

## RESEARCH ARTICLE

## Dim light pollution prevents diapause induction in urban and rural moths

Thomas Merckx<sup>1,2</sup>  | Matthew E. Nielsen<sup>2</sup>  | Tuomas Kankaanpää<sup>2</sup>  |  
Tomáš Kadlec<sup>3</sup> | Mahtab Yazdanian<sup>2</sup>  | Sami M. Kivelä<sup>2</sup> <sup>1</sup>Biology Department, Vrije Universiteit Brussel, Brussels, Belgium<sup>2</sup>Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland<sup>3</sup>Department of Ecology, Czech University of Life Sciences Prague, Prague-Suchbát, Czech Republic

## Correspondence

Thomas Merckx

Email: [thomas.merckx@vub.be](mailto:thomas.merckx@vub.be)

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## Abstract

1. Light pollution is increasingly affecting biodiversity and may also disrupt seasonal adaptations. Even dim artificial light, such as skyglow—which can spread far beyond urban areas—can interfere with using photoperiod as a seasonal cue.
2. Here, we test how light pollution impacts diapause induction and whether urban evolution counteracts it, by using common-garden experiments with a common, widespread geometrid moth (*Chiasmia clathrata*). We raised offspring from urban and rural populations from North- and Mid-European countries in treatments with and without dim light at night.
3. The dim light treatment strongly increased direct development overall—with no evidence for urban adaptation to it—but distinctly more so in Mid- than in North-European populations.
4. Because diapause induction is critical for surviving winter, these results indicate that dim but widespread light pollution may have detrimental effects on insect populations, especially so at mid-latitudes, and may hence explain part of the ongoing, large-scale insect declines globally.
5. *Synthesis and applications.* Latitudinal variation in sensitivity to light pollution means that its contribution to insect declines—and its conservation importance—should likewise vary among regions. In mid-latitude regions, where populations seem more sensitive to light pollution, mitigating light pollution should be a high priority for insect conservation. Reducing skyglow from cities should benefit both urban populations—which were just as susceptible as rural populations in our study—and rural populations—because skyglow extends far beyond the geographic boundaries of cities.

## KEYWORDS

artificial light at night, development time, dim light at night, global change, lepidoptera, phenotypic plasticity, skyglow, urban evolution

## 1 | INTRODUCTION

Light pollution introduces artificial light into the nocturnal environment, disrupting the natural daily light–dark cycle and hence

the biological circadian system. This artificial light at night (ALAN) is one of the most widespread forms of anthropogenic pollution and represents an emerging threat to global biodiversity because of its impacts at all levels of biological organization from

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cell to ecosystem (Gaston et al., 2013; Hölker et al., 2010; Koen et al., 2018). Although light pollution has regularly been characterized as an issue only affecting already heavily modified urban ecosystems, its impacts likely spread far beyond them (Gaston et al., 2021). For instance, skyglow—dim artificial light which occurs through atmospheric scattering of city lights—now covers nearly one-fourth of global land area (Falchi et al., 2016a). ALAN can have a strong biological impact, even the low 0.01–10-lux illuminance levels typically associated with skyglow (Jechow et al., 2021; Sanders et al., 2021). Impacts of light pollution at the organismal level (e.g. behaviour, physiology, development) can translate into negative ecological and ecosystem consequences, many of which we are only beginning to understand (Grubisic & van Grunsven, 2021; Owens et al., 2020; Sanders & Gaston, 2018). For example, comparative analyses indicate that light pollution may be an important, if understudied, factor contributing to contemporary insect declines and associated major ecosystem functions, such as pollination (van Langevelde et al., 2017).

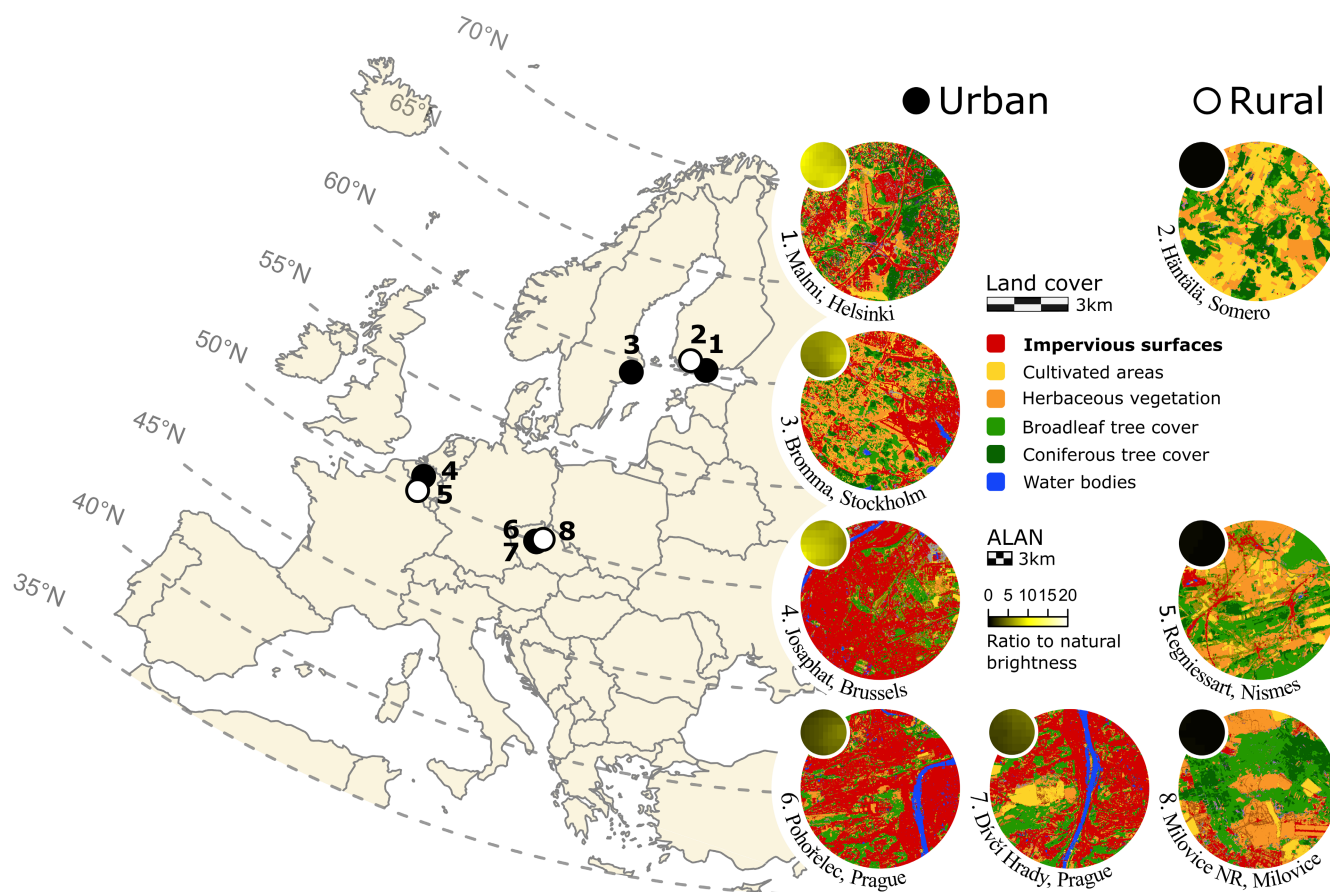
A primary reason why light pollution is so disruptive, even at low levels, is because it disrupts day–night cycles and their seasonal variation. Natural day–night cycles are the strongest and most predictable environmental signals that organisms typically rely on (Gaston et al., 2014, 2017). The diel cycle between day and night is used to regulate circadian systems by almost all organisms, allowing them to anticipate daily cycles in the environment and alter physiological and behavioural processes appropriately (Grubisic et al., 2019). Seasonal changes in photoperiod (i.e. the relative length of day and night) are, in turn, used to regulate a wide range of phenological changes over the course of the year (Bradshaw & Holzapfel, 2007; Meuti & Denlinger, 2013). Photoperiod is especially important as a seasonal cue in temperate and boreal regions, where it can be a much better predictor of future weather than current conditions (Way & Montgomery, 2015). These daily and seasonal cycles are often sensitive to very low levels of light, and thus can be heavily disrupted by artificial light (Desouhant et al., 2019; Grubisic et al., 2019; Owens & Lewis, 2018; Tidau et al., 2021). For instance, light pollution severely disrupts the synchronized diel vertical migrations of zooplankton (Ludvigsen et al., 2018) and causes birds to sing earlier in both the day and the year (Da Silva et al., 2014, 2015).

Diapause, a dormant state induced during ontogeny and used by many arthropods to survive winter (Hahn & Denlinger, 2011; Tauber et al., 1986), is a classic example of a trait often regulated by photoperiod, and thus highly likely to be disrupted by light pollution. Many insects use short photoperiods as a cue to indicate the approach of winter and, accordingly, short photoperiods typically induce diapause (Hand et al., 2016; Tauber et al., 1986). Individuals entering diapause cease development until after winter, investing in energy reserves and lowering their metabolic rate (Hahn & Denlinger, 2011). By extending perceived daylength, light pollution can repress the induction of diapause, potentially leading to direct development too late in the year with severe fitness consequences (Denlinger et al., 2017; Kerr et al., 2020; Van Dyck et al., 2015).

Dim ALAN averts diapause entry by *Mamestra brassicae* moths (7 lux: van Geffen et al., 2014) and mosquitoes (9–11 lux: Westby & Medley, 2020; 4 lux: Fyie et al., 2021); diapause entry of *Sarcophaga similis* flesh flies was affected by ALAN levels as low as 0.01 lux (Mukai et al., 2021). Thus, even very low intensities of skyglow could disrupt diapause, leading to potential impacts on rural populations in addition to urban ones.

Here, we test whether dim (0.7 lux), indirect ALAN impacts the photoperiodic induction of diapause in both urban and rural populations of the geometrid moth *Chiasmia clathrata* (Latticed heath). Although *C. clathrata* is a generalist species of meadow habitats, and hence common and widespread throughout its palaearctic range, populations appear to be declining. In Finland, *C. clathrata* decreased on average by 3.2% annually between 1993 and 2016, totalling a 53% decline in abundance (Hällfors et al., 2021). Between 1970 and 2016, the abundance of *C. clathrata* decreased by 85% in Britain and Ireland, and its distribution throughout this region decreased by 53% (Randle et al., 2019). Depending on latitude, *C. clathrata* flies in one to three generations per year; it overwinters as a diapausing pupa, and photoperiod is a key cue used to make this developmental decision during the larval stage (Merckx et al., 2021; Välimäki et al., 2013). Thus, alteration of photoperiod by light pollution could have severe negative impacts on this species, potentially contributing to its decline. On the other hand, previous research suggests that *C. clathrata* may be robust to the effects of artificial light. Specifically, light pollution is predicted to select for diapause induction at longer photoperiods in urban environments by artificially lengthening photoperiod; however, a previous study of Nordic *C. clathrata* found urban populations have instead evolved the opposite change—diapause induction only at shorter photoperiods, as predicted by the urban-heat-island effect (Merckx et al., 2021).

To test the effects of dim ALAN on diapause induction in *C. clathrata*, we performed a common-garden experiment on rural and urban populations, which should experience markedly different levels of nocturnal brightness. We raised F3-individuals descended from urban and nearby rural populations associated with multiple European cities with or without dim (0.7 lux) light during the night phase (Figure 1). If ALAN broadly disrupts the induction of diapause, we expected a higher proportion of directly developing individuals under the ALAN treatment than the control for all populations. Alternatively, if urban populations have adapted to the more prevalent light pollution found in cities, we expected a greater impact of our ALAN treatment in rural than urban populations. Moreover, while high levels of light pollution lead to nearly continuous day-like conditions in cities, bright nights also occur naturally at high latitudes during the summer. Thus, light pollution may not have as large of an effect in these regions as it does at lower latitudes because populations are already better adapted to short and bright nights. If *C. clathrata* also displays latitudinal variation in its sensitivity to brightened nights, we expect a smaller impact of the ALAN treatment on North- than on Mid-European populations.



**FIGURE 1** Location, surrounding land cover and light pollution level of the sampled populations. Map of Europe showing the locations of four urban (black dots), three rural (white dots) sampled populations as well as one 'semiurban' (site 7) sampled population. For each sampling site 3 km radius maps of land cover classes (large circles; Malinowski et al., 2020) and 3 km radius maps of light pollution levels (small circles; Falchi et al., 2016a, 2016b) are visualized.

## 2 | MATERIALS AND METHODS

### 2.1 | Common-garden skyglow manipulation experiment

Our study did not require ethical approval and permits to carry out fieldwork were not needed. *C. clathrata* females were hand netted in 2019 within urban and rural sites of two Mid-European countries (Belgium and Czech Republic), and two North-European countries (Finland and Sweden; Table S1; Figure 1). All sampled North-European and Mid-European populations are bivoltine. All females were taken to the University of Oulu, where they were kept at 21°C under 12L:12D conditions for egg laying in individual cups with access to sugar water. Newly hatched larvae were placed individually in cups (0.25 L translucent plastic). Each larva had ad libitum access to fresh, wild-collected shoots of a natural host plant, *Lathyrus pratensis*, and was reared until pupation at 21°C under 12L:12D. A layer of garden peat was added to the cups for pupation when larvae reached the final instar. Five days after pupation, the pupae were excavated from the peat, weighed and placed in a 0.25 L cup with *Sphagnum* spp. moss. After 10 months of overwintering in a dark refrigerator room at 5°C, the pupae were taken to 20°C and 18L:6D. Eclosed females

were placed with a nonsibling male from the same population in 0.25 L cups under 21°C and 18L:6D with access to sugar water and allowed to mate and lay eggs. Newly hatched F2-larvae from each population were singly placed in 0.25 L cups and reared under the same conditions as the F1-generation until the next generation of F3-individuals hatched in 2021, first the Mid-European individuals between 2 and 5 June, and next the North-European individuals between 11 and 14 July. Because we only managed to collect a few males and no females from rural Stockholm, our comparisons in the North-European individuals focus on the Finnish populations while retaining the urban Stockholm population for context. We aimed to test 140 individuals from seven families per population, but were not able to do so in all cases (the smallest per population sample was 60 individuals from three families; Table S1), leading to a total starting sample size of 989 individuals.

The offspring of each female was evenly divided among two climate rooms (Arctest Oy) at 21°C, one without (i.e. control treatment) and the other with an ALAN treatment. Mean illuminance level at daytime was 1423 lux (Figure S1). In order to produce a realistic amount of skyglow we used a 2 m strip of warm white (3500K) LED light source (120LED/m; luminous flux 400 lumen; Kempton). This light was mixed in a 2 m long black plastic duct

at 1.6 m height that we could adjust by rotating until a uniform, indirect light with mean intensity of 0.7 lux (measured with Ocean Optics USB2000 + RAD) was obtained on the table surface where the moth larvae were reared. The control room at night was characterized by dark conditions of only 0.038 lux (Figure S1). Brighter ALAN treatments were used in previous studies focusing on effects of dim ALAN on a noctuid moth (7 lux: van Geffen et al., 2014), on an ermine moth (5 lux: Cieraad et al., 2022) and on a mosquito (4 lux: Fyie et al., 2021).

For the North-European populations, the climate rooms had a photoperiodic regime of 20.5L:3.5D, whereas for the Mid-European populations this was 16L:8D. The North-European photoperiodic regime was the mean critical photoperiod (daylength when 50% of a population opts for direct development) of these populations, based on knowledge from a previous experiment (Merckx et al., 2021). In the absence of laboratory data on critical photoperiod, we selected the Mid-European photoperiodic regime based on citizen science phenological data for the species from both countries over a recent 10-year period, showing the final flight peak on 2 August in both Belgium and Czech Republic ([www.waarnemingen.be](http://www.waarnemingen.be) and <https://portal.nature.cz>). By choosing a 16L:8D photoperiodic regime, we targeted to obtain a mixture of directly developing and diapausing individuals in the control groups, which we achieved. In each climate room, each day began with 30 min of linearly brightening light conditions and ended with 30 min of linearly fading light conditions.

Date and nearest hour were noted when the experimental larvae were placed in the rearing cups, in which they were reared similarly to the previous generation. Final-instar larvae were checked at least twice a day, and the hour and date when the larvae burrowed into the peat for pupation were recorded. Five days after burrowing, pupae were excavated from the peat, weighed (Mettler Toledo MT5; precision: 0.01 mg) and sexed based on sex-specific genital scars. After pupation, each individual was kept under the same conditions as those experienced during larval development and monitored daily for eclosion for a minimum of 2 weeks. All individuals that did not eclose during that time and still appeared alive were considered to be in diapause. Monitoring of pupae concluded after no adults had eclosed for 6 days. We obtained developmental pathway information from 799 individuals (dataset: Merckx et al., 2023a).

## 2.2 | Data analyses

We analysed variation in probability of direct development with a GLMM fitted with the maximum likelihood method (Laplace approximation) by the function 'glmmTMB' (package 'glmmTMB'; Brooks et al., 2017) in R version 4.0.2 (R Core Team, 2020). Developmental pathway (1 for direct development; 0 for diapause) was set as the response variable, and we specified a binomial error distribution and a logistic link function. We set treatment (control/ALAN), environment of population origin (rural/urban), region (Mid-Europe/North-Europe), sex and all interactions among them as fixed effects, and family as a random effect. Model goodness-of-fit was confirmed by

a visual investigation of residual plots produced with the diagnostic tools in the package 'DHARMa' (Hartig, 2020).

Because the model predictions were essentially 0 or 1 for some combinations of fixed factors, Wald significance tests became unreliable due to inflated standard errors of model parameters. To overcome this, we ran a permutation test to derive empirical *p*-values for model parameters. We permuted the observations of the response variable to a random order 5000 times while keeping the explanatory variables unchanged, fitted the same GLMM to each of the permuted datasets, and saved the parameter estimates from each round to derive an empirical distribution for each parameter. We compared the parameter estimates based on the real data to the distributions derived from random data, and derived empirical *p*-values with the function 'ecdf'.

Due to the inflated standard errors of model parameters, it was not possible to derive confidence intervals for model predictions directly from the fitted model. Therefore, we used a bootstrap approach in confidence interval derivation. We took 5000 resamples with replacement from the original data, resampling being stratified so that the combinations of fixed factors defined the strata for resampling. The same GLMM was fitted to each of the 5000 datasets based on stratified resampling. The model did not converge for 1286 resampled datasets and these models were ignored in further considerations. From the 3714 converged models, we derived predictions for each combination of the fixed factors at the scale of the linear predictor with the function 'predict.glmmTMB' (Brooks et al., 2017). Then, we derived percentile confidence intervals for the estimates for each combination of the fixed factors by using the 0.025 and 0.975 quantiles of the factor-combination-specific bootstrap distributions of the predicted values as the lower and upper limits of 95% confidence intervals respectively. We used means of the bootstrap distributions as point estimates for each combination of fixed factors. Finally, we back-transformed the confidence limits and point estimates to the probability scale by using the inverse of the link function.

We repeated the above analysis both with the Dívčí Hradý population included and excluded, because whether this population is truly an urban population remains unclear (although only ~2 km away from Prague's city centre, and hence almost surrounded by urban areas, to the south-west it is directly connected to previously arable land converted into grassland in 2017). As the main conclusions were unaffected by this population, we present results from the analysis including all populations (Dívčí Hradý classified as urban) in the main text, while the results of analysis not including the Dívčí Hradý population are presented in Supporting Information (Table S2; Figure S2).

## 3 | RESULTS

We used a common-garden split-brood experiment to test whether the impacts of dim ALAN varied between urban and nearby rural populations from two North-European (Helsinki and Stockholm) and two Mid-European cities (Brussels and Prague; Figure 1). To

accommodate the strong latitudinal difference in critical photoperiod between North- and Mid-European populations, we raised Mid-European populations at a shorter photoperiod than North-European populations. Since we were unable to successfully sample a rural population near Stockholm, our urban–rural comparisons for the North-European region focus on the Finnish populations. We only retain the urban Stockholm population in a supplementary plot (Figure S2).

Using a GLMM, we tested how our ALAN treatments affected developmental pathway (diapause vs. direct development) in 691 F3-individuals from urban and rural populations from Belgium, Czech Republic and Finland. The ALAN treatment strongly increased the frequency of direct development, and distinctly more so in the Mid-European populations (Table 1; Figure 2; Figure S2). Specifically, the frequency of direct development increased from 40% to 68%,

**TABLE 1** Statistical model output explaining the probability of direct development. Fixed effects of a GLMM (with binomial error distribution and a logistic link function) explaining the probability of direct development in *Chiasmia clathrata* in relation to experimental artificial light at night (ALAN) in populations from rural versus urban environments within two regions (North-European vs. Mid-European) and for the two sexes. Empirical *p*-values were derived from a permutation test (see text for details) because inflated standard errors (not shown) rendered Wald tests meaningless. Significant *p*-values are depicted in bold. Sample sizes in different factor combinations are presented in Table S4.

Model parameter	Estimate	Empirical <i>p</i> -value
Intercept	−1.39	<b>0.0004</b>
Treatment (ALAN)	2.31	<b>&lt;0.0001</b>
Environment (Urban)	2.60	<b>&lt;0.0001</b>
Region (Mid-European)	−1.78	<b>0.0006</b>
Sex (male)	−0.430	0.24
Treatment (ALAN) × environment (Urban)	−0.750	0.18
Treatment (ALAN) × region (Mid-European)	25.0	<b>&lt;0.0001</b>
Environment (Urban) × region (Mid-European)	−1.60	<b>0.015</b>
Treatment (ALAN) × sex (male)	−1.06	0.10
Environment (Urban) × sex (male)	−1.08	0.094
Region (Mid-European) × sex (male)	0.928	0.099
Treatment (ALAN) × environment (Urban) × region (Mid-European)	0.848	0.20
Treatment (ALAN) × environment (Urban) × sex (male)	1.15	0.16
Treatment (ALAN) × region (Mid-European) × sex (male)	0.141	0.44
Environment (Urban) × region (Mid-European) × sex (male)	0.588	0.27
Treatment (ALAN) × environment (Urban) × region (Mid-European) × sex (male)	−1.39	0.16

averaged across the North-European populations, and from 14% to 100%, averaged across the Mid-European populations. The effect of ALAN was so strong on the Mid-European populations that no individuals entered diapause in this treatment. While strong evidence for an effect of our treatment, this lack of variation in the ALAN treatment limits our ability to interpret higher-order interactions of treatment with environment or region. Nevertheless, focusing on the factor combinations with <100% direct development, we did find a consistent difference between urban and rural populations (Table 1; Figure 2). In all cases, urban populations had significantly higher rates of direct development than corresponding rural populations, reflecting statistically clear genetic differentiation (Table 1; Figure 2). This urban–rural difference remained similar between the ALAN and control treatments (Table 1; Figure 2). We did not find a significant overall effect of sex, although there was a general trend towards higher diapause incidence in males. Because we were unsure whether the Dívčí Hrad population was truly an urban population, we repeated analyses removing this population, which led to almost identical results, with model predictions essentially remaining the same (Table S2; Figure S3).

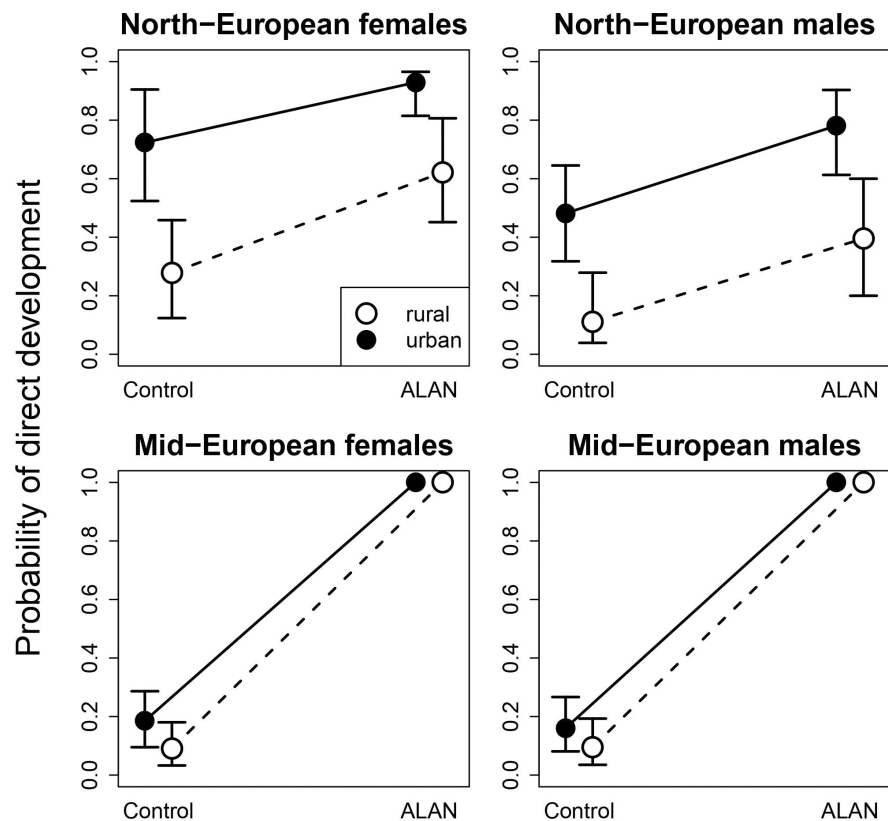
In addition to measuring diapause induction, we also measured larval development time and pupal mass (i.e. body size; Appendix S1). The ALAN treatment consistently resulted in a reduction of larval development time and a consistent but nonsignificant reduction of body size, independently of the developmental pathway, with both rural and urban populations responding similarly to ALAN (Appendix S1: Tables A1 and A2; Figures A1 and A2).

## 4 | DISCUSSION

Our large-scale common-garden experiment clearly demonstrates that indirect, dim ALAN greatly increases the probability of direct development compared to the same conditions with dark nights. Across seven populations from three countries, the impact of ALAN was much higher for mid-latitude populations than high-latitude populations (~50°N vs. 60°N, resp.), to the extent that no Mid-European individuals entered diapause when exposed to ALAN. This impact of our ALAN treatment occurred in both urban and rural populations, and we found no evidence that its impact differed between these populations, even though the baseline frequency of diapause was lower in urban populations (in line with adaptation to urban warming; Merckx et al., 2021). Hence, even low-intensity ALAN can avert diapause in *C. clathrata*, and given the severe fitness consequences of failing to enter diapause before winter, even dim light pollution is thus likely to create a developmental trap (Kerr et al., 2020; Van Dyck et al., 2015). Additionally, the ALAN treatment resulted in a reduction of larval development time and a small, but nonsignificant reduction in pupal mass, both independently of the urban–rural population origin and the induced developmental pathway. As such, *C. clathrata*'s widespread susceptibility to dim ALAN in terms of reduced diapause induction is likely to have strongly negative consequences for population viability, which may explain the drastic



**FIGURE 2** Probability of direct development by *Chiasma clathrata* individuals in relation to treatment (artificial light at night [ALAN] vs. control) and environment of origin (rural vs. urban). Top row shows probabilities for North-European populations and bottom row for Mid-European populations. Left column shows probabilities for females and right column for males. Probabilities (points) are means of bootstrap distributions based on stratified resampling and GLMM fitting (see statistical analyses for details), whiskers depicting 95% percentile CIs based on the same bootstrap distributions (note for ALAN-treated Mid-European populations that mean probability estimates and CI limits are all 1). Numerical values of the point estimates and their confidence limits are presented in Table S3.



reductions in observed abundance and distribution of this common, generalist species (Hällfors et al., 2021; Randle et al., 2019).

In addition to the effects we found on diapause, direct impacts of ALAN on physiology, development, movement, feeding and reproduction by insects have all been documented experimentally (Boyes et al., 2021a; Grubisic & van Grunsven, 2021; Kalinkat et al., 2021; Owens et al., 2020; Owens & Lewis, 2018; van Geffen et al., 2014, 2015; van Langevelde et al., 2017). Because of its negative consequences, light pollution is emerging as a major source of anthropogenic selection (Desouhant et al., 2019; Hopkins et al., 2018). Despite the potential for strong selection by artificial light, we found no evidence for adaptation to this selection by *C. clathrata* in urban areas: the ALAN treatment effect was not smaller for urban than for rural populations. Instead, we confirmed and generalized previous research indicating that urban populations have evolved reduced diapause induction to take advantage of the longer growing season created by the urban-heat-island effect (Merckx et al., 2021). The lack of evidence for urban adaptation to ALAN in our study could reflect an inability to rapidly adapt to light pollution—potentially due to insufficient genetic variation or stronger selection by other factors, such as urban warming. It could also reflect the pervasiveness of dim light pollution as an agent of selection; because skyglow can extend hundreds of kilometres from urban sources (Falchi et al., 2016a), both urban and rural populations are likely to be impacted by dim light pollution. Any associated adaptations should thus occur in both populations, which will thus not diverge in that regard. In the same vein, a recent study on the ermine moth *Yponomeuta cagnagellus* found that while ALAN negatively affected adult feeding and

sex pheromone signalling, adaptation to ALAN was absent (Cieraad et al., 2022). Nonetheless, suggestive evidence for adaptation to ALAN in flight-to-light behaviour exists in *Y. cagnagellus*: individuals from light-polluted areas are less likely to come to a light source (associated with high mortality risks: Longcore & Rich, 2004) than individuals from dark areas (Altermatt & Ebert, 2016).

Instead of finding differences between urban and rural populations in sensitivity to ALAN, we found strong differences in the effect of our ALAN treatment with latitude: the effect of ALAN on Mid-European populations was much greater than its effect on North-European populations. This smaller effect of ALAN at high-latitude environments may be because organisms at these latitudes are already adapted to naturally bright nights during spring and summer. If these populations have already evolved to perceive brighter conditions as night, they may be less sensitive to dim artificial light. This also seems to be the case in some songbirds, such as European robins and Common blackbirds, whose timing of dawn singing was less affected by light pollution at high than at lower latitudes (Da Silva & Kempenaers, 2017).

More taxa from different habitat types need to be tested to establish how common regional variation in sensitivity to light pollution is and the exact factors driving it, but, if widespread, latitudinal variation in sensitivity to light pollution has major implications for insect conservation. Abundance of *C. clathrata* appears to be declining sharply (Hällfors et al., 2021; Randle et al., 2019), as is the case for significant proportions of other (once-)common and widespread insects (e.g. Fox et al., 2021; Hällfors et al., 2021). Areas where relatively recent insect declines are most conspicuous are typically

characterized by multiple stressors occurring simultaneously, with the principal stressors being land-use and climate change, industrial agricultural practices, invasive species spread, nitrification and pollution (Wagner et al., 2021). Alongside these threats, light pollution could be a major contributor to these insect declines given this strong evidence of its disruptive impact (Boyes et al., 2021a, 2021b; Cardoso et al., 2020; Eggleton, 2020; Grubisic et al., 2018; Kalinkat et al., 2021; Owens et al., 2020; Sanders & Gaston, 2018; van Grunsven et al., 2020; Wagner, 2019), particularly in areas like nature reserves (e.g. Hallmann et al., 2017) where other anthropogenic pressures like pesticides and habitat loss are virtually absent, but where artificial light due to skyglow can be changing the night-time environment (Gaston, 2018). Support for this claim is evidenced by recent research showing that light pollution directly and indirectly reduces the abundance of macro-moths (Boyes et al., 2021b; Coulthard et al., 2019; Macgregor et al., 2017; van Grunsven et al., 2020; van Langevelde et al., 2018; Wilson et al., 2018). Variation in sensitivity to light pollution across regions means that its contribution to insect declines should likewise vary among regions, and its conservation importance in turn. In mid-latitude regions, where we demonstrated that populations are highly sensitive to ALAN (e.g. Mid-Europe), and where most global light pollution is concentrated (Falchi et al., 2016a), mitigating light pollution should be a high priority for insect conservation. In contrast, if further research generalizes our results that populations are less sensitive to light pollution in high-latitude regions (e.g. North-Europe), mitigating light pollution will still likely be important for these areas, but it may be less of a priority than other interventions to halt insect declines.

In cases where dim light pollution has detrimental effects on insect populations, mitigating its impacts should not only help halting global declines of insect populations, but should also improve the functioning of global food webs with impacts on ecosystem functioning that extend beyond nocturnal communities and outside illuminated areas (Davies & Smyth, 2017; Grubisic & van Grunsven, 2021; Sanders et al., 2021). Light pollution is known to not only impact insects (Owens et al., 2020; Owens & Lewis, 2018), but for example also plants and plant-insect interactions (Bennie et al., 2018; Knop et al., 2017; Macgregor et al., 2017). In turn, restored insect populations will allow for better ecosystem functioning and ecosystem services, with moths for instance being important prey items, herbivores, parasitoid hosts and pollinators (Fox et al., 2021). Given that marked reductions in extent and intensity of skyglow could already be achieved by simply limiting outdoor artificial lighting to places where it is required by people and to only necessary levels (Garrett et al., 2020), restoring the dark night sky should be considered low-hanging fruit as a conservation measure. As the main source of skyglow, cities have a key role to play in implementing these mitigation measures, such as motion-activated lighting, dimming protocols and banning light spots that are directed upwards (Gaston & Sánchez de Miguel, 2022; Kyba et al., 2014; Nguyen & Gupta, 2022). Because of the susceptibility we found to dim artificial light in both urban and rural populations, reducing urban skyglow will have benefits that extend far beyond the city limits.

## AUTHOR CONTRIBUTIONS

Thomas Merckx and Sami M. Kivelä conceived the research idea and designed the methodology; Tomáš Kadlec organized sampling in the Czech Republic; Thomas Merckx, Sami M. Kivelä, Tuomas Kankaanpää and Mahtab Yazdanian collected the data; Sami M. Kivelä analysed the data; Tuomas Kankaanpää provided the maps figure; Thomas Merckx, Matthew E. Nielsen and Sami M. Kivelä wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.866t1g1vc>

(Merckx et al., 2023a). R scripts of analyses available via the Zenodo Repository <https://doi.org/10.5281/zenodo.7661423> (Merckx et al., 2023b).

## ORCID

Thomas Merckx  <https://orcid.org/0000-0002-6195-3302>

Matthew E. Nielsen  <https://orcid.org/0000-0002-0388-1187>

Tuomas Kankaanpää  <https://orcid.org/0000-0003-3269-0299>

Mahtab Yazdanian  <https://orcid.org/0000-0001-8182-2142>

Sami M. Kivelä  <https://orcid.org/0000-0002-6844-9168>

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## SUPPORTING INFORMATION

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