The effect of artificial light at night on the biomass of caterpillars feeding in urban tree canopies

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Abstract

Alternation of day and night is the oldest cycle on Earth, which is increasingly disturbed by the accelerating rate of urbanization and technological development. Despite the ubiquity of light pollution in cities, many aspects of its influence on urban ecosystems are still poorly understood. Here we studied the effect of artificial light at night (ALAN) on the biomass of arboreal caterpillar populations, which are a major component of the diet of many insectivorous animals. We predicted that increasing ALAN intensity is associated with reduced caterpillar biomass, because ALAN may increase predation risk for both caterpillars and adult lepidopterans (i.e. moths), and can also hinder the moths' reproductive rate. We estimated caterpillar biomass from frass samples (n= 3061) collected from 36 focal trees in two cities in Hungary during four consecutive years. To quantify ALAN we measured light intensity during night at each focal tree (range of illumination: 0.69 – 3.18 lux). We found that caterpillar biomass of individual trees was repeatable over the four years. This temporal consistency in prey biomass production may be important for birds because it can help predict territory quality, especially in cities where caterpillar abundance is generally low. Our results did not support the negative effect of ALAN on urban caterpillar populations, because ALAN intensity was not related to caterpillar biomass, and this lack of effect was consistent between study sites and tree species. We suggest that the effect of ALAN on urban caterpillar biomass is either weak and thus can be masked by other, local environmental factors, or light pollution may have antagonistic effects acting during different stages of the lepidopteran life cycle. Another explanation could be that even the lower levels of our sites' public lighting are strong enough to cause serious detrimental effects for caterpillars, resulting in their uniformly low biomass.

Introduction

The day-night cycle is one of the oldest natural cycles on Earth. Most living organisms are influenced by light or its absence, hence the natural light-dark cycles are vital for them. Light pollution by artificial light at night (ALAN) alters this cycle. Although light pollution is a longstanding concern and the evidence for its wide-ranging negative effects on the biota is continuously mounting, the amount of ALAN is still increasing globally with an average of ca. 6% per year (0 to 20 % depending on location, Hölker et al. 2010; Gaston et al. 2013; Davies and Smyth 2018), mostly as a consequence of urbanization. The effects of ALAN can be observed at every level of biological organization: it affects cells (e.g. by disrupting circadian rhythm of cell division), individuals (e.g. by changing behaviour during orientation, reproduction or communication) and even communities (by affecting competition, predation), and it is also listed as a major threat to biodiversity (Woelfle et al. 2004; Rich and Longcore 2006; Hölker et al. 2010; Brown 2014; Knop et al. 2017).

ALAN can have particularly strong effects on nocturnal organisms that are attracted to light sources, such as adult lepidopterans (Schacht and Witt 1986; Simon and Bradstreet 1991; Eisenbeis and Hänel 2009), potentially disturbing all aspects of their life cycle. For example, light pollution negatively affects moth reproduction via multiple mechanisms: it can inhibit the release of female sex pheromones (Sower et al. 1970; Van Geffen et al. 2015), and it is also likely to disrupt mate finding behaviour when males favour approaching light sources over the pheromone signals of females (Delisle et al. 1998). Furthermore, ALAN can also suppress oviposition (Nemec 1969), inhibit pupal diapause and reduce the size and age at the pupation of caterpillars (Van Geffen et al. 2014), ultimately resulting in their decreased fitness. The predation rate of moths (by bats, birds and predatory arthropods) also can be higher near light sources, for at least two reasons. First, because high density of prey attracts higher number of predators (Simon and Bradstreet 1991; Rydell 1992), and second, because ALAN hinders moths' defensive behaviour against bats by impeding the moths' ultrasound detection and emittance, leading to increased susceptibility to bat predation (Acharya and Fenton 1999). Light sources in cities artificially increase the length of natural photoperiod which in turn has been demonstrated to greatly increase larval growth rates – however, fast-growing larvae were also significantly more prone to predation, revealing a trade-off between growth rate and predation risk (Gotthard 2000). Additionally, birds residing at more illuminated territories have prolonged daily activity periods (Tarlow et al. 2003; Dominoni et al. 2013, 2014) which might lead to increased foraging times, thus elevated predation rates on moths and caterpillars. Combined together, these ALAN-induced processes can greatly contribute to the local and regional decline of lepidopteran populations. For example, in Germany during a single summer the number of moths killed by light sources was estimated to reach the scale of 10^{11} (Bauer 1993).

Despite the obvious negative effects documented in some populations (see above), other studies argue that ALAN does not necessarily have a strong influence on lepidopterans. For example, a study comparing natural (ALAN free) and urban populations of the small ermine moth (*Yponomeuta cagnagella*) found that urban populations living under long term exposure to ALAN are less attracted to light sources, perhaps as a consequence of an adaptive response (Altermatt and Ebert 2016). Similarly, the experiment of Van Grunsven et al. (2014) demonstrated that, when released from the close proximity of an artificial light source, almost 75% of moth individuals (including different species) were not attracted by the experimental light source. The spectral composition of the emitted light is also very important, as lamps emitting shorter wavelengths (around 380 nm, i.e. blue and violet) attract significantly more moths (species and individuals alike) than light sources with longer wavelengths (617 nm, i.e. red; van Langevelde et al. 2011). The severity of ALAN's impacts on nocturnal moth communities varies considerably between studies, as it depends on factors like species composition of local communities (because susceptibility to light pollution differs between moth taxa; van Langevelde et al. 2011; Van Grunsven et al. 2014) and local characteristics of the natural and artificial light circumstances (Eisenbeis and Hänel 2009).

These studies clearly illustrate the complex and diverse effects of ALAN on lepidopterans; thus, to get a better understanding on its actual impacts, it is necessary to conduct more studies in different environments, on more species and communities, involving different stages of the lepidopteran life cycle. As the significant majority of ALAN comes from urban areas, it is important to explore the impacts of light pollution on lepidopterans in our built-up environment. Furthermore, although several studies tested the effects of ALAN on adult moths, relatively few studies focused on their larvae, the caterpillars, and these produced contrasting results. Welbers et al. (2017) studied the effect of ALAN in a deciduous forest, with experimentally altering light conditions by street lamps emitting different colours of lights. This study found significantly higher peak caterpillar abundances in trees with green and white light than with red light or without light. Van Geffen et al. (2014), by contrast, found a negative effect of green and white light on the development of caterpillars: male caterpillars had lower body mass and pupated earlier than under red light or dark treatments. A third study found that the length of the illumination can also have influence on the abundance of caterpillars, because of its effect on the level of predation by predatory insects Gotthard (2000).

Caterpillars are important food items for several insectivorous bird species occupying urban habitats (e.g. great tit *Parus major*, blue tit *Cyanistes caeruleus*, Naef-Daenzer and Keller 1999) and for predatory arthropods (Ferrante et al. 2014), while at their imago life stage they are preferred preys of urban-dwelling bat species (e.g. common noctule *Nyctalus noctule* or common pipistrelle *Pipistrellus pipistrellus*; Rydell 2006), and also play an important role as pollinators (Macgregor et al. 2015). Therefore, in this study our aim is to investigate the effect of artificial light at night on tree-dwelling caterpillar populations in urban areas. Due to the various negative effects that ALAN can exert on both adult moths and caterpillars (see above) we predict decreased caterpillar biomass on trees that are exposed to higher intensity of ALAN. To explore the relationship between caterpillar biomass and light pollution, we collected data on caterpillar biomass from several tree species throughout four consecutive years (2014-217), from two cities with differing urban environments.

Materials and methods

Study sites and selected tree species

We conducted our study in two cities in Hungary, Balatonfüred (46°57'30"N, 17°53'34"E) and Veszprém (47°05'17"N, 17°54'29"E). Both cities are characterized by typical urban vegetation, i.e. maintained green areas such as public parks, street tree lines, and suburban gardens. However, the two urban sites differ in their intensity of urban development: the study site in Balatonfüred is an urban park with continuous and relatively dense vegetation, and typically has detached, single-storeyed houses, whereas the study site in Veszprém consists of more roads, impervious surfaces and apartment blocks, and scattered patches of less dense vegetation (Electronic Supplementary Material, Fig S1). Following the study setup of Seress et al. (2018) we identified the three most common tree species in each study site (by field survey conducted in 2013) and selected six individual trees per species as focal individuals (n=18 trees in Balatonfüred and n=18 in Veszprém; see ESM, Fig. S1). We used these focal trees for caterpillar biomass monitoring and light intensity measurements (see below). In Balatonfüred, the selected tree species were small-leaved lime (*Tilia cordata*), sessile oak (*Quercus partea*) and Norway maple (*Acer palatanoides*), whereas in Veszprém we chose silver linden (*Tilia tomentosa*), horse-chestnut (*Aesculus hippocastanum*) and Norway maple. The rationale behind this sampling strategy was to estimate caterpillar abundance as experienced by foraging birds (Seress et al. 2018). Furthermore, the sampling of the most common tree species at each study site increased our chance to get a general picture on urban caterpillar abundance and its response to ALAN intensity for each site, compared to a sampling regime that would focus on a single common tree species at both sites (e.g. the Norway maple). The trees in our two urban locations are characterized by significantly lower level of caterpillar abundance than forest trees, and this result of low amount of caterpillars is consistent with the findings of several other studies (see Seress et al. 2018 for a detailed discussion of caterpillar biomass in urban areas).

Caterpillar biomass

To quantify arboreal caterpillars' biomass, we used the commonly applied frassfall method (Tinbergen and Dietz 1994) and collected frass (insect droppings) samples from our focal trees. The method has been described in detail in Seress et al. (2018), here we summarize it only briefly. From February, we monitored the leaf emergence phenology individually for each focal tree and started sampling frass when >50% of the buds had emerged and the shape of the leaves was clearly recognizable. We suspended frassfall traps (cheese cloth net attached to a 0.5 x 0.5 m wooden frame) under the canopies of the focal trees (one trap per tree) and collected frass samples from the traps every 3-5 days (depending on the prevailing weather conditions) between March and June in four consecutive years (from 2014 to 2017). This sampling period corresponds to the breeding season of great tits and several other insectivorous birds for whom caterpillars provide the main component of nestling diet. The collected frass samples were dried at room temperature (additional drying was not required, for further details see Seress et al. 2018)), sorted (i.e., debris and powder removed) and weighed to the nearest mg. From the dry frass mass and temperature data (recorded by weather loggers (Voltcraft DL 101T) throughout the whole sampling period) we calculated caterpillar biomass expressed as hourly caterpillar biomass ($mg/h/0.25m^2$) using the equation of Tinbergen and Dietz (1994). From Balatonfüred we had 397 (2014), 447 (2015), 390 (2016), 296 (2017) frass samples and from Veszprém 386 (2014), 429 (2015), 404 (2016) and 312 (2017) samples.

Because canopy volume above the frassfall traps can directly affect the amount of frass production, and canopy height is usually correlated with canopy volume (Troxel et al. 2013), we estimated the height of each focal tree's canopy (to the nearest m) to control for the potential differences in canopy height (for further details of the field methods see Seress et al. 2018). Because vegetation density in the surroundings of our focal trees can also influence caterpillar abundance (Blair and Launer 1997), to control for this variable, we also calculated the percentage of area covered by tree canopies in the 30 m radius of each focal tree (henceforth 'canopy cover') from orthophotos taken in 2015 using the QGIS software (QGIS Development Team 2016).

Night light intensity measurements

We characterized the focal trees' night light regimes by conducting light intensity measurements in 2017, between 12 January and 8 April, intentionally before foliage development, to avoid the shading effect). The public lighting system in our study area consists mostly of high-pressure sodium lamps (HPS lamps with orange light, i.e. a narrow emitting spectrum peaking around 600 nm), both on streets and in park areas, with only a small fraction of the surveyed light sources being LED lights (three lamps, 6% at Veszprém, and none at Balatonfüred). Given that there were no significant changes in the physical structure (e.g. number of buildings, roads and density of vegetation) and street-lighting system of our study sites between 2014 and 2017, we assume that our focal trees' night light environment did not change between the study years. We recorded the level of ALAN (in lux) during one whole night for each focal tree with a purpose-built, calibrated light-logger (for its detailed description see ESM, 'Additional details on methods: light logger description') which was suspended in the focal tree's canopy at 2.5-3 m above ground and ca. 1.5-2 m from the tree trunk in order to reduce the shading effect. The logger had three sensors around its perimeter, enabling us to detect light sources from every direction, and each sensor recorded light intensity every second (range of sensitivity: $188*10^{-6}$ – $88*10^{3}$ lux). Light intensity measurements were conducted during the astronomical night (i.e., when the center of the Sun is below the horizon with 18 degrees; starting and ending times were determined separately for each date from the timeanddate.com database, Time and Date AS © (www.timeanddate.com). The very high number of recordings per tree [mean ± SE = 17755 ± 2799, range: 12999 – 20821] yielded a detailed picture of the ALAN regimes for each focal tree (for visualised light intensity recording examples see: ESM, Fig. S2). To characterize ALAN intensity for each focal tree, we used the mean light intensity calculated as the mean of all recordings of the three sensors.

To assess the validity of our light intensity measurements, we performed two sets of analyses. First, to test the repeatability of the light-logger's recordings, we selected five test points in our study site in Veszprém and conducted five repeated light measurements on each of them (i.e. during 25 consecutive nights) as follows. After each night (measurement) the light-logger was relocated to a different test point, and after one set of measurements (i.e. one measurement per each point, 5 nights), we again hung the logger to the first test point to start the next set of measurements. We found that the mean light intensity values were highly repeatable between these consecutive measurements (intra class correlation, using the R '*ICC*' (Matthew and Maintainer Matthew 2015) and function ICCest, r_{ICC}= 0.84; CI: 0.62 – 1.05; N=5, k=5), indicating that the variability of measured light levels on the same tree was much lower than the variability between trees. Additionally, to test if there was any consistent bias in the mean values of the repeated measurements (e.g. due to a several days long cloudy period followed by a several days long moon-lit period), we built a linear mixed-effects model (LME, using the function 'lme' of the package '*nlme*'; Pinheiro et al. 2014)that contained mean light intensity as dependent variable, measurement set ID as a fixed five-level factor and test point ID as a random factor. This model indicated no significant differences between the repeated measurements (F=2.02, df=16, p=0.14). Because of the high repeatability of measurements, we decided to record light intensity for only one night for each focal tree to describe the intensity of ALAN in their surroundings.

Second, after sunset we surveyed the number of artificial light sources (street lamps and household light sources) within the 25 m radius around each focal tree, and tested the correlation between the number of light sources and the mean light intensity values recorded by the light-logger (see above). The rationale behind using an area of 25 m radius for the light source survey was that a street lamp is typically capable to illuminate its immediate surrounding area with 5 lux (corresponding to the Hungarian recommendations for outdoor lighting; Arató 2003), and light intensity drops close to zero at 25 m distance from the source. Our survey indicated that the number of artificial light sources ranged between 0 – 9 per focal tree within 25 m (ESM, Fig. S2), and the number of light sources was significantly and positively correlated with light intensity recorded by our light-logger for the same focal trees (Kendall's rank correlation, τ=0.365, p<0.01, n= 36 trees).

Statistical analyses

We tested the repeatability of caterpillar biomass measured on the focal tree individuals across the four study years using a generalized linear mixed-effects approach as implemented by the 'rpt' command of package '*rptR*' (Nakagawa and Schielzeth 2010). In this model the dependent variable was the log transformed mean amount of caterpillar biomass (mg/h/0.25m^2) of individual trees calculated for each year separately, the predictors were the year of sample collection (as a factor) and the tree species, and the random factor was the trees' ID.

Because the urban habitat characteristics of the two sites differed markedly (see study site descriptions above), we compared the ALAN regimes between the study sites. In order to do so, we compared the mean light intensity values measured for individual trees by a Mann-Whitney U Test, due to the non-normal distribution of the data.

Finally, we investigated the relationship between mean night light intensity and caterpillar biomass in an LME model. In the initial model, caterpillar biomass ((mg/h/0.25m^2 values were log-transformed using the formula $\log_e(x+0.0001)$) was the dependent variable (using the mean value of each tree from each sampling year, i.e. the annual mean biomass of each individual tree), while predictors were mean light intensity, study site, year of sample collection (as a factor), tree species, canopy height and canopy cover. The model also included the light intensity × study site and light intensity × tree species interactions and tree ID as random factor. Our idea behind testing the light intensity × study site interaction was that light pollution could have different effect on the two study sites' caterpillar populations because of their different habitat characteristics. We tested the light intensity × tree species interaction because different tree species may have different caterpillar fauna that could have different responses to ALAN. The initial model was reduced by backwards stepwise model selection, excluding the term (interaction or main effect) with the highest P-value in each step until only significant ($p<0.05$) terms remained. Additionally, by conducting pairwise *post-hoc* tests (using the emmeans function from the '*emmeans*' package; (Lent 2018) we also compared the mean caterpillar biomass (with Tukey method) between tree species and sampling years as estimated from the results of the final LME model. Because of the spatial structure of our sampling locations both within and among sites, we built an additional model to test spatial autocorrelation using the package '*ncf*'(Bjornstad 2019). We controlled for spatial autocorrelation by updating our LME models described above with data on the spatial coordinates of the trees. All statistical analyses were performed in the R statistical environment (R Core team 2018).

Results

We found that focal tree individuals consistently differed in their caterpillar biomass production: the repeatability of caterpillar biomass of individual trees across the four years was low but statistically significant ($R= 0.279$, $p< 0.001$).

Mean night light intensity and its standard deviation in the canopy of trees was 1.52 ± 0.79 lux (range: 0.69 – 3.18 lux) in Veszprém, whereas tree canopies in Balatonfüred were darker, with a mean value and standard deviation of 0.76 ± 0.1 lux (range: 0.68 – 1.05). The difference between the two sites was statistically significant ($W = 295$, $p< 0.01$, Mann-Whitney U Test).

Caterpillar biomass was not related to the night light intensity measured on the same focal trees (Table 1), and this lack of effect seems robust. First, light intensity was unrelated to caterpillar biomass when the two study sites were analysed together in a model that controlled for the effects of potential confounding variables (Table 1, Fig. 1). Second, we got similar results when the two study sites were analysed separately (ESM, Table S1). Third, the light intensity × study site and light intensity × tree species interactions were non-significant (Table 1), indicating that the relationship between light intensity and caterpillar biomass did not change between sites or between different tree species. In our final LME model, only tree species and study year had significant effects on caterpillar biomass (Table 1). Similarly, light intensity was consistently unrelated to caterpillar biomass when we analysed the tree species separately (ESM, Table S2). The pairwise *post-hoc* comparisons indicated that sessile oaks supported the highest caterpillar biomass, differing significantly from every other tree species, except for the silver linden (ESM, Table S3; Fig. S3). The pairwise *post-hoc* comparisons between years showed that caterpillar biomass was significantly lower in 2016 compared to all other years (ESM, Table S4; Fig. S4), but it did not differ significantly between the other years. We detected spatial autocorrelation in the data in both locations, but caterpillar biomass remained unrelated to light intensity in the models that controlled for this effect (ESM, Table S5).

Discussion

Light pollution is a global environmental problem to which a broad range of organisms are very sensitive. Here we used correlational data from two urban study sites to explore whether ALAN influences the population sizes of arboreal caterpillars that play important roles in many ecosystems including forested urban areas. Although ALAN is thought to have various impacts on both adult and larval lepidopterans (see Introduction), we found no strong effects of light pollution on local caterpillar abundances. We believe this result is robust for several reasons.

First, our analyses produced consistent conclusions between two urban sites and between different tree species. In both study sites, the range of light intensity values we recorded (0.68 – 3.18 lux) were within the expected and recommended outdoor street lighting levels(Arató 2003; Fotios and Goodman 2012). Another study investigating the effect of ALAN on avian reproductive physiology used the same lighting range to mimic urban night light conditions (Dominoni et al. 2013). Light intensity levels (mean lux values) differed significantly among our study sites, which can be explained with the size and the structure of the two cities: Veszprém is larger and the distribution of sampled trees in the city is more scattered, thus trees are more exposed to street lights. In Balatonfüred all sampled trees were in a continuous, central park region where street lighting has lower intensity and the vegetation is denser. Despite this difference between the two study sites in lighting levels, the effect of ALAN was consistently non-significant in both cities.

Second, we found that the caterpillar biomass of individual trees was significantly repeatable across the four study years. Considering the dependence of caterpillar biomass on the climatic conditions (Reynolds et al. 2007) and also that environmental conditions often strongly fluctuate between years, this detectable consistency within individual trees is remarkable. The repeatability cannot be explained by differences between tree species, since we controlled for that effect in the analysis. Our results also do not support that it is simply related to canopy height and canopy cover, since these factors did not influence the measured caterpillar biomass in our study sites. It may be explained, however, by other tree traits like age, or nutritional and immune state (Kaitaniemi and Ruohomäki 2001; Howe and Jander 2008) that we did not assess in our study. This year-to-year consistency in prey biomass of individual trees may be important for birds and other predators of arboreal caterpillars because it can help them to predict territory quality, especially in urban environments where caterpillar abundance is generally low.

For the lack of association between light pollution intensity and caterpillar biomass in our study system there are several possible explanations. One potential reason can be that other environmental and ecological factors that we were not able to control for could have masked ALAN’s effects, by having stronger impacts on caterpillar biomass than the recorded variation in ALAN. One such environmental factor is the altered urban vegetation, including the presence of non-native species that replace caterpillars’ original host plants (Burghardt et al. 2010), as well as variation in vegetation structure, since denser or more open parts of the canopies provide different habitat qualities for caterpillars (Roland 1993; Dulaurent et al. 2011). Further possible detrimental effects may result from intensive urban vegetation management practices, like frequent mowing of grass and removal of leaf litter (typical in our study sites), as these activities reduce the availability of suitable locations for caterpillars to pupate. Furthermore, local microclimate, which depends on multiple factors, can also have great influence on caterpillar abundance (Casey et al. 1988; Moore et al. 1988; Savilaakso et al. 2009) and may be highly variable within cities. The health status of trees (Miller et al. 2006; Dale and Frank 2014) and as a consequence their nutrition content or resistance ability against herbivores (Kaitaniemi and Ruohomäki 2001) is also among the important caterpillar biomass determining factors, just like the local predation pressure (Kozlov et al. 2017). All of these diverse factors could affect microhabitat quality to a different extent and their interactions may further increase the small-scale spatial heterogeneity.

Another possible explanation for the absence of ALAN's effect on caterpillar biomass is that light pollution could have antagonistic effects on the same lepidopteran populations, e.g. during their different life stages. For example, while ALAN has many potentially detrimental effects on adults (moths, see Introduction), it could have some beneficial effects during the larval stages. For example, ALAN could positively affect caterpillars' development directly, by accelerating larval growth rates (Gotthard 2000) or indirectly, via enhancing host plant quality as a food source (Ouzounis et al. 2015), either by increasing plants' growth rate (Cathey and Campbell 1975), or seasonally advancing the timing of budburst (Ffrench-Constant et al. 2016). A recent study conducted in an oak forest found that green and white LED light has a major positive effect on local caterpillar biomass compared to plots with red light or no artificial illumination (Welbers et al. 2017). Interestingly, the effect of ALAN on peak caterpillar biomass was prominent only at the study site with highest caterpillar abundance and not in other study sites with evergreen vegetation and much lower caterpillar abundance. To which extent could be these results generalized in urban ecosystems, is an open question however, as in many cities (including our study sites) HPS lamps, producing orange light, are the most common public light sources, and several studies reported significantly lower caterpillar biomass in urban compared to forested areas (reviewed by Seress et al. 2018) – these differences might all contribute to that we did not find any apparent effect of artificial light pollution on caterpillar biomass.

In our analyses, tree species was a significant predictor of caterpillar biomass, and other studies also showed that e.g. oak species in general support higher amounts and diversity of phytophagous arthropods compared to other tree species (Csóka 2004), similarly to that we have found here. Thus, it is also possible that our sampled tree species differ in their local moth faunas, and the variability in different moth species' responses to ALAN result in that we found no overall relationship when all trees species were analysed together. Our results do not support this theory, however. We did not find a significant interaction effect between light intensity and tree species on caterpillar biomass (Table 1), and the effect of light intensity was also non-significant for any of the sampled tree species, including oaks, when these were analysed separately (ESM, Table S2). Our knowledge on the Hungarian moth fauna further supports this conclusion, because usually only a few common species contributes to the major part of the annual moth biomass (Valtonen et al. 2017).

It is important to note that in our case even the lowest recorded lux values (0.68 lux at site Balatonfüred) were still at least 6 times brighter than natural night light conditions. Thus, a further explanation for our results could be that even very low levels of public lighting (e.g. similar to the lower values of the range in our survey) are strong enough to cause serious detrimental effects in arboreal caterpillar populations, resulting in uniformly low caterpillar biomass on urban trees.

Finally, it is also possible that the abundance of caterpillars in urban areas is less responsive to ALAN intensity than we previously thought. Local caterpillar abundances are strongly depending on the behaviour of adults, and several studies imply that not all moth species are sensitive to light or light pollution (e.g. see van Langevelde et al. 2011; Van Geffen et al. 2014; Altermatt and Ebert 2016). This idea is also supported by the review of Fox (2013) that investigated the potential causes of declines in moth populations in Great Britain, and failed to find any direct evidence for ALAN being a major cause. Furthermore, perhaps urban moth populations are less susceptible to light pollution either due to the differences in species composition between urban and non-urban lepidopteran communities (New 2015; Lizee et al. 2016), or due to local adaptations to the urban habitats (i.e. if the individuals most sensitive to ALAN are selected against). In line with these assumptions, a recent study found that individuals from urban moth populations living under an increased exposure to ALAN for a long time are significantly less attracted by light sources compared to individuals from pristine populations (Altermatt and Ebert 2016).

In summary, our results show no significant effect of ALAN on urban caterpillar biomass, suggesting that other ecological factors are more important drivers of variation in caterpillar abundance in cities – thus, their effects should be investigated in more detail. However, we feel important to note that our conclusions are based on correlational results, and this approach may have limited power for detecting the effect of ALAN either due to various confounding environmental factors or due to possible antagonistic effects of light pollution (see above). To have a clearer knowledge on how and to which extent light pollution affects urban caterpillar populations we would definitely need more experimental studies, for example in which ALAN intensity is experimentally manipulated around urban trees.

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Compliance with Ethical Standards

Our research did not involve any experiments on human participants or on animals. All procedures were in accordance with Hungarian laws, licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission numbers: 31559/2011 and 24861/2014). We have no conflict of interest.

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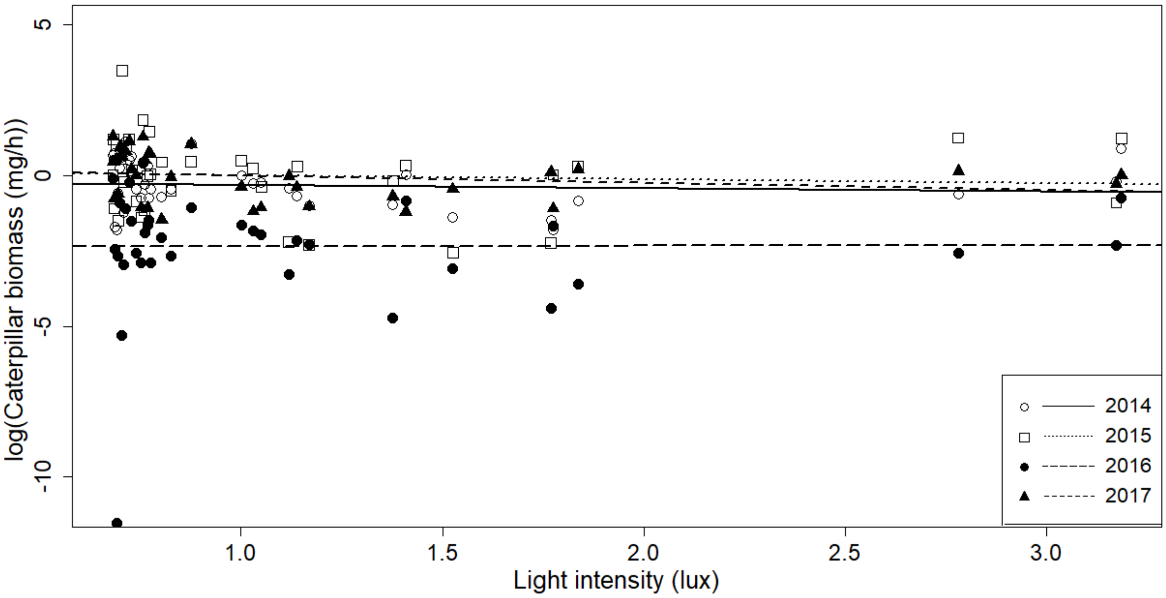
Table 1

Results of the (a) full and (b) final LME models for caterpillar biomass (log[mg/h/0.25m^2]). The final model includes only the significant variables (highlighted by bold).

(a) Full model	**numDF**	**denDF**	**F-value**	**p-value**
(Intercept)	1	105	0.446	0.51
Light intensity	1	23	0.101	0.75
Year	3	105	38.693	**<0.0001**
Tree species	4	23	10.111	**<0.0001**
Light intensity x Tree species	4	23	1.221	0.33
Canopy height	1	23	2.379	0.13
Canopy cover	1	23	0.642	0.43
Study site	1	23	0.002	0.96
Light intensity x Study site	1	23	0.097	0.76
(b) Final model				
(Intercept)	1	105	0.018	0.89
Year	3	105	38.693	**<0.0001**
Tree species	4	31	11.824	**<0.0001**

Fig.1 Scatterplot showing the relationship between light intensity and caterpillar biomass (log [mg/h/0.25m^2]), points showing up as mean values of focal trees per year, with regression lines illustrating the direction of the trends separately for the four years.



Electronic supplementary material

The effect of artificial light at night on the biomass of caterpillars feeding in urban tree canopies

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Keywords: artificial light at night, light pollution, caterpillar abundance, frass, urbanization, birds

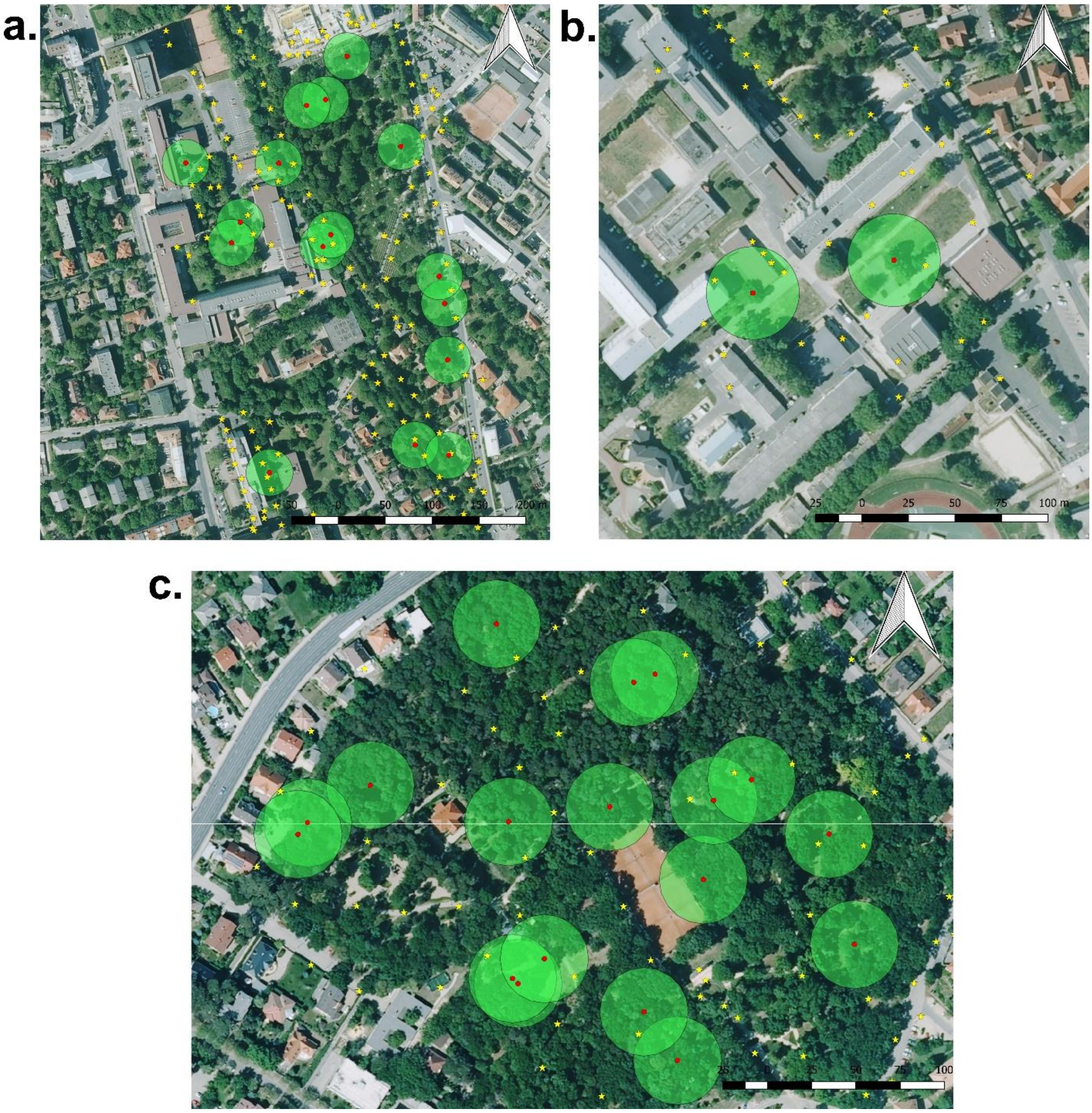

Fig. S1 Examples of maps of the study sites with the sampled trees (red dots), their 25m radius (green circles) and the light sources trees (yellow stars). (a) Veszprém: park, cemetery, university lower campus, (b) Veszprém: university upper campus, and (c) Balatonfüred: park.

Additional details on methods: light logger description

To estimate ALAN intensity to which arboreal caterpillars are exposed on our focal trees, we used a purpose-constructed light-logger containing three High Dynamic Range Digital Light Sensors (TSL2591, Adafruit, USA, for detailed description of the sensor see: https://www.adafruit.com/product/1980) facing three directions on the instrument, closing 120° angle with each other. The light-logger also contained a real time clock (Maxim Integrated: DS3232, for the detailed data sheet see: https://datasheets.maximintegrated.com/en/ds/DS3232.pdf). Recorded data was saved to a micro SD card, and the device was powered by four 3.7 V lithium ion batteries. The light-logger recorded data every 2 seconds in clockwise circular alternation.

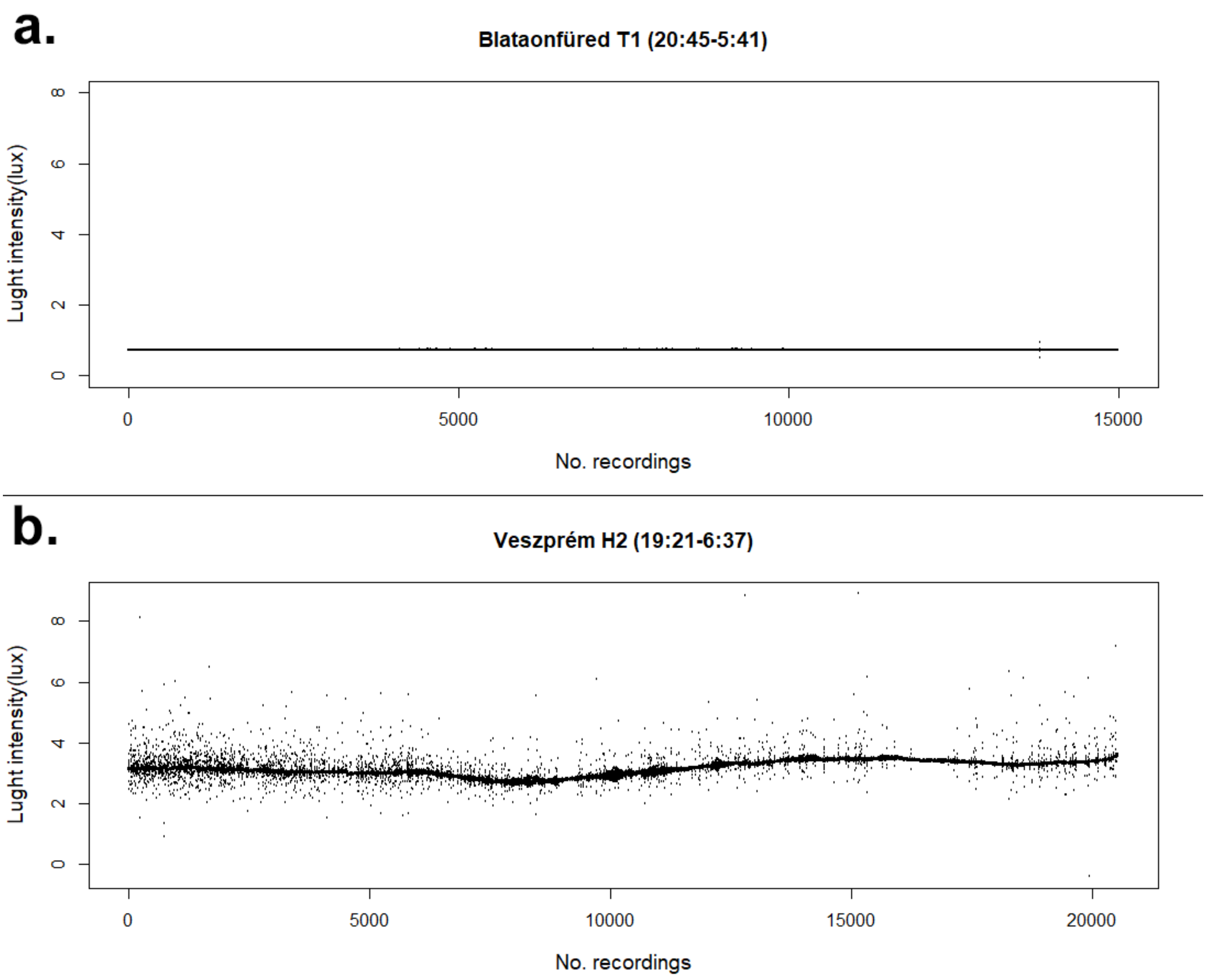

Fig. S2 Two visualized light intensity measurement examples typical to the study sites. At (a) Balatonfüred we recorded constantly lower values of light intensity, whereas at (b) Veszprém the overall light intensity and the variance was higher in the majority of the focal trees.

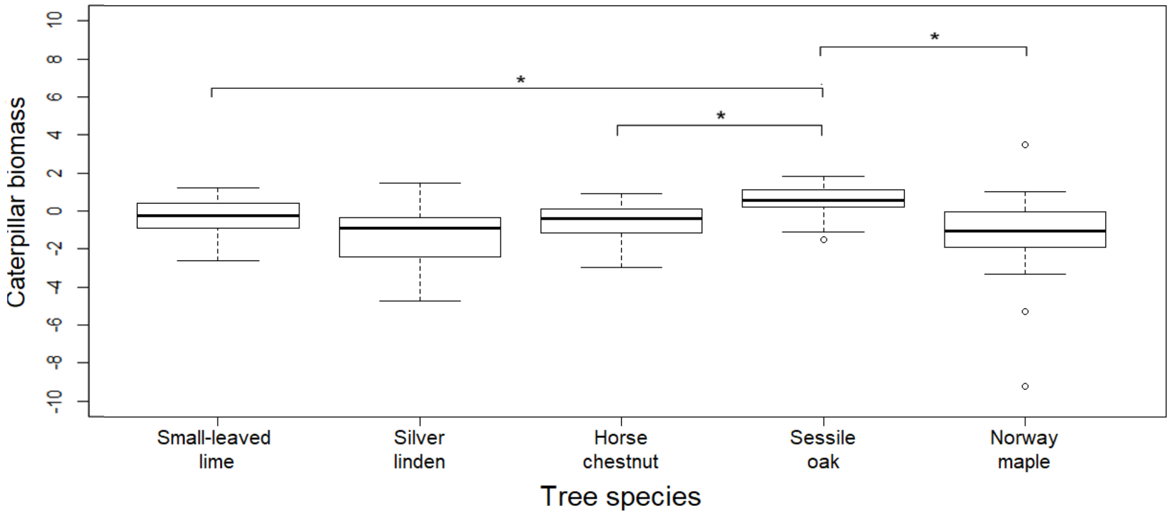

Fig. S3 Pairwise *post-hoc* comparisons of caterpillar biomass (log (mg/h/0.25m^2)) between tree species. Lines above the boxplots indicate statistically significant ($p< 0.05$) differences. Medians and interquartile ranges are indicated by the thick middle lines and the boxes, respectively.

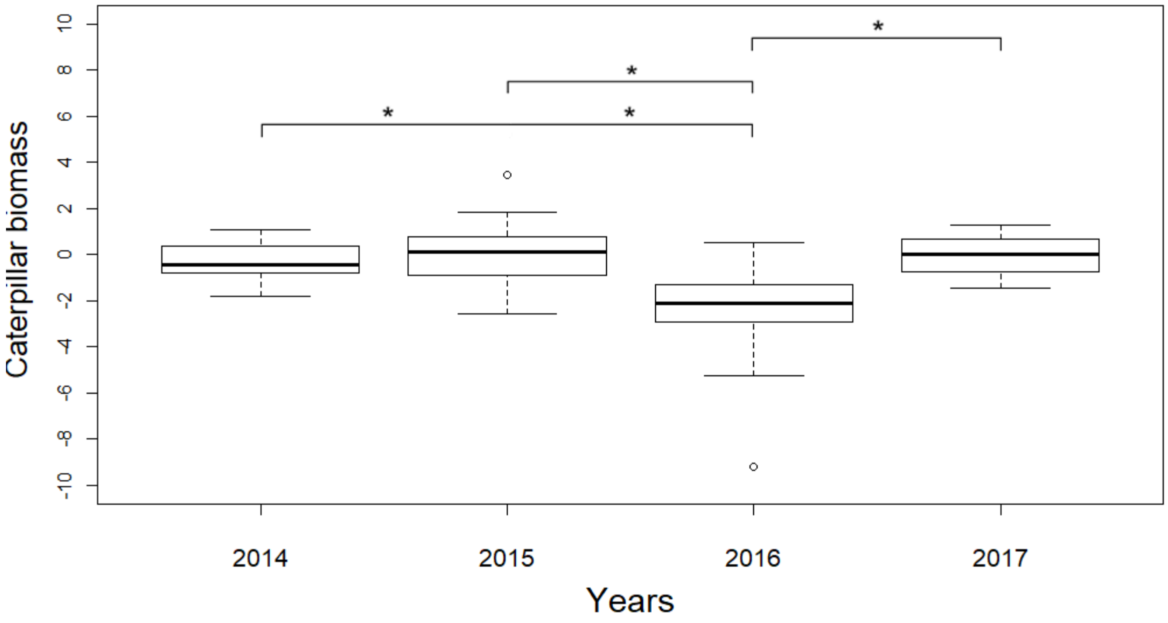

Fig. S4 Pairwise *post-hoc* test results in caterpillar biomass (log[mg/h/0.25m^2]) between study years. Lines above the boxplots indicate statistically significant ($p< 0.05$) differences between groups. Medians and interquartile ranges are indicated by the thick middle lines and the boxes, respectively.

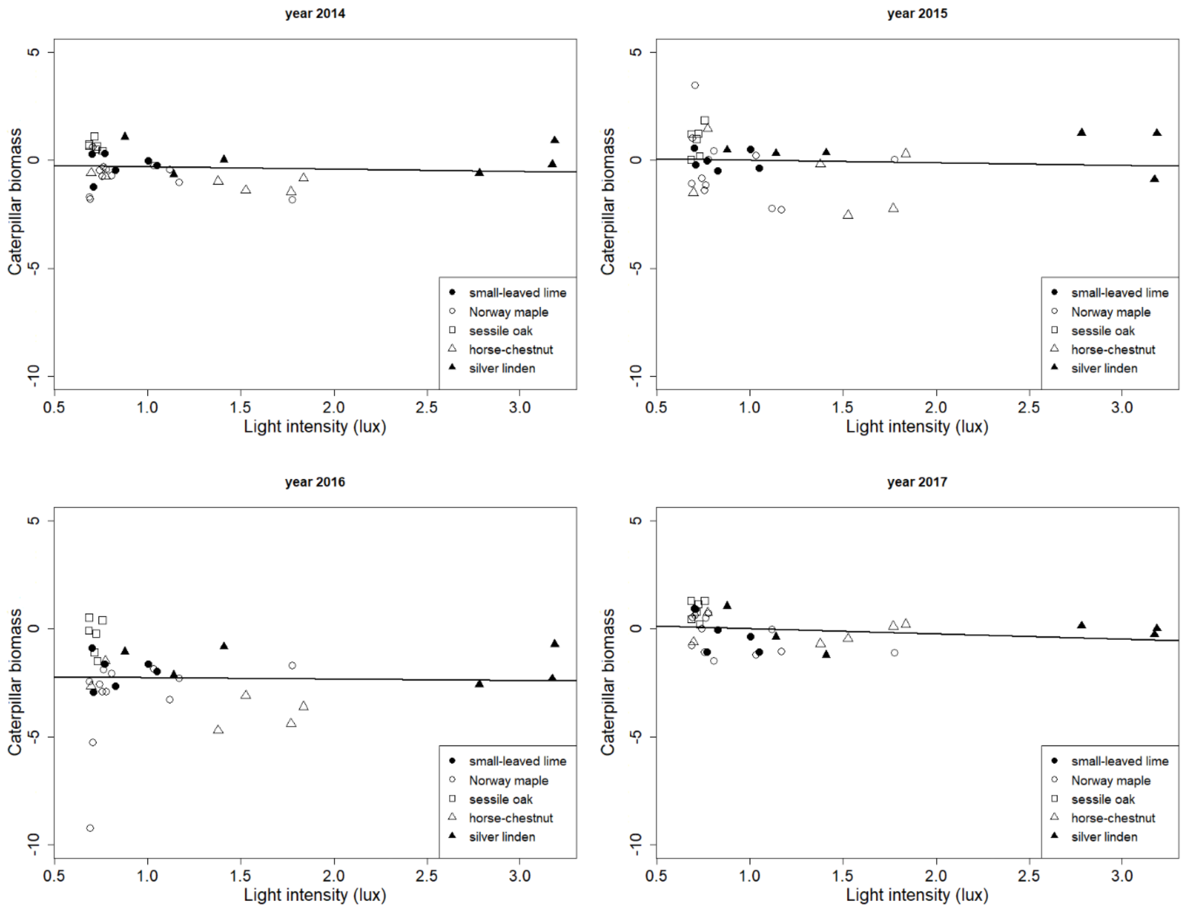

Fig. S5 Scatterplot showing the relationship between light intensity and mean values of caterpillar biomass (log(mg/h/0.25m^2)) of sampled tree individuals, separately for each study year. The regression lines are from LME models, illustrating the direction of the trends, and tree species are represented by different symbols. See Table S2 for separate analyses of the different tree species.

Table S1. The results of initial (full) and final linear mixed-effects models testing the relationship between caterpillar biomass (log[mg/h/0.25m^2]) and mean night light intensity, when the two study sites, (a) Balatonfüred and (b) Veszprém were analyzed separately. Statistically significant ($p<0.05$) effects are highlighted by bold.

(a) Balatonfüred				
Full model	numDF	denDF	F-value	p-value
(Intercept)	1	51	1.275489	0.264
Year	3	51	17.1987	**<0.0001**
Tree species	2	10	0.39333	0.684
Tree species x Light intensity	2	10	0.331593	0.725
Canopy height	1	10	1.491848	0.249
Canopy cover	1	10	1.927764	0.195
Light intensity	1	10	0.546728	0.476
Final model				
(Intercept)	1	51	0.553931	0.460
Year	3	51	17.25676	**<0.0001**
Tree species	2	15	12.36121	**0.001**

(b) Veszprém				
Full model	numDF	denDF	F-value	p-value
(Intercept)	1	51	1.147	0.289
Year	3	51	25.374	**<0.0001**
Tree species	2	10	0.055	0.947
Tree species x Light intensity	2	10	1.24	0.330
Canopy height	1	10	1.951	0.193
Canopy cover	1	10	0.002	0.962
Light intensity	1	10	0.756	0.405
Final model				
(Intercept)	1	51	0.038	0.847
Year	3	51	25.374	**<0.0001**
Tree species	2	15	5.217	**0.019**

Table S2. The results of linear mixed-effects models testing the relationship between caterpillar biomass (dependent variable, log(mg/h/0.25m^2)) and ALAN, separately for each tree species. The models also include year, canopy height, canopy cover, and (in the case of the Norway maple) study site. Statistically significant effects are highlighted by bold.

(a) sessile oak

	numDF	denDF	F-value	p-value
(Intercept)	1	15	0.011	0.918
Year	3	15	7.276	**0.003**
Canopy height	1	2	0.008	0.937
Canopy cover	1	2	0.365	0.607
Light intensity	1	2	<0.001	0.989
(b) small-leaved lime				
(Intercept)	1	15	0.042	0.84
Year	3	15	13.964	**<0.001**
Canopy height	1	2	3.803	0.190
Canopy cover	1	2	0.243	0.671
Light intensity	1	2	3.053	0.223
(c) Norway maple				
(Intercept)	1	33	0.411	0.526
Year	3	33	10.406	**<0.001**
Canopy height	1	8	0.321	0.587
Canopy cover	1	8	0.233	0.643
Light intensity	1	8	0.012	0.916
(d) Norway maple (study site included)				
(Intercept)	1	33	1.107	0.3
Year	3	33	10.164	**<0.001**
Study site	1	6	0.835	0.396
Study site x Light intensity	1	6	0.721	0.428
Canopy height	1	6	0.504	0.504
Canopy cover	1	6	0.028	0.873
Light intensity	1	6	0.66	0.448
(e) horse-chestnut				
(Intercept)	1	15	0.503	0.489
Year	3	15	16.416	**<0.001**
Canopy height	1	2	0.193	0.704
Canopy cover	1	2	0.667	0.500
Light intensity	1	2	0.02	0.902
(f) silver linden				
(Intercept)	1	15	7.847	0.013
Year	3	15	13.632	**<0.001**
Canopy height	1	2	13.191	0.068
Canopy cover	1	2	0.308	0.635
Light intensity	1	2	7.923	0.106

Table S3. Pairwise *post-hoc* comparisons of tree species in caterpillar biomass (log [mg/h/0.25m^2]), statistically significant ($p<0.05$) differences are highlighted by bold. Abbreviations used for tree species: SL - silver linden, SLL - small-leaved lime, SO - sessile oak, NM - Norway maple, HC - horse-chestnut.

Contrast	Estimate ± SE	t	p-value
SL-HC	**1.159 ± 0.35**	**3.27**	**0.0213**
SL-SLL	0.526 ± 0.40	1.36	0.6937
SL-SO	-0.553 ± 0.42	-1.32	0.6874
SL-NM	**1.088 ± 0.36**	**3.01**	**0.0391**
HC-SLL	-0.633 ± 0.34	-1.88	0.3574
HC-SO	**-1.712 ± 0.34**	**-4.98**	**0.0002**
HC-NM	-0.071 ± 0.29	-0.25	1.0000
SLL-SO	**-1.08 ± 0.32**	**-3.34**	**0.0175**
SLL-NM	0.561 ± 0.28	2.01	0.2975
SO-NM	**1.641 ± 0.28**	**5.83**	**<0.0001**

Table S4. Pairwise *post-hoc* test results of differences in caterpillar biomass (log[mg/h/0.25m^2]) between study years. Statistically significant ($p<0.05$) differences are highlighted by bold.

Contrast	Estimate ± SE	t	p-value
2014 - 2015	-0.316 ± 0.25	-1.28	0.576
2014 - 2016	**1.946 ± 0.25**	**7.9**	**<0.0001**
2014 - 2017	-0.289 ± 0.25	-1.17	0.645
2015 - 2016	**2.262 ± 0.25**	**9.18**	**<0.0001**
2015 - 2017	0.027 ± 0.25	0.11	1
2016 - 2017	**-2.234 ± 0.25**	**-9.07**	**<0.0001**

Table S5. Results of linear mixed-effects model testing the relationship between caterpillar biomass and night light intensity. Note that the model structure is the same as that of in the main text (see Table 1), with the only exception that here we included spatial data of the focal trees to consider and control for spatial autocorrelation (see the main text for further details).

(a) the two urban study sites (Balatonfüred and Veszprém) analyzed together

	numDF	denDF	F-value	p-value
(Intercept)	1	22	0.214	0.649
Tree species	4	22	0.348	0.843
Tree species x Light intensity	1	22	0.652	0.428
Canopy height	1	22	3.747	0.066
Canopy cover	1	22	0.055	0.817
Study site	1	22	0.62	0.440
Study site x Light intensity	4	22	0.631	0.646
Light intensity	1	22	0.577	0.455

(b) the two urban study sites (Balatonfüred and Veszprém) analyzed separately

Veszprém				
(Intercept)	1	10	0.019	0.894
Tree species	2	10	0.403	0.679
Tree species x Light intensity	2	10	0.501	0.620
Canopy height	1	10	1.735	0.217
Canopy cover	1	10	0.028	0.871
Light intensity	1	10	0.621	0.449
Balatonfüred				
(Intercept)	1	10	1.524	0.245
Tree species	2	10	0.254	0.781
Tree species x Light intensity	2	10	0.878	0.445
Canopy height	1	10	2.013	0.186
Canopy cover	1	10	0.121	0.735
Light intensity	1	10	1.137	0.311