1	Title: Anthropogenic lighting affects moth abundance
2	and diversity differently across ecosystems
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12 13	Highlights
14 15	$\cdot$ Light traps with known lighting properties were used in two different ecosystems.
16 17	$\cdot$ Abundance and diversity of captured moths were higher in forests than grasslands.
18 19	$\cdot$ Environmental factors had greater effects on attraction to light in grasslands.
20 21	$\cdot$ Different moth families showed varying attraction to light traps across ecosystems.
22 23	$\cdot$ The findings suggest the need for ecosystem-specific mitigation strategies.
24 25 26	<b>Keywords:</b> light pollution; nocturnal; insects; Crambidae; Geometridae; Noctuidae; artificial lighting

#### Graphical abstract 27

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# How light pollution affects moths in forests & grasslands

### **Field experiment**

We used insect light traps (LED 3000K) and an exposure area of 13 m<sup>2</sup> above 0.3 lux

The lights were used in ecosystems.



Forest: two different Higher abundance. Greater species richness.



Grassland: Lower abundance and richness. Higher abiotic influence.

### **Recommendations**



# 2 Abstract

3 Light pollution poses a significant threat to nocturnal insects, yet our understanding of how 4 insects are affected by lighting across ecosystems is limited. The purpose of this study was to 5 investigate differences in light-induced attraction in abundance and diversity of moths in forest 6 and grassland ecosystems. This study presents a novel comparison of moth attraction between 7 these ecosystems using identical light traps with known lighting properties across 32 sites. We 8 found significantly higher moth abundance and diversity (species richness) in forests compared 9 to open grasslands, where environmental factors such as temperature and cloudiness had 10 stronger effects on moth attraction in grasslands. Notably, moth families showed varying 11 responses across ecosystems, suggesting potential sampling biases in light attraction studies. 12 Our findings point to the need for ecosystem-specific approaches in light pollution mitigation 13 strategies and provide a methodological approach for future research on the impacts of 14 anthropogenic light on biodiversity. The results have important implications for conservation 15 planning and the management of anthropogenic lighting in diverse landscapes. 16

# 17 **1.** Introduction

The human need for illumination and the desired benefits of lighting our surroundings has led to 18 19 an increased use of light at night (Boyce, 2019). This has resulted in light pollution, which refers 20 to the adverse effects of anthropogenic light (CIE, 2020). Light pollution is recognised as a 21 pervasive environmental problem with serious consequences worldwide, including reduced 22 ability for astronomical observations of celestial objects (Kocifaj et al., 2023) and far-reaching 23 implications for most species and their ecosystems (Jägerbrand and Spoelstra, 2023). Light 24 pollution is a serious environmental problem impacting the majority of economically developed 25 regions across the globe (Falchi et al., 2016a). The problem of anthropogenic nighttime lighting 26 is escalating in almost all countries worldwide, with an annual rise of 2.2% in upward light 27 emissions in already lit areas (Kyba et al., 2017).

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29 A group of organisms significantly affected by nocturnal light are insects, whose responses to 30 anthropogenic lighting have been extensively reviewed (Bruce-White and Shardlow, 2011; Boyes 31 et al. 2020; Owens and Lewis, 2018; van Langevelde et al., 2018). Insects, the most species-rich 32 animal group on Earth, play essential roles in ecosystems by providing services such as 33 pollination, decomposition, soil formation, and pest control (Schowalter et al., 2018). Numerous 34 studies have documented substantial declines in insect diversity and biomass (Hallman et al., 35 2017; Sánchez-Bayo and Wyckhuys, 2019; van Klink et al., 2020; Wagner et al., 2021; van Langevelde et al., 2018). These declines are linked to various factors, including habitat 36 37 destruction and degradation, climate change, land use changes and habitat fragmentation (e.g., 38 Sánchez-Bayo and Wyckhuys, 2019), as well as the potential impacts of anthropogenic light at 39 night (Boyes et al., 2020; van Grunsven et al., 2020).

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41 Many nocturnal insects are often attracted to light, a phenomenon known as phototaxis (Jekely,

42 2009; Gorostiza et al., 2016). Such attraction to light may cause mortality through circling,

43 exhaustion, injury and increased predation risk when exposed in the light (Eisenbeis, 2006).

Thus, anthropogenic light may potentially affect ecosystem services such as pollination and
 biodiversity (e.g., Macgregor and Scott-Brown, 2020). Insect attraction to light sources is

46 influenced by several factors, including light intensity (Jägerbrand et al., 2023), spectral power

47 distribution (e.g. Longcore et al., 2015; Niermann and Brehm, 2022), flickering (Barroso et al.,

48 2017), light distribution and optics of the luminaire (Bolliger et al., 2022). However, very little is

1 known about how the attraction of nocturnal insects to light sources is affected by the spatial 2 context, such as the surrounding ecosystems. For instance, studies of moth attraction to 3 anthropogenic light has been conducted in different types of ecosystems such as grasslands 4 (Wakefield et al., 2016; Degen et al., 2016), urban environments (Straka et al., 2021), prairies 5 (Grenis et al., 2023), woodland edges (Wakefield et al., 2018) and aquatic ecosystems (Meyer 6 and Sullivan, 2013). However, as single studies in most cases are confined within the same 7 ecosystem, test different light sources and are conducted at different times of the year, 8 comparisons between results from different ecosystems are hard to make. Still, understanding 9 differences in responses to light between different ecosystems is important to predict 10 differences in responses in biodiversity and ecosystem services. 11 12 Grasslands, covering up to 40% of Earth's terrestrial surface, and forests, covering 30% and 13 accounting for most of the terrestrial primary production and biomass, are both crucial biomes 14 providing essential ecosystem goods and services globally (Blair et al., 2014; Pan et al., 2013). 15 Due to differences in topography and elevation of physical features, these ecosystems exhibit 16 varying light distributions and exposures for organisms. Forest ecosystems typically experience 17 dim light conditions as vegetation filters and absorbs light, allowing limited light to reach the 18 forest floor (Veilleux and Cummings, 2012). In contrast, open grasslands lack these filtering 19 effects, allowing unobstructed light to dominate the landscape. These differences between 20 closed forests and open grasslands may also result in varied exposure of insects to 21 environmental factors such as weather conditions and moonlight. For instance, lower 22 temperatures may significantly reduce moth catches in light traps, while increased cloud cover 23 can increase them (Yela and Holyoak, 1997). It has also been shown that trap catches of moths 24 can be considerably higher near the period of the new moon compared to full moon (Williams 25 and Sing, 1951). Consequently, environmental factors can affect insect activity differently 26 across ecosystems with potential interactive effects from anthropogenic light. Therefore, it is 27 essential to consider confounding factors like weather conditions and moonlight exposure in studies of the effects of anthropogenic light attraction in different ecosystems. 28 29 In this study, we compare insect attraction to light in two different ecosystems, open grasslands

30 31 and forests. Our objective was to investigate differences in light-induced attraction regarding 32 abundance, richness, and diversity of moths between these ecosystems. For this purpose, we 33 sampled moths in grassland and forest ecosystems with light traps using identical light exposure (same light sources, intensities and distributions). We used "spot" lamps and shielding to limit 34 35 vertical light spread, creating a light cone confined to the nearby ground. This setup allowed us 36 to implement identical attraction radii, enabling a comparison of abundance, richness and 37 diversity per square meter of exposed area (above a threshold value for full moon/insects, see 38 Jägerbrand et al., 2023). This approach is novel in studying insect attraction to light at night and 39 facilitates comparisons between ecosystems.

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### 41 2. Methods

#### 42 2.1 Study area

43 The study area is situated south of Stockholm, in Huddinge, Haninge, and Botkyrka

44 municipalities. The study area consists of boreo-nemoral mixed heterogeneous landscape

45 types, such as forests with mixed evergreen and deciduous species, lakes, agricultural areas

46 and open field grasslands. The forest ecosystem was dominated by for example *Picea abies*,

47 *Populus tremula, Betula* spp. and *Corylus avellana*. The grassland ecosystem consisted of more

48 or less managed meadows with dominance of various grasses, such as *Phleum pratense*,

49 Festuca spp., Hypericum spp. Trifolium spp. and Achillea millefolium.

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- 2 The brightest field site experience sky brightness of 2.64 mcd/m<sup>2</sup> (Vårby), medium bright sites
- 3 had a mean value of 1.10 mcd/m<sup>2</sup> (five sites) and the darkest situated sites had 0.60 mcd/m<sup>2</sup>
- 4 according to the New World Atlas of Artificial Night Sky Brightness (Falchi et al., 2016a, b). In the
- 5 three municipalities, more than 1500 species of Lepidoptera have been recorded in accordance
- 6 with the Species Observation System (SLU Swedish Information Center, 2024a) out of
- 7 approximately 2700 resident species in Sweden (Eliasson et al., 2005).

#### 2.2 Experimental set-up 8

- 9 We performed a field experiment on nocturnal moths using light traps. We used funnel traps
- 10 with an attached net bag originally designed for the LepiLed light source (Brehm, 2017) (Fig. 1).
- However, we used a LED lamp (3000K 3.8W 350 lm Osram Germany) as the light source in the 11
- 12 experiment (to simulate road lighting which does not have as much UV and blue light as LepiLed
- 13 have) which was attached to the top lid of the funnel trap. To avoid vertical spread of light from
- 14 the lamp, the upper surface on the lid of the funnel trap was covered with duct tape. The trap
- 15 was mounted on a stand consisting of metal frames usually used for portable greenhouses (Fig.
- 16 1). We used portable power banks as the power supply for the LED lights. We documented
- 17 luminance of the light trap and its surroundings (Fig. 1B), and detailed measurements of the
- 18 illuminance at various distances and heights from the trap is presented in Appendix A.
- 19
- 20



23 Figure 1. A) Close-up photo of insect trap with light that was used. B) Luminance photo of the insect light trap in the 24 forest. Luminance photos were taken using LMK Mobile Advanced imaging luminance photometer (based on a Canon EOS 550D) and the associated computer software LMK labsoft ver. 12.7.23 (Techno Team Bildverarbeitung GmbH, Ilmenau, Germany). Note that the luminance photo (2B) uses false color to represent luminance values for clearer visualization of the distribution.

- 29
- 30 The experimental procedures were as follows. Light traps were mounted in late afternoons-early 31 evenings (1-2 hours before sunset) at each site. We sampled two sites per night, one site 32 situated in an open grassland and one site situated inside a forest. The mean distance between 33 traps in open grassland and the nearest forest was 41 m (range 15-160 m). Potential sites had 34 been identified beforehand from studies of aerial photographs. For each site we also used a 35 control trap mounted identical to the light trap but with no light source. These control traps were 36 placed in the vicinity of the light traps at each site, but never closer than 25 m. In the following 37 morning, the traps were revisited and all moth individuals captured were photographed. All 38 moths were released after documentation. This procedure was performed for a total of 16 nights 39 between 26 July and 5 September 2022, resulting in sampling of moths at a total of 32 sites. All

1 moths captured in the traps were identified to species using adequate literature and online

2 databases (Sterling et al., 2012, Elmquist et al., 2011, SLU Swedish Species Information Center, 3 2024b).

4

5 At each sampling location, alongside with the installation of the light traps, we took notes on the

6 prevailing weather conditions using the weather app provided by the Swedish Meteorological

- 7 and Hydrological Institute (SMHI). We recorded the temperature (in Celsius) and wind speed (in
- 8 meters/second) from the weather app. In addition, we also noted if the sky was cloudy or clear
- 9 (as a binary variable) and also obtained information about the lunar phase (moon visibility, in %)
- 10 during the night from the app Moon Phases and Lunar Calender (Kinetic stars).
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#### 2.3 Data and statistical analysis 12

13 All statistical analyses were conducted using R 4.1.0. (R Development Core Team, 2021). We

- 14 analyzed the response variables moth abundance and moth richness at the sites with
- 15 generalized linear mixed effects models (in the package lme4 (Bates et al., 2015)). In addition,
- 16 we analyzed species diversity using linear mixed effects models. For all response variables, we
- 17 included the fixed effects of the ecosystem (forest vs. grassland), temperature, cloudiness
- 18 (cloudy vs. not cloudy), lunar phase (in %), and wind velocity (m/s). The sampling date was
- 19 included as a random variable in all analyses. Since there is a possibility that environmental
- 20 variables may affect trap catches differently in the ecosystems, we included the two-way
- 21 interactions between the ecosystem and the environmental variables (i.e., temperature,
- 22 cloudiness, wind velocity, and lunar phase). We used a backward stepwise selection procedure,
- 23 removing non-significant variables from the full models. The resulting models were then
- 24 compared using Akaike's Information Criterion (AIC) to determine the best-fitting model,
- 25 continuing until no further improvement in AIC was possible. Species diversity (Hill's effective
- number of species) of insects in forest and open ecosystems was assessed using Hill's diversity 26 27
- index (e.g., Chao et al., 2014). We calculated q = 0 (species richness), q = 1 (the exponential of
- 28 Shannon's diversity) and q = 2 (the inverse of Simpson's concentration index). All taxa are listed 29 in Appendix C.
- 30

#### 3. Results 31

The field experiment yielded 172 moth individuals from 54 species. Species richness at the 32 33 investigated sites ranged from 1 to 8 species, with abundance ranging from 1 to 21 individuals. 34 Of the 32 sampled sites, six sites captured no moths. Geometridae was the most species-rich 35 family with 13 species (43 individuals), followed by Noctuidae with 11 species (46 individuals) 36 and Crambidae with 10 species (47 individuals). None of the control traps (with no light source) 37 captured any moths.

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39 The total abundance and species richness of the captured moths was significantly higher in the

40 forest compared to the open grassland (Table 1, Fig. 2). Abundance and species richness

- 41 increased with increased cloudiness whereas abundance also increased with higher
- 42 temperatures (Table 1, Fig. 3). Furthermore, trap catches in the open grassland increased at
- 43 nights with higher temperatures and slow wind, as indicated by significant ecosystem by
- 44 temperature and ecosystem by wind interactions (Table 1).
- 45
- 46 In Crambidae, abundance was significantly higher in the forest (Table 1, Fig. 4a) and increased
- 47 with temperature and cloudiness, and there were significant two-way interactions between
- 48 ecosystem and temperature and wind, where trap catches in open grasslands increased with

- temperature and decreased with wind (Table 1). However, species richness of Crambidae were
  only affected by increased cloudiness (Table 1, Fig. 4b).
- 3

4 In Geometridae, we found no significant main effect of the ecosystem for abundance or species

- 5 richness (Table 1, Fig. 4), but abundance increased significantly with an increased cloudiness.
- Furthermore, there was a significant ecosystem by cloudiness interaction effect, where species
   richness of Geometridae decreased in open grasslands with increased cloudiness (Table 1, Fig.
- richness of Geometridae decreased in open grasslands with increased cloudiness (Tal4).
- 9

10 In Noctuidae, we found no main significant effect of the ecosystem on abundance or species

11 richness (Table 1, Fig. 4). However, for abundance we found significant interaction effects

- 12 between ecosystem and temperature, cloudiness and moon phase, where abundance
- 13 increased in open grasslands with temperature and cloudiness and decreased with moon phase
- 14 (Table 1). Species richness of Noctuidae was only significantly affected by temperature (Table1).
- 15 16
- 17 In species diversity, q=1 (exponential of Shannon diversity, effective number of species)
- 18 increased significantly with cloudiness and a negative interaction effect by ecosystem and wind
- 19 (Table 2, Fig. 5). However, in species diversity q=2 (reciprocal of Simpson index) we found no
- 20 significant effects (Table 2, Fig. 5).
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Table 1. Results from the generalized linear mixed effects models on abundance and number of species on moths
 (total), Crambidae, Geometridae and Noctuidae.

Total abundance	Estimate (standard error)	z	P
Intercept	-1.84 (1.20)	-1.53	0.13
Ecosystem (open)	-3.51 (1.47)	-2.38	0.017
Temperature	0.13 (0.06)	2.10	0.035
Cloudiness	1.18 (0.49)	2.42	0.015
Wind speed	0.11 (0.21)	0.51	0.61
Ecosystem (open) x Temperature	0.24 (0.09)	2.82	<0.01
Ecosystem (open) x Wind speed	-0.66 (0.30)	-2.21	0.027
Total number of species	Estimate (standard error)	z	Ρ
Intercept	-0.76 (0.78)	-0.98	0.33
Ecosystem (open)	-3.00 (1.27)	-2.36	0.018
Temperature	0.05 (0.04)	1.33	0.18
Cloudiness	1.04 (0.31)	3.33	<0.001

Wind speed	0.11 (0.13)	0.80	0.43	
Ecosystem (open) x Temperature	0.21 (0.08)	2.80	<0.01	
Ecosystem (open) x Wind speed	-0.59 (0.24)	-2.42	0.016	
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Crambidae abundance	Estimate (standard error)	z	Р	
Intercept	-6.44 (1.48)	-4.34	<0.001	
Ecosystem (open)	-8.98 (1.66)	-5.41	<0.001	
Temperature	0.20 (0.09)	2.14	0.032	
Cloudiness	2.10 (0.92)	2.27	0.023	
Wind speed	0.22 (0.47)	0.46	0.65	
Ecosystem open x Temperature	0.66 (0.12)	5.36	<0.001	
	1 77 (0 00)	2 05	<0.01	

Crambidae number of species	Estimate (standard error)	z 💙	Р
Intercept	-5.27 (2.30)	-2.29	0.022
Ecosystem (open)	-0.56 (0.44)	-1.26	0.21
Temperature	0.17 (0.10)	1.82	0.07
Cloudiness	2.03 (1.00)	2.04	0.042
	>		
Geometridae abundance	Estimate (standard error)	z	Р
Intercept	-2.77 (1.68)	-1.65	0.1
Ecosystem (open)	0.02 (0.99)	0.02	0.98
Temperature	0.13 (0.08)	1.65	0.01
Cloudiness	1.98 (0.90)	2.20	0.028
Moon phase	-0.03 (0.01)	-2.09	0.037

-1.94 (1.00)

-1.95 0.051

Ecosystem (open) x Cloudiness

h			1
Ecosystem (open) x Moon phase	0.02 (0.01)	1.60	0.11
Geometridae number of species	Estimate (standard error)	z	Р
Intercept	-2.05 (1.31)	-1.57	0.12
Ecosystem (open)	0.69 (0.87)	0.80	0.42
Temperature	0.09 (0.06)	1.51	0.13
Cloudiness	1.28 (0.76)	1.69	0.091
Moon phase	-0.02 (0.01)	-1.87	0.061
Ecosystem (open) x Cloudiness	-2.08 (1.03)	-2.02	0.044
		L	
Noctuidae abundance	Estimate (standard error)	z	Р
Intercept	-1.88 (2.55)	-0.74	0.46
Ecosystem (open)	-7.67 (4.09)	-1.87	0.061
Temperature	-0.006 (0.13)	-0.05	0.96
Cloudiness	-0.50 (1.22)	-0.41	0.68
Moon phase	0.03 (0.02)	1.42	0.15
Ecosystem (open) x Temperature	0.46 (0.22)	2.04	0.042
Ecosystem (open) x Cloudiness	2.29 (1.12)	2.04	0.041
Ecosystem (open) x Moon phase	-0.04 (0.02)	-2.01	0.045
		I	1
Noctuidae number of species	Estimate (standard error)	z	Р
Intercept	-3.28 (1.31)	-2.50	0.012
Ecosystem (open)	0.85 (0.49)	1.74	0.08
Temperature	0.20 (0.08)	2.41	0.016
Wind speed	-0.55 (0.29)	-1.91	0.06
	i		1

- Table 2. Results from the linear mixed effects models on species diversity (Hill's effective number of species) of moths (total), Crambidae, Geometridae and Noctuidae. q =1 (exponential of Shannon diversity, effective number of species) and q = 2 (inverse of Simpson's concentration index).
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Diversity q=1	Value (standar error)	d.f.	t	Ρ
Intercept	-1.33 (1.61)	12	-0.83	0.43
Ecosystem (open)	-0.94 (1.86)	12	-0.50	0.62
Temperature	0.10 (0.09)	12	1.05	0.31
Cloudiness	2.90 (0.76)	12	3,81	0.0025
Wind speed	0.34 (0.34)	12	1.02	0.33
Ecosystem (open) x Temperature	0.20 (0.11)	12	1.92	0.079
Ecosystem (open) x Cloudiness	-1.47 (0.88)	12	-1.67	0.12
Ecosystem (open) x Wind speed	-0.99 (0.39)	12	-2.56	0.025
		1		1

Diversity q=2	Value (standar error)	d.f.	t	Р
Intercept	5.19 (1.78)	8	2.91	0.02
Ecosystem open	-3.76 (2.53)	5	-1.49	0.20
Temperature	-0.11 (0.09)	8	-1.13	0.29
Wind speed	0.29 (0.32)	8	0.93	0.38
Ecosystem (open) x Temperature	0.29 (0.13)	5	2.23	0.076
Ecosystem (open) x Wind speed	-1.13 (0.47)	5	-2.38	0.063





Noctuidae), divided between forest and open grassland ecosystems. The numbers shown in bars represent the

**Figure 3.** 3D graphs of abundance (A) and number of species (B) for all moths in forest and open grassland



Species richness of Crambidae, Geometridae and Noctuidae in relation to temperature and cloudiness. Error bars

represent standard error.



**Figure 5.** Species diversity (Hill's effective number of species) of insects in forest and open grassland ecosystems. q =1 (exponential of Shannon diversity, effective number of species) and q = 2 (inverse of Simpson's concentration index). For q=0 (species richness) see figure 4b. ENS represents the effective number of species. Error bars indicate 95% confidence intervals.

#### 4. Discussion

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Our study offers novel insights into moth attraction to anthropogenic light across different 8 9 ecosystems, revealing significant ecological implications. We observed marked differences in 10 moth abundance and species richness between traps placed in grassland and forest 11 ecosystems, with forest ecosystems generally yielding higher catch rates. Forests act as thermal 12 buffers, moderating temperatures (De Frenne et al., 2019) and providing shelter from winds, thus 13 creating a more stable and favorable microclimate for insects. This stable environment 14 facilitates extended periods of insect activity, which may explain our findings. 15 Moth abundance and species richness in open grasslands increased with higher temperatures 16 and increased cloudiness, approaching levels comparable to those observed in forest 17 ecosystems. Our findings align with previous studies demonstrating reduced catches at lower 18 temperatures and decreased cloudiness (Yela and Holyoak, 1997). Importantly, our study further 19 reveals that forest environments exhibit less variation in catch rates across different weather 20 conditions. 21

22 To the best of our knowledge, our comparison of light attraction across different ecosystems is 23 the first of its kind. Previous studies on the effects of anthropogenic light at night on moths have 24 primarily focused on behavior and attraction (e.g., Truxa and Fiedler, 2012; van Geffen et al., 25 2015; Degen et al., 2016; Altermatt and Ebert, 2016; van Langevelde et al., 2017; Boyes et al., 26 2020, Gaydecki, 2019, Fabian et al., 2024; Longcore et al., 2015). However, these studies have 27 not focused on investigating variations in ecosystem responses using standardized insect traps 28 and lighting setups. While no studies have directly compared different ecosystems, some 29 research has examined smaller-scale effects and explored the impact of trees on insect 30 catches. A field study by Niermann and Brehm (2022) demonstrated differences in 31 microhabitats, with higher abundance and species richness in catch traps at moderately 32 sheltered sites (closer to bushes) compared to exposed sites (i.e. more than 10 m from bushes). 33 Similarly, Straka et al. (2021) used UV-light traps to catch moths in dry grassland ecosystems 34 with differing tree cover and impervious surface amounts along an urbanization gradient with 35 presence of outdoor lighting. They found a positive effect of tree cover density on species 36 abundance and richness, although this effect was primarily driven by results from a single site.

1 These findings, along with our results, underscore the importance of considering ecosystem

- 2 variability when studying the impacts of light pollution on moth populations.
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4 In our study, we observed distinct differences in catches among various taxonomic groups 5 across forest and open grassland ecosystems. In forests, we caught higher numbers of 6 Geometridae (30) and Crambidae (26) compared to open grasslands (12 and 21, respectively), 7 while Noctuidae showed similar abundance in both ecosystems (22 in forest, 24 in open). 8 Species richness also varied, with forests hosting more Geometridae (17) and Crambidae (14) 9 species than open grasslands (8 for both), while Noctuidae showed higher species richness in 10 open grasslands (14) compared to forests (6). These findings align with the findings of Merckx 11 and Slade (2014), who demonstrated family-specific sampling areas (attraction radii) and 12 efficiencies for light traps. They found that erebids were attracted from up to 27 m, geometrids 13 from up to 23 m, and noctuids from up to 10 m, with varying capture rates among families. While 14 the specific mechanisms for the family-specific differences in attraction to light traps in different 15 ecosystems in our study cannot simply be explained, it may depend on various ecological traits 16 among taxonomic groups. The varied responses across families and ecosystems could 17 potentially bias results if not accounted for in light attraction studies. Therefore, it is important to 18 evaluate trap efficiency differences among families when interpreting results (Merckx and Slade, 19 2014). 20 Our study found fewer moths captured compared to previous studies, likely due to the lower 21 22 intensity, less attractive wavelengths, and smaller exposure area of our light sources, since we 23 aimed to simulate the attraction of modern electric lighting in natural ecosystems, for example 24 road lighting. We caught five individual moths per trap per night, whereas Niermann and Brehm 25 (2022), using UV light traps, caught approximately 63 individuals per trap per night in open

grasslands and orchards in Germany. This underscores the importance of considering lighting
 design (intensity, spectra, distribution, direction, height, luminaire) when comparing results

across studies. It is also important to use lighting designs which simulate currently used electric
 lighting when aiming to study attraction of anthropogenic lighting rather than using light sources
 designed for maximal attraction of insects.

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In our study, we measured light distribution at different heights and distances from the light trap, 32 33 providing detailed knowledge about light exposure around it and ensuring repeatability. This 34 aspect is rarely addressed in other studies investigating insect attraction to light. It has been 35 suggested from a controlled lab experiment that a threshold for impacts of light at night in the 36 Greater wax moth (Galleria mellonella) is approximately 0.3 lux (Jägerbrand et al., 2023). We 37 used a light trap that emitted light that exceeded that of bright full moonlight (0.3 lux. The 38 illumination was measured vertically at different heights, with the light meter pointing toward the 39 light trap. The light intensity exceeded 0.3 lux over an circular area with a 2 meter radius at 40 different heights from the ground (see also Appendix B), resulting in an estimated insect 41 attraction area of approximately 12.56 m<sup>2</sup>. This approach allows for a more precise 42 quantification of the affected area and the relationship between light intensity and insect 43 attraction, addressing a significant gap in the existing literature. By establishing a defined area of 44 influence, we can better estimate the attraction radius and also quantify light attraction through 45 dose-effect responses, with the potential to extrapolate these findings to larger-scale lighting 46 scenarios. Our methodological approach, using light traps with known lighting properties offers 47 a reproducible framework for future research on the impacts of anthropogenic light on 48 biodiversity, enabling other researchers to compare their results across ecosystems. 49 50 Our results suggest that anthropogenic lighting may potentially have a greater negative impact

51 on moth populations in open ecosystems, such as grasslands. Adult moths are active for short

52 periods, and unfavourable weather conditions further limit their time for mating and

2 ecosystems further shortens this critical activity window, reducing opportunities for foraging and 3 reproduction. This highlights the need for tailored light pollution management, particularly 4 during periods of insect activity. For example, adaptive lighting systems could be programmed to 5 dim during key periods of insect activity, helping to mitigate the impact on foraging and 6 reproduction. Forest ecosystems buffer weather conditions, promoting insect activity through 7 natural light filtering and protection, making consistent and long-term mitigation strategies the 8 most effective approach to reduce the impact of outdoor lighting. Our findings emphasize the 9 importance of ecosystem-specific approaches to enhance the effectiveness of light pollution 10 mitigation strategies. Using general approaches for light pollution reductions may not be 11 sufficient to protect photo-sensitive species such as nocturnal moths from negative impacts on 12 reproduction in all ecosystems. Further research across ecosystems with varied microclimates 13 could reveal greater differences and lead to more effective mitigation strategies.

reproduction (Persson, 1972). The added disruption caused by outdoor lighting in open

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#### 15 5. Conclusions

16 This study provides the first direct comparison of moth attraction to identical light traps in forest 17 and grassland ecosystems, revealing significant ecological differences. Our findings 18 demonstrate higher catch rates in forests compared to grasslands, with environmental factors 19 such as temperature and cloudiness exerting a stronger influence on moth attraction in open 20 grassland ecosystems. We also observed family-specific variations in light trap catches between 21 ecosystems, highlighting potential sampling biases that should be considered in future 22 research. Our method, with precise measurements of lighting around traps, enables reliable 23 comparisons across ecosystems and provides a clear framework for studies on the impact of 24 light pollution on biodiversity and informing conservation planning and lighting management. 25 These results have important implications for developing tailored light pollution mitigation strategies, emphasizing the need to consider specific ecosystem characteristics. We suggest 26 27 that future research should explore the mechanisms underlying such ecosystem-dependent differences in moth responses to light. 28

29

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33

# 34 Author contribution statement

PA and AJ contributed equally to this study, collaborating on the conception and design, data
collection, analysis and interpretation of results, and preparation of the first draft manuscript.
PA took a leading role in the fieldwork component of the research. Both authors were involved in
reviewing the results and approving the final version of the manuscript.

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## 40 Declaration of competing interests

41 The authors declare no competing interests.

42

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# 3 Appendix

4 5



Figure A1. Spectral power distribution of the LED light source used in the insect light trap. The correlated colour temperature (CCT) was 2961K. Measurements were performed using a JeTi Spectro-Radiometer (specbos 1201).

#### 10

#### 11 Appendix B. Field measurements of the insect light trap

12 Light measurements were taken under field conditions on 14-15 November 2022 in a mixed 13 forest and a relatively open meadow in Gustavsberg, Sweden, with overcast and ca 5-10°C, and 14 moon in waning gibbous (57–68%). According to the New World Atlas of light pollution the site 15 has an artificial sky brightness of 1380 µcd/m<sup>2</sup> (Falchi et al., 2016b, Falchi et al., 2016a). 16 Detailed measurements were conducted for the forest and control measurements were done in 17 the meadow. For the forest ecosystem, illuminance measurements were performed in all four 18 directions (north, south, west, east) from the light trap, to investigate light distribution in the 19 vicinity of the light trap. Vertical illuminances were taken at heights of 0.5 m, 1.0 m, 1.5 m, 2.0 m 20 and at distances of 0.5—5.0 m from the light source at 0.5 m intervals. 21 Measurements show that at a distance of 1.5 m the vertical illuminance for heights of 1.5 m and 22 2.0 m is equal to or below 0.3 lux, and at a distance of 2.0 m, it is equal to or below 0.3 lux at 23 heights of 0.5 m and 1.0 m (Table 1). Horizontal illuminances were measured on the ground (5.5 24 cm above the ground) and at 2 m height, at the same distances from the light trap as vertical 25 measurements were taken (0.5-5.0 m). Again, illuminance was below 0.30 lux at a 2 m distance 26 (Table 2). However, the horizontal illuminance at 2 m did not seem to be influenced by the light 27 from the insect trap and therefore, only a few control points were measured, and the illuminance 28 was found to be 0.04 lux. In the meadow, the vertical illuminance at 1.0 m height and 2.0 m 29 distance from the insect trap was found to be on average 0.29 lux and the horizontal illuminance 30 at 2 m height was 0.11 lux (not shown).

**Table B1.** Vertical illuminance (lux) at different heights and distances from the insect light trap in the forest ecosystem. Mean values from four different directions (north, south, west, east). Mean values  $\pm$  standard deviation (SD). Bold indicates illuminance values equal to or below 0.30 lux.

				Heig	ht (m)				
	0	.5		1	1	.5	2	2	
Distance (m)	mean	SD	mean	SD	mean	SD	mean	SD	
0.5	0.96	0.168	3.86	0.579	1.96	0.359	0.31	0.062	31
1	1.25	0.187	1.12	0.067	0.68	0.072	0.36	0.091	
1.5	0.52	0.049	0.48	0.069	0.30	0.041	0.27	0.018	
2	0.30	0.026	0.27	0.035	0.20	0.014	0.17	0.019	
2.5	0.19	0.029	0.17	0.025	0.14	0.014	0.13	0.026	
3	0.14	0.021	0.12	0.017	0.10	0.013	0.09	0.015	
3.5	0.10	0.017	0.09	0.013	0.08	0.013	0.08	0.014	
4	0.08	0.017	0.07	0.013	0.07	0.010	0.06	0.017	
4.5	0.06	0.013	0.06	0.010	0.05	0.013	0.06	0.014	

5 0.05	0.013	0.05	0.008	0.05	0.014	0.05	0.012
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- Table B2. Horizontal illuminance (lux) on the ground at distances from the insect light trap. Mean
- 2 3 4 values from four different directions (north, south, west, east). Mean values ± standard deviation (SD).
- Bold indicates illuminance values equal to or below 0.30 lux.

Distance from light source	Mean	SD	
0.5	0.64	0.126	
1.0	0.41	0.054	
1.5	0.40	0.019	
2.0	0.18	0.010	
2.5	0.06	0.054	
3.0	0.07	0.022	
3.5	0.06	0.014	
4.0	0.05	0.006	
4.5	0.05	0.010	
5.0	0.05	0.010	

- Photos taken with a commercial triple-lens camera with LiDAR sensor for light detection and
- 7 ranging, shows the forest and open meadow sites where measurements were performed under

natural conditions with low light (Figure B1 a-b). Photos in figure B1 c-d shows the luminance
 distribution for the insect light trap in the field under natural low light conditions.



- Figure B1. a) Photo of the insect light trap in forest. B). Photo of the insect light trap in the open meadow. c)
   Luminance photo of the insect light trap in forest, d) luminance photo of the insect light trap in the open meadow.
- 5 Illuminance and luminance were measured with Hagner<sup>™</sup>s Universal Photometer S5. with
- 6 Measurement function of illuminance and luminance (1°) of Hagner S5 are 0.01—199.900 lux
- 7 and cd/m<sup>2</sup> and have an accuracy better than  $\pm$ 3%. The lowest detectable value of
- 8 measurements is 0.01 cd/m<sup>2</sup> or lux. Operating temperature range is  $-5^{\circ}$ C  $+50^{\circ}$ C.
- 9 Luminance photos were taken using LMK Mobile Advanced imaging luminance photometer
- 10 (based on a Canon EOS 550D) and the associated computer software LMK labsoft ver. 12.7.23
- 11 (Techno Team Bildverarbeitung GmbH, Ilmenau, Germany). Canon EOS 550D is a digital single-

lens reflex camera with a CMOS sensor with 18.0 effective megapixels resolution and has a
 working temperature range of 0–40°C and working humidity of 85% or less. The LMK Mobile
 Advance is designed to convert images directly into luminance values with assistance of a

4 software programme and calibration file.

#### 5 6 7

#### Appendix C

Table C1. Taxon list from the field experiment.

8	3
9	)

Species	Family	Number
Acleris emargana	Tortricidae	1
Acrocercops brongniardellus	Gracillariidae	1
Aethes smeathmanniana	Tortricidae	1
Agriphila inquinatella	Crambidae	19
Agriphila selasella	Crambidae	1
Agriphila straminella	Crambidae	2
Agriphila tristella	Crambidae	11
Apamea crenata	Noctuidae	1
Catoptria falsella	Crambidae	4
Cerapteryx graminis	Noctuidae	6
Chiasmia clathrata	Geometridae	1
Clostera pigra	Notodontidae	3
Cosmorhoe ocellata	Geometridae	1
Crambus perlellus	Crambidae	2
Crocallis elinguaria	Geometridae	1
Eana osseana	Tortricidae	1
Eilema depressum	Erebidae	1
Epinotia trigonella	Tortricidae	1
Eudonia truncicolella	Crambidae	4
Eulithis testata	Geometridae	5
Eupithecia centaureata	Geometridae	1
Eupithecia pusillata	Geometridae	7
Eupithecia vulgata	Geometridae	1
Geometra papilionaria	Geometridae	4
Helcystogramma rufescens	Gelechiidae	3
Hydraecia micacea	Noctuidae	1
Hydriomena furcata	Geometridae	1
Idaea straminata	Geometridae	2
Lathronympha strigana	Tortricidae	1
Lithosia quadra	Erebidae	1
Lymantria monacha	Erebidae	1
Mniotype satura	Noctuidae	1
Mythimna impura	Noctuidae	1
Nematopogon robertellus	Adelidae	1

Species	Family	Number	]
Noctua pronuba	Noctuidae	1	
Notocelia roborana	Tortricidae	2	
Notocelia sp.	Tortricidae	1	-
Nymphula nitidulata	Crambidae	1	
Oncocera semirubella	Pyralidae	1	
Parapoynx stratiotata	Crambidae	2	
Patanis ruralis	Crambidae	1	
Pennithera firmata	Geometridae	4	
Phragmatobia fuliginosa	Erebidae	1	
Rivula sericealis	Erebidae	5	
Schrankia costaestrigalis	Erebidae	2	
Scotopteryx chenopodiata	Geometridae	11	
Thalpophila matura	Noctuidae	5	
Tholera decimalis	Noctuidae	2	
Xanthia togata	Noctuidae	3	
Xanthorhoe ferrugata	Geometridae	4	
Xestia sexstrigata	Noctuidae	1	
Xestia xanthographa	Noctuidae	24	
Yponomeuta evonymellus	Yponomeutidae	8	
Ypsolopha nemorella	Ypsolophidae	2	

#### 3 References

Altermatt, F. and Ebert, D. 2016. Reduced flight-to-light behaviour of moth populations exposed
to long-term urban light pollution. Biology Letters 12(4):20160111.

6

Barroso, A., Haifig, I., Janei, V., da Silva, I., Dietrich, C., Costa-Leonardo, A. 2017. Effects of
flickering light on the attraction of nocturnal insects. Lighting Research & Technology 49(1):100-

9 110. doi:10.1177/1477153515602143

10

Bates, D., Mächler, M., Bolker, B., Walker, S. 2015. Fitting Linear Mixed-Effects Models Using
 lme4. Journal of Statistical Software 67:1. https://doi.org/10.18637/jss.v067.i01

13

Blair, J., Nippert, J., Briggs, J. 2014. Grassland ecology. In: Monson, R.K. (ed.), Ecology and the
Environment, The Plant Sciences 8, pp. 389-423. https://doi.org/10.1007/978-1-4614-7501-9\_14

16

Bolliger, J., Haller, J., Wermelinger, B., Blum, S. & Obrist, M. K. 2022. Contrasting effects of street
light shapes and LED color temperatures on nocturnal insects and bats. Basic and Applied
Eastern C4, 1, 10, https://doi.org/10.1010/j.heast.2020.07.000

- 19 Ecology 64, 1-12. https://doi.org:10.1016/j.baae.2022.07.00220
- 21 Boyce, P. R. 2019. The benefits of light at night. Building and Environment 151:356-367.
- 22 https://doi.org:10.1016/j.buildenv.2019.01.020
- 23

1 Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S. Pocock, M.J. 2020. Is light pollution driving moth 2 population declines? A review of causal mechanisms across the life cycle. Insect Conservation 3 and Diversity 14:167-187. doi: 10.1111/icad.12447 4 5 Brehm, G. 2017. A new LED lamp for the collection of nocturnal Lepidoptera and a spectral 6 comparison of light- trapping lamps. Nota Lepidopterologica 40:87-108. 7 https://doi.org/10.3897/nl.40.11887 8 9 Bruce-White, C., Shardlow, M. 2011. A Review of the Impact of Artificial Light on Invertebrates. 10 Buglife, Peterborough. 11 12 Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. Ellison, A.M. 2014. 13 Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in 14 species diversity studies. Ecological Monographs, 84:45-67. https://doi.org/10.1890/13-0133.1 15 16 CIE S 017/E:2020. ILV: International lighting vocabulary, 2nd edition. Commission Internationale 17 de l'Éclairage, Vienna, Austria. 18 19 Degen, T., Delb, T., Oelke, H. Schade, J. 2016. Street lighting: sex-independent impacts on moth 20 movement. Journal of Animal Ecology 85:1352-1360. https://doi.org/10.1111/1365-2656.12540 21 22 De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F. et al. 2019. Global buffering of temperatures 23 under forest canopies. Nature Ecology & Evolution 3:744–749. https://doi.org/10.1038/s41559-24 019-0842-1 25 Eisenbeis, G. 2006. Artificial night lighting and insects: Attraction of insects to streetlamps in a 26 27 rural setting in Germany. In: Rich, C., Longcore, T. (eds.), Ecological Consequences of Artificial 28 Night Lighting, pp. 281–304. Island Press. 29 Eliasson, C.U., Ryrholm, N., Holmer, M., Jilg, K., Gärdenfors, U. 2005. Nationalnyckeln till 30 31 Sveriges flora och fauna. Fjärilar: Dagfjärilar. Hesperiidae-Nymphalidae. ArtDatabanken, SLU. 32 Uppsala. 33 34 Elmquist, H., Liljeberg, G., Top-Jensen, M., Fibiger, M. 2011. Sveriges fjärilar – en fälthandbok 35 över Sveriges samtliga dag- och nattfjärilar. Bugbook Publishing. 36 Fabian, S. T., Sondhi, Y., Allen, P.E., Theobald, J.C., Lin, H-T. 2024. Why flying insects gather at 37 38 artificial light. Nature Communications 15:689. 39 40 Falchi, F., Cinzano. P., Duriscoe. D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B.A., 41 Rybnikova, N.A., Furgoni, R. 2016a. The new world atlas of artificial night sky brightness. Science 42 Advances 2(6):e1600377. doi: 10.1126/sciadv.1600377. 43 44 Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B., 45 Rybnikova, N.A., Furgoni, R. 2016b. Supplement to: The New World Atlas of Artificial Night Sky 46 Brightness. V. 1.1. GFZ Data Services. <u>https://doi.org/10.5880/GFZ.1.4.2016.001</u> 47 48 Gaydecki, P. 2019. Automated moth flight analysis in the vicinity of artificial light. Bulletin of 49 Entomological Research 109:127–140. DOI: https://doi.org/10.1017/S0007485318000378 50 51 Gorostiza, E.A., Colomb, J., Brembs, B. 2016. A decision underlies phototaxis in an insect. Open 52 Biology 6(12):160229. doi: 10.1098/rsob.160229

1	
2 3 4 5	Grenis, K., Nufio, C., Wimp, G.M., Murphy, S.M. 2023. Does artificial light at night alter moth community composition? Philosophical Transactions of the Royal Society B: Biological Sciences 378 (2023). <u>https://doi.org/10.1098/rstb.2022.0365</u>
6 7 8	Hallmann, C.A., Sorg, M., Jongejans, E., et al. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12(10): e0185809.
9 10 11	Jekely, G. 2009. Evolution of phototaxis. Philosophical Transactions of the Royal Society B: Biological Sciences 364:2795–2808.
12 13 14	Jägerbrand, A. K., Spoelstra, K. 2023. Effects of anthropogenic light on species and ecosystems. Science 380:1125-1130. <u>https://doi.org/10.1126/science.adg3173</u>
15 16 17 18	Jägerbrand, A., Andersson, P., Nilsson Tengelin, M. 2023. Dose–effects in behavioural responses of moths to light in a controlled lab experiment. Scientific Reports 13. https://doi.org:10.1038/s41598-023-37256-0
19 20 21 22	Kocifaj, M., Wallner, S., Barentine, J. C. 2023. Measuring and monitoring light pollution: Current approaches and challenges. Science 380:1121-1124. https://doi.org/10.1126/science.adg0473
23 24 25	Kyba, C. C. M., Mohar, A., Ziegler, D., et al. 2017. Artificially lit surface of Earth at night increasing in radiance and extent. Science Advances 3, e1701528. <u>https://doi.org:10.1126/sciadv.1701528</u>
26 27 28 29	Longcore, T. et al. 2015. Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. Philosophical Transactions of the Royal Society B: Biological Sciences 370, 20140125. <u>https://doi.org:10.1098/rstb.2014.0125</u>
30 31 32 33	Macgregor, C.J., Scott-Brown, A.S. 2020. Nocturnal pollination: an overlooked ecosystem service vulnerable to environmental change. Emerging Topics in Life Sciences 4:19–32. https://doi.org/10.1042/ETLS20190134
34 35 36 37	Merckx, T., Slade, E.M. 2014. Macro-moth families differ in their attraction to light: implications for light-trap monitoring programmes. Insect Conservation and Diversity 7:453-461. https://doi.org/10.1111/icad.12068
38 39 40	Meyer, L.A., Sullivan, S.M.P. 2013. Bright lights, big city: influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. Ecological Applications 26(3): 1322-1330.
40 41 42 43 44	Niermann, J., Brehm, G. 2022. The number of moths caught by light traps is affected more by microhabitat than the type of UV lamp used in a grassland habitat. European Journal of Entomology 119: 36-42. doi: 10.14411/eje.2022.004
44 45 46 47	Owens, A.C.S., Lewis, S.M. 2018. The impact of artificial light at night on nocturnal insects: A review and synthesis. Ecology and Evolution 8, 11337-11358. <u>https://doi.org:10.1002/ece3.4557</u>
48 49 50 51	Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B. 2013. The structure, distribution and biomass of the world's forests. Annual Review of Ecology, Evolution, and Systematics 44:593-622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

1 Persson, B. 1972. Longevity of Noctuid Moths in Relation to Certain Day-Time Weather Factors. 2 Oikos 23(3):394-400. 3 4 R Development Core Team 2021. R: A language and environment for statistical computing, 5 R Foundation for Statistical Compution. URL http://R-project.org. 6 7 Sánchez-Bayo, F., Wyckhuys, K.A.G. 2019. Worldwide decline of the entomofauna: A review of its 8 drivers. Biological Conservation 232:8-27. https://doi.org/10.1016/j.biocon.2019.01.020 9 10 Schowalter, T.D., Noriega, J.A., Tscharntke, T. 2018. Insect effects on ecosystem services -Introduction. Basic and Applied Ecology 26: 1-7. 11 12 13 SLU Swedish Species Information Center 2024a. Species Information System. Source: 14 https://www.artportalen.se/ 15 16 SLU Swedish Species Information Center 2024b. Artfakta. Source: https://artfakta.se/ 17 18 Sterling, P., Parsons, M., Lewington, R. 2012. Field guide to the micromoths of Great Britain and 19 Ireland. British Wildlife Publishing. 20 Straka, T. M. et al. 2021. Light pollution impairs urban nocturnal pollinators but less so in areas 21 22 with high tree cover. Science of The Total Environment 778, 146244. 23 https://doi.org/10.1016/j.scitotenv.2021.146244 24 25 Truxa, C., Fiedler, K. 2012. Attraction to light - from how far do moths (Lepidoptera) return to 26 weak artificial sources of light? European Journal of Entomology 109:77-84. 27 28 van Geffen, K.G., van Eck, E., de Boer, R.A., van Grunsven, R.H.A., Salis, L., Berendse, F., 29 Veenendaal, E.M. 2015. Artificial light at night inhibits mating in a Geometrid moth. Insect 30 Conservation and Diversity 8:282-287. 31 van Grunsven, R.H.A., van Deijk, J.R., Donners, M., Berendse, F., Visser, M.E., Veenendaal, E., 32 33 Spoelstra, K. 2020. Experimental light at night has a negative long-term impact on macro-moth 34 populations. Current Biology 30:R694-R695. doi: 10.1016/j.cub.2020.04.083. 35 36 van Klink, R. et al. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater 37 insect abundances. Science 368, 417–420. 38 39 van Langevelde, F., van Grunsven, R.H.A., Veenendaal, E.M., Fijen, T.P.M. 2017. Artificial night 40 lighting inhibits feeding in moths. Biology Letters 13:20160874. 41 42 van Langevelde, F. et al. 2018. Declines in moth populations stress the need for conserving dark 43 nights. Global Change Biology 24, 925–932. 44 45 Veilleux, C.C., Cummings, M.E. 2012. Nocturnal light environments and species ecology: 46 implications for nocturnal color vision in forests. Journal of Experimental Biology 215:4085-47 4096. 48 49 Wakefield, A., Broyles, M., Stone, E. L., Jones, G., Harris, S. 2016. Experimentally comparing the 50 attractiveness of domestic lights to insects: Do LEDs attract fewer insects than conventional 51 light types? Ecology and Evolution 6:8028-8036. https://doi.org/10.1002/ece3.2527 52

- Wakefield, A., Broyles, M., Stone, E.L., Harris, S., Jones, G. 2018. Quantifying the attractiveness
   of broad-spectrum street lights to aerial nocturnal insects. Journal of Applied Ecology 55:714–
- 3 722. <u>https://doi.org/10.1111/1365-2664.13004</u>
- Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., Stopak, D. 2021. Insect decline
- 6 in the Anthropocene: Death by a thousand cuts. Proceedings of the National Academy of
- 7 Sciences USA 118(2), e2023989118.
- 8
- 9 Williams, C. B., Sing, B. P. 1951. Effect of moonlight on insect activity. Nature 167: 853.
- 10
- 11 Yela, J.L., Holyoak, M. 1997. Effects of Moonlight and Meteorological Factors on Light and Bait
- 12 Trap Catches of Noctuid Moths (Lepidoptera: Noctuidae). Environmental Entomology13 26(6):1283-1290.
- 14 15