pos_6**	**pos_7**
Araneae	Pseudoscorp.							
	Opiliones							
	Araneae							
Crustaceae / Myriapoda	Isopoda							
	Diplopoda							
	Chilopoda							
Coleoptera	Carabidae							
	Staphylinidae							
	Coleop.Rest							
	Necrophorus							
	Geotrupes							
Heteroptera	Heteroptera							
Homoptera	Psyllidae							
	Cicadina							
	Aphidina							
Hym-Symphyta	Symphyta							
Hym-Apocrita	Apocrita							
Hym-Formicidae	Formicidae							
Neuropterida	Raphidiopt.							
	Neuroptera							
	Megaloptera							

	Mecoptera							
Diptera	Nematocera							
	Brachycera							
Saltatoria	Ensifera							
	Caelifera							
Lepidoptera	Lepidoptera							
Trichoptera	Trichoptera							
Ephemeroptera	Ephemerop.							
Plecoptera	Plecoptera							
Rest_2	Dermaptera							
	Psocoptera							
	Blattodea							
	Odonata							
	Lumbricidae							
Rest_3	Thysanoptera							
	Larven-holo.							
	Collembola							
	Acarina							
	Rest							
Gastropoda	Gastropoda							
Amphibien	Amphibien							
Reptilien	Reptilien							
Mäuse	Mäuse							
Bemerkung:								

Table A3: Regression results for nocturnal insect abundance (Birmensdorf, Lägern, Alpthal combined).
Explanatory variables: Luminaire shape (enhanced horizontal light emission (LePlex) compared to standard vertical light emission (Le)), LED color temperature (2200K compared to 3000K, and 2200K compared to 4000K), light level (dimmed light level (50%) compared to fully lit light (100%)), mean nightly temperature, nightly precipitation sum, mean vegetation height in a radius of 3m around the luminaires. R^2: total R^2 (fixed and random factors), AIC: Akaike information criterion of the total model. Statistical levels of significance: *** < 0.001, ** < 0.01, * < 0.05.

All insects	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.088	0.083	13.103	< 2e-16 ***	0.7044	8895
3000K-2200K	0.0118	0.1019	0.116	0.908		

4000K-2200K	-0.0288	0.1021	-0.282	0.7781		
50%-100%	-0.233	0.0831	-2.803	0.0051 **		
Mean temperature	-0.0223	0.017	-1.313	0.1893		
Sum precipitation	0.013	0.0066	1.982	0.0475 *		
Mean vegetation height	0.0096	0.0048	1.986	0.047 *		

Diptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.1788	0.085	13.874	< 2e-16 ***	0.7097	8572
3000K-2200K	-0.0129	0.1043	-0.124	0.9015		
4000K-2200K	0.0162	0.1044	0.156	0.8764		
50%-100%	-0.2486	0.0851	-2.923	0.0035 **		
Mean temperature	-0.0702	0.0176	-3.987	6.7e-05 ***		
Sum precipitation	0.0107	0.0071	1.515	0.1298		
Mean vegetation height	0.01	0.005	2.013	0.0441 *		

Coleoptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.7488	0.1217	6.155	7.49e-10 ***	0.5898	3757
3000K-2200K	-0.0177	0.1487	-0.119	0.9053		

4000K-2200K	-0.3282	0.15	-2.188	0.0287 *		
50%-100%	-0.1194	0.1218	-0.980	0.3269		
Mean temperature	0.2319	0.0286	8.124	4.53e-16 ***		
Sum precipitation	0.0291	0.0121	2.415	0.0157 *		
Mean vegetation height	-0.0296	0.0073	-4.051	5.11e-05 ***		

Lepidoptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.0565	0.1331	7.938	2.05e-15 ***	0.529	3730
3000K-2200K	0.1742	0.1631	1.068	0.2855		
4000K-2200K	0.0297	0.1637	0.182	0.8559		
50%-100%	-0.1388	0.133	-1.043	0.2967		
Mean temperature	0.0773	0.0186	4.160	3.18e-05 ***		
Sum precipitation	0.0026	0.0071	0.365	0.7155		
Mean vegetation height	0.0182	0.0077	2.373	0.0176 *		

Hymenoptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.3529	0.14	2.521	0.0117 *	0.5269	3107
3000K-2200K	-0.0068	0.1717	-0.039	0.9685		

4000K-2200K	-0.1941	0.1721	-1.128	0.2592		
50%-100%	-0.3269	0.1401	-2.333	0.0196 *		
Mean temperature	0.2776	0.02	13.868	<2e-16 ***		
Sum precipitation	0.02	0.0101	1.976	0.0481 *		
Mean vegetation height	0.0097	0.0079	1.223	0.2215		

Heteroptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.8193	0.1416	5.787	7.16e-09 ***	0.4866	994
3000K-2200K	0.2657	0.1704	1.560	0.1189		
4000K-2200K	0.2203	0.1687	1.306	0.1916		
50%-100%	-0.2483	0.136	-1.825	0.0679		
Mean temperature	0.4592	0.0366	12.552	< 2e-16 ***		
Sum precipitation	0.0349	0.0239	1.460	0.1443		
Mean vegetation height	-0.0168	0.0084	-1.991	0.0464 *		

Homoptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.395	0.1701	2.322	0.0202 *	0.2379	1140
3000K-2200K	-0.2324	0.2035	-1.142	0.2535		

4000K-2200K	-0.4087	0.2091	-1.955	0.0506		
50%-100%	-0.1802	0.1699	-1.060	0.2889		
Mean temperature	0.2145	0.0324	6.619	3.62e-11 ***		
Sum precipitation	0.0142	0.0209	0.676	0.4991		
Mean vegetation height	0.0085	0.0097	0.879	0.3793		

Trichoptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.6889	0.2961	2.327	0.02 *	0.3972	961
3000K-2200K	-0.3961	0.3573	-1.108	0.2677		
4000K-2200K	-0.6804	0.3612	-1.884	0.0596		
50%-100%	-0.0535	0.299	-0.179	0.858		
Mean temperature	0.1643	0.0435	3.780	0.0002 ***		
Sum precipitation	0.0339	0.0142	2.386	0.017 *		
Mean vegetation height	-0.0991	0.0186	-5.325	1.01e-07 ***		

Neuropterida	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.0059	0.2349	4.282	1.86e-05 ***	0.1979	748
3000K-2200K	0.1161	0.2769	0.419	0.675		
4000K-2200K	-0.0553	0.2828	-0.196	0.845		

50%-100%	-0.1857	0.2288	-0.811	0.417		
Mean temperature	0.1947	0.0389	5.003	5.65e-07 ***		
Sum precipitation	0.0421	0.0211	1.995	0.046 *		
Mean vegetation height	0.0111	0.013	0.858	0.391		

Ephemer-optera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.7718	0.5667	1.362	0.1733	0.0242	424
3000K-2200K	-0.5414	0.6833	-0.792	0.4282		
4000K-2200K	-1.0212	0.7034	-1.452	0.1466		
50%-100%	0.1212	0.571	0.212	0.832		
Mean temperature	0.1393	0.0713	1.953	0.0509		
Sum precipitation	0.086	0.018	4.766	1.88e-06 ***		
Mean vegetation height	-0.1188	0.0414	-2.870	0.0041 **		

Plecoptera	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.0257	0.3544	2.895	0.0038 **	0.8536	225
3000K-2200K	-1.1033	0.4055	-2.721	0.0065 **		
4000K-2200K	-1.2058	0.4246	-2.840	0.0045 **		

50%-100%	-1.2612	0.4208	-2.997	0.0027 **		
Mean temperature	-1.2227	0.3021	-4.048	5.17e-05 ***		
Sum precipitation	-0.012	0.1208	-0.100	0.9206		
Mean vegetation height	-0.0156	0.035	-0.446	0.656		

Table A4: Regression results for nocturnal insect abundance (Birmensdorf, Lägern, Alpthal separate).
Explanatory variables: Luminaire shape (enhanced horizontal light emission (LePlex) compared to standard vertical light emission (Le)), LED color temperature (2200K compared to 3000K, and 2200K compared to 4000K), light level (dimmed light level (50%) compared to fully lit light (100%)), mean nightly temperature, nightly precipitation sum, mean vegetation height in a radius of 3m around the luminaires. R^2: total R^2 (fixed and random factors), AIC: Akaike information criterion of the total model. Statistical levels of significance: *** < 0.001, ** < 0.01, * < 0.05.

All insects - Birmensdorf	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.1258	0.1108	10.159	< 2e-16 ***	0.8456	2575
3000K-2200K	0.1444	0.142	1.017	0.309		
4000K-2200K	0.0493	0.1431	0.344	0.73		
50%-100%	-0.1431	0.1152	-1.242	0.214		
Mean temperature	0.2156	0.0471	4.579	4.68e-06 ***		
Sum precipitation	0.0028	0.02	0.139	0.889		
Mean vegetation height	-0.0069	0.02	-0.344	0.731		

All insects - Lägern	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	1.1213	0.066	16.984	< 2e-16 ***	0.8533	2874
3000K-2200K	-0.0883	0.0795	-1.11	0.267		
4000K-2200K	0.0186	0.086	0.216	0.8286		
50%-100%	-0.0997	0.0651	-1.53	0.126		
Mean temperature	0.1856	0.0295	6.29	3.18e-10 ***		
Sum precipitation	0.1282	0.0272	4.718	2.38e-06 ***		
Mean vegetation height	0.0192	0.0084	2.276	0.0229 *		

All insects - Alpthal	**Regression diagnostics**				**Regression performance**	
	Estimate	**Std. error**	**z-ratio**	***p*-value**	**R^2**	**AIC**
LePlex-Le	0.9412	0.1378	6.832	8.35e-12 ***	0.8286	2974
3000K-2200K	-0.0861	0.17	-0.506	0.6126		
4000K-2200K	-0.1141	0.1685	-0.677	0.4984		
50%-100%	-0.3759	0.1401	-2.684	0.0073 **		
Mean temperature	0.1922	0.0562	3.422	0.0006 ***		
Sum precipitation	0.0197	0.0175	1.128	0.2595		
Mean vegetation height	0.0016	0.0138	0.115	0.9083		

Table A5: VIF values for nocturnal insect abundances.

Insect group	Explanatory variables	GVIF	Df	GVIF^(1/(2*Df))
All insects	Luminaire shape	1.000666	1	1.000333
	LED color temperature	1.010738	2	1.002674
	Light level	1.003994	1	1.001995
	Mean nightly temperature	1.052029	1	1.025685
	Nightly precipitation sum	1.000697	1	1.000348
	Mean vegetation height (radius 3 m)	1.066749	1	1.032836
Diptera	Luminaire shape	1.000592	1	1.000296
	LED color temperature	1.011054	2	1.002752
	Light level	1.003905	1	1.001951
	Mean nightly temperature	1.053646	1	1.026473
	Nightly precipitation sum	1.000316	1	1.000158
	Mean vegetation height (radius 3 m)	1.068627	1	1.033744
Coleoptera	Luminaire shape	1.000862	1	1.000431
	LED color temperature	1.013518	2	1.003362
	Light level	1.005945	1	1.002968
	Mean nightly temperature	1.147010	1	1.070986
	Nightly precipitation sum	1.016737	1	1.008334
	Mean vegetation height (radius 3 m)	1.144316	1	1.069727
Lepidoptera	Luminaire shape	1.001660	1	1.000830
	LED color temperature	1.009480	2	1.002362
	Light level	1.003199	1	1.001598
	Mean nightly temperature	1.064780	1	1.031882
	Nightly precipitation sum	1.029830	1	1.014806
	Mean vegetation height (radius 3 m)	1.048308	1	1.023869
Hymenoptera	Luminaire shape	1.002118	1	1.001058
	LED color	1.013601	2	1.003383

	temperature			
	Light level	1.004482	1	1.002239
	Mean nightly temperature	1.109733	1	1.053439
	Nightly precipitation sum	1.057832	1	1.028510
	Mean vegetation height (radius 3 m)	1.067718	1	1.033304
Heteroptera	Luminaire shape	1.003149	1	1.001573
	LED color temperature	1.037465	2	1.009237
	Light level	1.005410	1	1.002701
	Mean nightly temperature	1.480436	1	1.216732
	Nightly precipitation sum	1.102390	1	1.049948
	Mean vegetation height (radius 3 m)	1.393918	1	1.180643
Homoptera	Luminaire shape	1.001351	1	1.000675
	LED color temperature	1.027876	2	1.006897
	Light level	1.005055	1	1.002525
	Mean nightly temperature	1.242248	1	1.114562
	Nightly precipitation sum	1.112974	1	1.054976
	Mean vegetation height (radius 3 m)	1.147803	1	1.071356
Trichoptera	Luminaire shape	1.004221	1	1.002108
	LED color temperature	1.020799	2	1.005160
	Light level	1.022968	1	1.011419
	Mean nightly temperature	1.095683	1	1.046749
	Nightly precipitation sum	1.019910	1	1.009906
	Mean vegetation height (radius 3 m)	1.106128	1	1.051726
Neuropterida	Luminaire shape	1.003406	1	1.001702
	LED color temperature	1.025977	2	1.006432
	Light level	1.004949	1	1.002471
	Mean nightly temperature	1.236736	1	1.112086
	Nightly precipitation sum	1.117248	1	1.057000

	Mean vegetation height (radius 3 m)	1.143977	1	1.069568
Ephemeroptera	Luminaire shape	1.003460	1	1.001729
	LED color temperature	1.058787	2	1.014383
	Light level	1.014533	1	1.007240
	Mean nightly temperature	1.140512	1	1.067948
	Nightly precipitation sum	1.064806	1	1.031894
	Mean vegetation height (radius 3 m)	1.118584	1	1.057631
Plecoptera	Luminaire shape	1.032293	1	1.016018
	LED color temperature	1.012607	2	1.003137
	Light level	1.264231	1	1.124380
	Mean nightly temperature	1.090864	1	1.044444
	Nightly precipitation sum	1.022948	1	1.011409
	Mean vegetation height (radius 3 m)	1.379297	1	1.174435

Table A6: Contrasts for regression results of nocturnal insect abundance (luminaire shape x LED color temperature x light level).
Complete set of contrasts for two luminaire shapes (Le = standard vertical light emission (falt), LePlex = enhanced horizontal light emission (diffused)), three LED color temperatures (2200K, 3000K, 4000K) and two light levels (100%, 50%).

Insect group	**Contrast**	**Estimate**	**Std. error**	**z-ratio**	***p*-value**
All insects	Le 2200 100 - LePlex 2200 100	-1.0880	0.0830	-13.1031	< 0.0001
	Le 2200 100 - Le 3000 100	-0.0118	0.1019	-0.1156	1.0000
	Le 2200 100 - LePlex 3000 100	-1.0998	0.1317	-8.3527	< 0.0001
	Le 2200 100 - Le 4000 100	0.0288	0.1021	0.2819	1.0000
	Le 2200 100 - LePlex 4000 100	-1.0593	0.1317	-8.0406	< 0.001
	Le 2200 100 - Le 2200 50	0.2330	0.0831	2.8030	0.1785
	Le 2200 100 - LePlex 2200 50	-0.8550	0.1175	-7.2739	< 0.0001
	Le 2200 100 - Le 3000 50	0.2212	0.1314	1.6842	0.8758

	Le 2200 100 - LePlex 3000 50	-0.8668	0.1556	-5.5700	< 0.0001
	Le 2200 100 - Le 4000 50	0.2618	0.1313	1.9944	0.6975
	Le 2200 100 - LePlex 4000 50	-0.8263	0.1555	-5.3139	< 0.0001
	LePlex 2200 100 - Le 3000 100	1.0763	0.1312	8.2002	< 0.0001
	LePlex 2200 100 - LePlex 3000 100	-0.0118	0.1019	-0.1156	1.0000
	LePlex 2200 100 - Le 4000 100	1.1168	0.1314	8.4978	< 0.0001
	LePlex 2200 100 - LePlex 4000 100	0.0288	0.1021	0.2819	1.0000
	LePlex 2200 100 - Le 2200 50	1.3210	0.1174	11.2480	< 0.0001
	LePlex 2200 100 - LePlex 2200 50	0.2330	0.0831	2.8030	0.1785
	LePlex 2200 100 - Le 3000 50	1.3093	0.1552	8.4368	< 0.0001
	LePlex 2200 100 - LePlex 3000 50	0.2212	0.1314	1.6842	0.8758
	LePlex 2200 100 - Le 4000 50	1.3498	0.1551	8.7003	< 0.0001
	LePlex 2200 100 - LePlex 4000 50	0.2618	0.1313	1.9944	0.6975
	Le 3000 100 - LePlex 3000 100	-1.0880	0.0830	-13.1031	< 0.0001
	Le 3000 100 - Le 4000 100	0.0406	0.1016	0.3990	1.0000
	Le 3000 100 - LePlex 4000 100	-1.0475	0.1312	-7.9846	< 0.0001
	Le 3000 100 - Le 2000 50	0.2448	0.1317	1.8590	0.7847
	Le 3000 100 - LePlex 2000 50	-0.8432	0.1555	-5.4216	< 0.0001
	Le 3000 100 - Le 3000 50	0.2330	0.0831	2.8030	0.1785
	Le 3000 100 - LePlex 3000 50	-0.8550	0.1175	-7.2739	< 0.0001
	Le 3000 100 - Le 4000 50	0.2736	0.1311	2.0870	0.6322
	Le 3000 100 - LePlex 4000 50	-0.8145	0.1552	-5.2493	< 0.0001
	LePlex 3000 100 - Le 4000 100	1.1286	0.1313	8.5958	< 0.0001
	LePlex 3000 100 - LePlex 4000 100	0.0406	0.1016	0.3990	1.0000

	LePlex 3000 100 - Le 2200 50	1.3328	0.1558	8.5538	< 0.0001
	LePlex 3000 100 - LePlex 2200 50	0.2448	0.1317	1.8590	0.7847
	LePlex 3000 100 - Le 3000 50	1.3210	0.1174	11.2480	< 0.0001
	LePlex 3000 100 - LePlex 3000 50	0.2330	0.0831	2.8030	0.1785
	LePlex 3000 100 - Le 4000 50	1.3616	0.1552	8.7746	< 0.0001
	LePlex 3000 100 - LePlex 4000 50	0.2736	0.1311	2.0870	0.6322
	Le 4000 100 - LePlex 4000 100	-1.0880	0.0830	-13.1031	< 0.0001
	Le 4000 100 - Le 2200 50	0.2042	0.1320	1.5471	0.9274
	Le 4000 100 - LePlex 2200 50	-0.8838	0.1559	-5.6702	< 0.0001
	Le 4000 100 - Le 3000 50	0.1925	0.1315	1.4633	0.9503
	Le 4000 100 - LePlex 3000 50	-0.8956	0.1556	-5.7548	< 0.0001
	Le 4000 100 - Le 4000 50	0.2330	0.0831	2.8030	0.1785
	Le 4000 100 - LePlex 4000 50	-0.8550	0.1175	-7.2739	< 0.0001
	LePlex 4000 100 - Le 2200 50	1.2923	0.1561	8.2806	< 0.0001
	LePlex 4000 100 - LePlex 2200 50	0.2042	0.1320	1.5471	0.9274
	LePlex 4000 100 - Le 3000 50	1.2805	0.1555	8.2369	< 0.0001
	LePlex 4000 100 - LePlex 3000 50	0.1925	0.1315	1.4633	0.9503
	LePlex 4000 100 - Le 4000 50	1.3210	0.1174	11.2480	< 0.0001
	LePlex 4000 100 - LePlex 4000 50	0.2330	0.0831	2.8030	0.1785
	Le 2200 50 - LePlex 2200 50	-1.0880	0.0830	-13.1031	< 0.0001
	Le 2200 50 - Le 3000 50	-0.0118	0.1019	-0.1156	1.0000
	Le 2200 50 - LePlex 3000 50	-1.0998	0.1317	-8.3527	< 0.0001
	Le 2200 50 - Le 4000 50	0.0288	0.1021	0.2819	1.0000
	Le 2200 50 - LePlex 4000 50	-1.0593	0.1317	-8.0406	< 0.0001
	LePlex 2200 50 - Le 3000 50	1.0763	0.1312	8.2002	< 0.0001

	LePlex 2200 50 - LePlex 3000 50	-0.0118	0.1019	-0.1156	1.0000
	LePlex 2200 50 - Le 4000 50	1.1168	0.1314	8.4978	< 0.0001
	LePlex 2200 50 - LePlex 4000 50	0.0288	0.1021	0.2819	1.0000
	Le 3000 50 - LePlex 3000 50	-1.0880	0.0830	-13.1031	< 0.0001
	Le 3000 50 - Le 4000 50	0.0406	0.1016	0.3990	1.0000
	Le 3000 50 - LePlex 4000 50	-1.0475	0.1312	-7.9846	< 0.0001
	LePlex 3000 50 - Le 4000 50	1.1286	0.1313	8.5958	< 0.0001
	LePlex 3000 50 - LePlex 4000 50	0.0406	0.1016	0.3990	1.0000
	Le 4000 50 - LePlex 4000 50	-1.0880	0.0830	-13.1031	< 0.0001

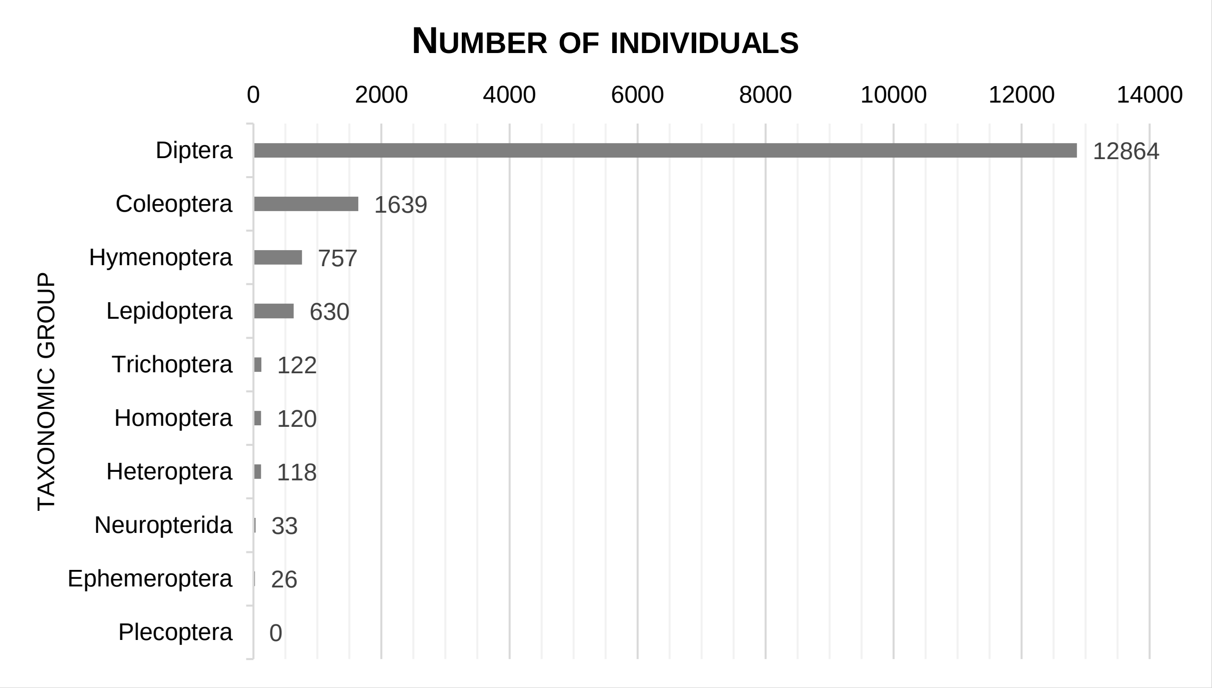

Figure A1: Number of caught insect individuals in Birmensdorf assigned to ten taxonomic insect groups.

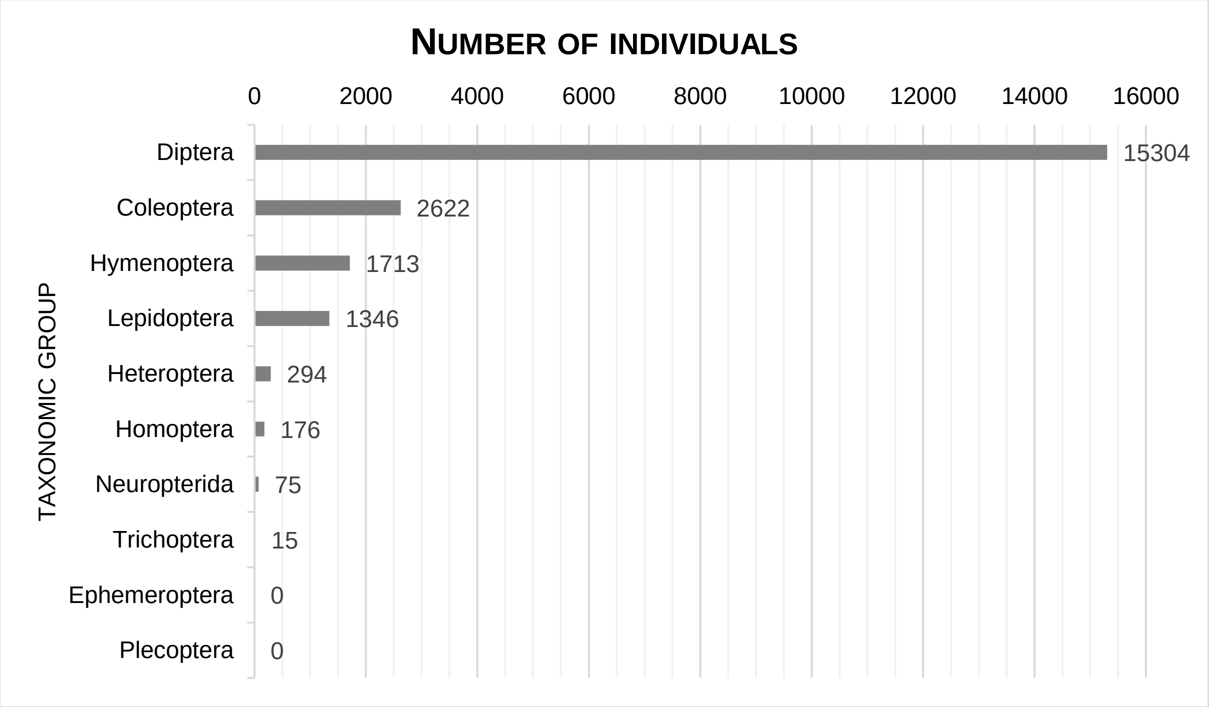

Figure A2: Number of caught insect individuals in Lägern assigned to ten taxonomic insect groups.

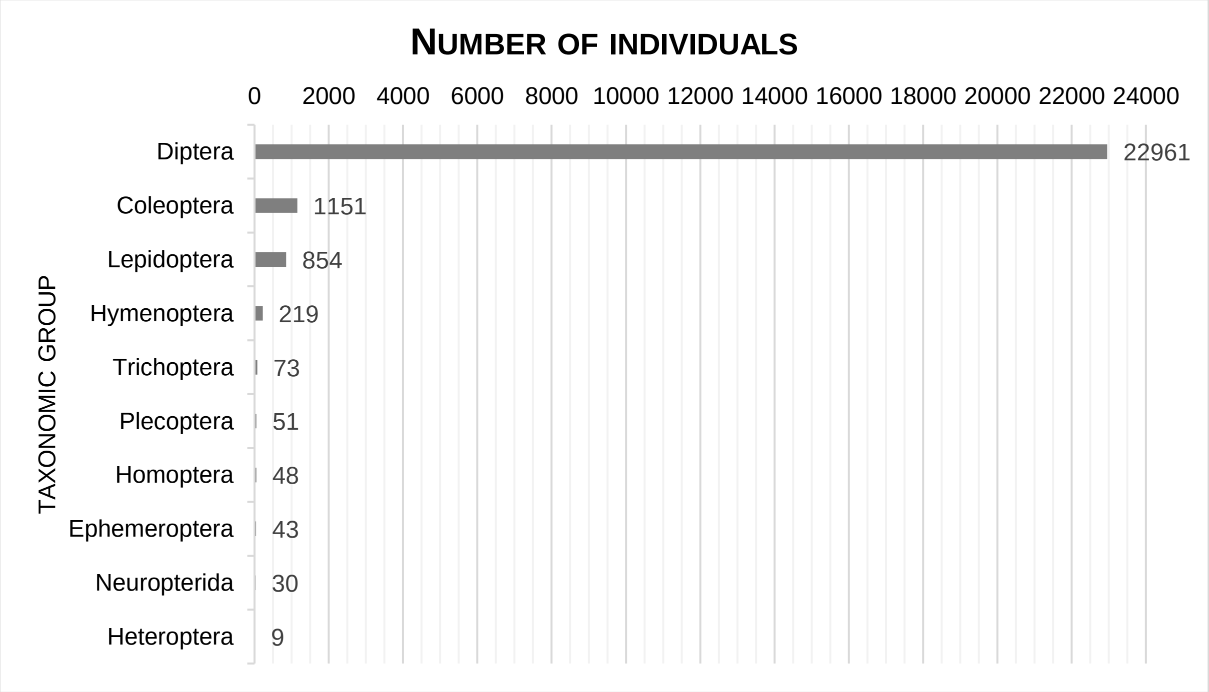

Figure A3: Number of caught insect individuals in Alpthal assigned to ten taxonomic insect groups.

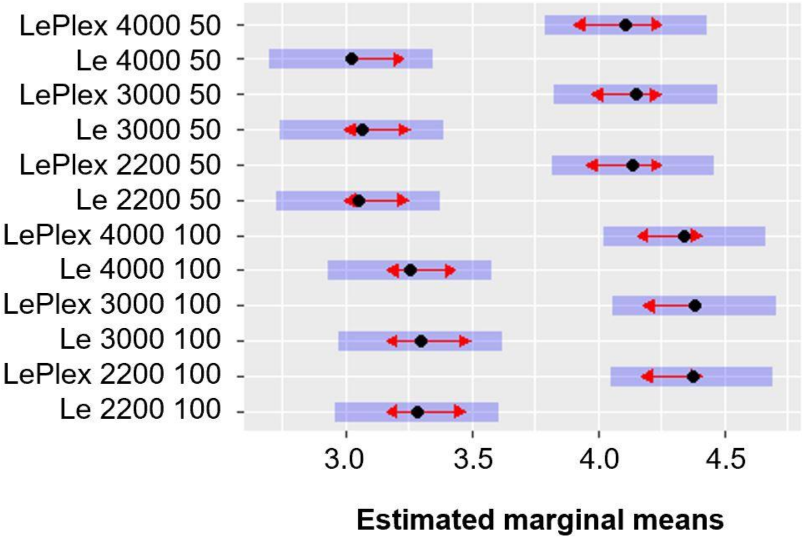

Figure A4: Contrasts for regression results of nocturnal insect abundance (luminaire shape x LED color temperature x light level). Contrasts for two luminaire shapes (Le = standard vertical light emission (flat), LePlex = enhanced horizontal light emission (diffused)), three LED color temperatures (2200K, 3000K, 4000K), and two light levels (100%, 50%). Blue bars are confidence intervals for estimated marginal means. Red arrows are for the comparisons among the means. No overlap between red arrows visualizes statistical significance ($p < 0.05$).