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Cieraad, E.; Strange, E.F.; Flink, M.; Schrama, M.J.J.; Spoelstra, K.

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RESEARCH ARTICLE

Artificial light at night affects plant–herbivore interactions

Ellen Cieraad^{1,2}  | Emily Strange¹  | Melanie Flink¹ | Maarten Schrama^{1,3}  |
Kamiel Spoelstra⁴ ¹Institute of Environmental Science,
Leiden University, Leiden, The
Netherlands²Nelson-Marlborough Institute of
Technology - Te Pūkenga, Nelson, New
Zealand³Naturalis Biodiversity Center, Leiden, The
Netherlands⁴Department of Animal Ecology,
Netherlands Institute of Ecology (NIOO-
KNAW), Wageningen, The Netherlands

Correspondence

Ellen Cieraad

Email: ellen.cieraad@nmit.ac.nz

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Abstract

1. Artificial light at night (ALAN) affects species' physiology and behaviour, and the interactions between species. Despite the importance of plants as primary producers, it remains poorly understood whether and how effects of ALAN on plants cascade through the food web.
2. We assess the extent to which ALAN of different spectra result in plant-mediated insect herbivory damage. In a 6-month field experiment, we exposed plants of differing palatability to three colours of ALAN and a dark control, and assessed plant traits (growth rate, leaf size, foliar density and thickness) and insect herbivory (represented by insect damage as loss of foliage to leaf-chewing insects, and gall abundance by phloem-feeding herbivory).
3. We found evidence for plant trait-mediated ALAN effects on herbivory for oak, but not for blueberry. In oak, ALAN of different colours changed the direction of relationships of insect damage with relative growth rate and with leaf thickness. Moreover, we found that the effects of ALAN on herbivory damage differed markedly between forest types within the same locale, particularly in the red light treatment.
4. *Synthesis and applications.* Our results provide evidence that continuous night-time light, as provided by street lighting around the world, affects food web interactions. The nature of these effects differed by species and appeared to depend on forest type and the light spectrum employed, thus underlining the context dependency of ALAN in different ecosystems and environmental settings. These findings highlight the complexity of using spectral manipulation as a mitigation measure, and the need for further consideration of ALAN in environmental management and planning, to limit the exposure and impact of cascading effects of artificial light at night on food webs and communities.

KEYWORDS

artificial light at night, cascading effects, context dependency, food web, herbivory

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1 | INTRODUCTION

For eons, the natural light–dark cycle has provided highly consistent and predictable cues that have guided behavioural patterns of many species. However, over the last century, the emission of artificial light at night (ALAN) is increasingly disrupting these natural patterns. ALAN is an anthropogenic change with a higher speed of increasing disruption than any other anthropogenic change, and its impacts include direct mortality by attraction, habitat loss, changes in daily and seasonal timing and effects on the food web (Gaston et al., 2021). However, our understanding of the impact of ALAN on most species, and species' interactions, is still limited. The majority of research has focussed on individual organisms, mostly animals and their behaviour (e.g. see Sanders et al., 2021 for a recent overview). ALAN can also affect different levels of organisation and interactions in biological systems (Bennie et al., 2015; Knop et al., 2017; Manfrin et al., 2017). However, few studies have assessed effects of ALAN on plants as primary producers, at the fundament of the ecological food web (Bennie et al., 2016). This severely hampers our ability to understand and mitigate the ecosystem-level impacts of ALAN, despite many natural areas in the world, and more than two-thirds of key biodiversity areas, being affected by night-time lighting (Garrett et al., 2020).

Light induces a series of highly conserved physiological processes in plants (Jackson, 2009). Since plant physiology and phenology affect primary productivity, and if ALAN affects physiology and phenology, it stands to reason that the impacts of ALAN on plants flow through to organisms higher in the food web. However, whether and how the effects of ALAN on plant physiology cascade through the food web remains poorly understood (Bennie et al., 2015; Heinen, 2021). In a mesocosm study, an increased intensity of ALAN resulted in increased plant biomass coincided with increased aphid abundance, but parasite–aphid relationships showed a more complex relationship with ALAN (Sanders et al., 2018). Few other studies have assessed the effect of ALAN on plant palatability and resulting herbivory. Murphy et al. (2022) found that ALAN can increase leaf toughness and alter C:N ratios, which in turn affect host plant quality, but these impacts are species specific. Grenis and Murphy (2019) found that streetlights directly reduced larval biomass and also indirectly affected larval growth by reducing host plant quality. Crump et al. (2021) showed that at low intensities, ALAN increased grass growth initially (without affecting the physiology), but that increased herbivory under light offset any biomass gains. ALAN can affect higher trophic levels through a multitude of pathways, including direct and indirect impacts on plants, herbivores and predators (Figure 1), but these pathways and processes have not yet been studied in a field setting.

Plant traits have been suggested as useful tools to improve the understanding of herbivory across gradients and treatments (Andrew et al., 2012). Physical traits, including leaf size, thickness and density are relatively cheap and easy to measure, and provide important determinants of herbivory (Muiruri et al., 2019). Leaf traits also have been shown to respond to a large variety of environmental factors, and have been shown to be altered by ALAN as well (Murphy et al., 2022). Structural leaf toughness depends on material toughness and lamina

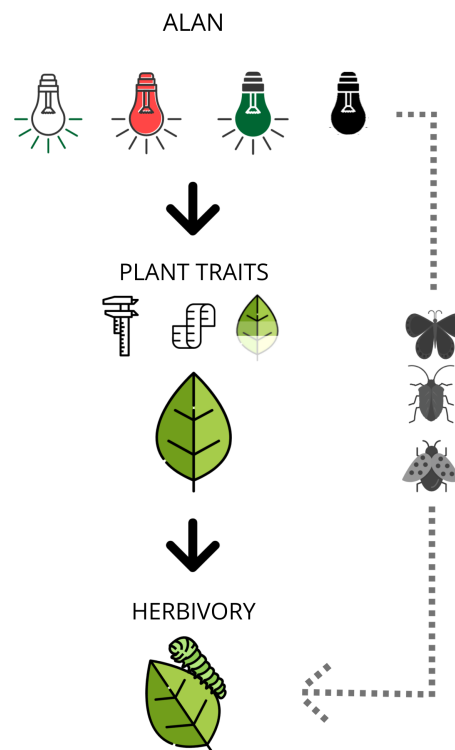


FIGURE 1 Potential pathways of effects of artificial light at night (ALAN) of different colours on plant insect herbivory damage. Plant-mediated effects, through effects on relative growth rates, and leaf size, thickness and density, are shown in solid arrows. Dashed arrows indicate that ALAN can also affect insect damage through its effects on insect communities (which herbivore species are present and active), insect behaviour (e.g. the location and activity of egg-laying moths and caterpillars) and insect predators (e.g. birds and bats) and parasites.

thickness and density, and these traits may provide resistance against chewing insects (Brunt et al., 2006; Caldwell et al., 2016). Leaves are most vulnerable to herbivory during leaf expansion, and smaller, faster expanding, leaves may be less susceptible to herbivory damage than larger leaves (Moles & Westoby, 2000). All these physical traits are affected by the quantity and quality of daytime light through changes to phytohormonal pathways (Lazzarin et al., 2021). As such, these traits can be expected to be important in mediating effects of ALAN via plants to higher trophic levels.

Here, we assess the extent to which ALAN of different spectra result in plant-mediated insect herbivory damage. In a field experiment, we exposed plants of differing palatability to three colours of ALAN and dark control during the growing season, and assessed plant traits (growth rate, leaf size, density and thickness) and foliar insect herbivory (represented by loss of foliage to leaf-chewing insects, and gall abundance by phloem-feeding herbivory).

1.1 | Hypotheses

Given the lack of a comprehensive understanding of the impact of ALAN colours on plants and their interaction with herbivores, our

hypotheses draw heavily from the existing (daytime) literature. Night-time light intensities under streetlight illumination are high enough to allow photosynthesis, so we expect ALAN to affect plant growth rates. Since the growth-defence trade-off demands prioritisation towards either growth or defence (Huot et al., 2014), we expected that herbivory damage is affected by ALAN indirectly through its effect on plant traits, including growth rate (growth) and leaf thickness and density (defence). We expect that any light at night will result in higher herbivory damage than in the natural dark conditions, as increased growth through additional photosynthesis will be traded off with a reduction in defences.

The spectral composition of daytime light strongly affects the efficiency of light absorption and CO₂ fixation and is an important determinant of growth (Lazzarin et al., 2021). During daytime in natural canopies, vegetation absorbs red light for photosynthesis and reflects far-red light. Under the canopy, the resulting reduced red: far-red ratio is perceived by photoreceptors and signals shading and light competition from neighbouring plants. Plants respond to a low red: far-red ratio with an increased growth (e.g. elongation) response to avoid the shade (Meijer et al., 2022). A low ratio also results in a downregulation of immune responses, so that plants prioritise shade avoidance over defence responses, and this hence generally increases herbivory damage (Ballare, 2014; de Vries et al., 2017; Lazzarin et al., 2021). The red: far-red ratio of the lights in our experiment is relatively low for the white and green treatments, and high for the red treatment (see Appendix S1 in Supporting Information). Foliar defence in red light (high red: far-red light ratio) is high (Shibuya et al., 2010). Based only on this, we would hence expect higher foliar damage under white and green light, and lowest under red light. At the same time, green lights attract insects (van Langevelde et al., 2011), a feature greenhouse horticulture exploits to reduce herbivory by attracting insects away from plants to green lights (Lazzarin et al., 2021). Hence, taken together, we expect insect damage is highest under white light, followed by green and red light, with the lowest damage in the dark control.

Phenolic compounds and leaf toughness partially determine palatability to insect herbivores. Both increase in response to light, at least in daytime environments (Lazzarin et al., 2021). Since we lack any evidence of such relationships during the night, we assume similar nocturnal relationships to exist. If so, we would expect a dampening effect of ALAN on the insect damage for more palatable species. That is, highly palatable species (with low phenolic content and/or soft leaves) will be less attractive under ALAN, while insect damage of highly unpalatable species is less affected by ALAN (as these species already have very tough leaves and/or high phenolic content).

We predict ALAN affects gall abundance through its effect on leaf thickness, as thicker leaves reduce gall abundance (Muiruri et al., 2019). Moreover, the plant vigour hypothesis predicts that gall-inducing insects perform better on faster growing plants than on less vigorous plants (Price, 1991). Combined, we hypothesise that green light leads to the lowest gall intensity.

2 | MATERIALS AND METHODS

2.1 | Experimental setup

This study was conducted at the experimental 'Light on Nature' sites in the Netherlands, using a dedicated set-up to assess plant growth and herbivory. Rows with 4 m tall light posts were placed in forest edge habitat, with each row randomly assigned one of four light treatments: white, green or red or the row remained unlit as a dark control. Lights were commercially available street light armatures available from Philips (Amsterdam, The Netherlands), more details are available in the Supplementary Information S1. The study sites had four rows (with all four treatments) placed in deciduous broadleaf forest, and four rows (also with all four treatments) placed in coniferous forest. We used two posts along each row, so a total of 16 posts. The experimental set-up is described in detail in Spoelstra et al. (2015). Our study did not require ethical approval. Site access was provided by Staatsbosbeheer (permit number GBOinv201869/5.0.cr.4.06.1).

In spring 2019, pots with 3-year-old saplings of two plant species of differing palatability were purchased at a nursery. We used European blueberry *Vaccinium myrtillus* (approximately 10 cm tall) and saplings of the common oak *Quercus robur* (approximately 100 cm tall) to represent species of medium and low palatability respectively. Both species naturally occur at the site. We included a third species, the highly palatable rapeseed *Brassica napus* (originally, but it was exposed to such severe herbivory across treatments that it could not be included in the results). Ten blueberry plants, and 12 oak saplings were placed within 2 m from the base of each of the posts in direct illumination. Under the posts in the dark control, we placed 10 extra plants. The pots were randomly placed in a small grid within species blocks, and re-randomised every fortnight. All plants were watered throughout the growing season when required.

It is important to measure leaf traits at a similar stage of leaf development across treatments. The phenology of blueberry and oak is mainly affected by temperature, but may also be altered by ALAN (in the order of days, to a week, French-Constant et al., 2016). To minimise any possible confounding effects of our treatments on the phenology and leaf traits, we started our experiment prior to budburst and completed it 6 months later (end of the growing season). Herbivory damage was measured at the end of the experiment, and hence describes the cumulative effects over the whole growing season.

2.2 | Measurements

2.2.1 | Plant traits

Plant growth rates are expected to affect herbivory due to variation in energy investment in different defence mechanisms. Relative height growth rate (RGR) was calculated using Pérez-Harguindeguy et al. (2013):

$$\text{RGR} = (\ln H_2 - \ln H_1) / (t_2 - t_1), \quad (1)$$

where H_1 and H_2 refer to the plant height (in mm) at the start (t_1) and a second time point during the experiment (t_2) respectively. For blueberry, t_2 was the end of the growing season ($t_2 - t_1 = 177$ days); for oaks, we used an additional mid-season measurement ($t_2 - t_1 = 77$ days), because just before the end of the experiment, the tops of several oaks had suffered deer browse, resulting in negative height growth over the whole growing season.

Mid-lamina leaf thickness was measured (in mm) on 10 freshly harvested leaves of each plant, selected randomly, using a portable thickness gauge (Top cloud-agri technology). Leaf density was assessed as the dry leaf weight per cm² of leaf, where leaf area was determined using image analysis of harvested leaves (Davidson, 2011, see also below), and dry weight was assessed after drying at 60°C until constant weight. Leaf size was determined from digital images (see below). All leaf traits were measured once, at the end of the growing season.

2.3 | Insect herbivory damage

We used two metrics to represent insect herbivory in this study: (1) foliar insect damage (also referred to as insect damage) and in the case of the oaks, also by (2) the gall abundance (number of leaves with galls). For foliar insect damage, we estimated the fraction of foliage lost for each plant. Insects are assumed to be responsible for all the foliar damage analysed here, in particular chewing insects (as opposed to phloem sucking insects). Deer browse affected some of the plants, but this resulted in removal of the whole meristem of the plant. No evidence of other browse (rabbits, hares) was found on the experimental plants throughout the growing season. Using a desktop scanner, we took one image of at least 10 randomly selected leaves per plant, and analysed these images in Fiji version X (Schindelin et al., 2012). Preliminary analyses showed thresholds of at least 200 contiguous pixels for blueberry and 5000 for oak resulted in consistent assessment of the number of leaves, with and without damage. In each image, the number of leaves and the leaf area ('original leaf area') were obtained by determining the number of dark pixels using the analyse particle option following Davidson (2011). Then, for each damaged leaf on each image, the predicted leaf edge was manually drawn following the natural shape of the leaf using the pencil tool, and the full leaf area was filled (representing the 'leaf area without damage'). The difference between the leaf area without damage and the original leaf area corresponded to holes and foliar margin damage, that is, the leaf area lost to herbivory over the whole growing season. Our response variable 'insect damage' was expressed as this leaf area lost as a fraction of the leaf area without damage. Average leaf size per plant was calculated as the estimated leaf area without damage divided by the number of leaves.

2.4 | Statistical analyses

All analyses were performed in R version 3.5.2 (R Core Team, 2021). We used multiple regression to assess whether any effect of ALAN on herbivory damage was mediated by plant traits. We used generalised linear models with a beta distribution for the herbivory damage, represented as the fraction of total leaf area consumed, using the BETAREG package (Cribari-Neto & Zeileis, 2010), and a negative binomial distribution for the abundance of galls on oak foliage, using the MASS package (Venables & Ripley, 2002). We did not include a random nested factor (light post within treatment), as the extremely small variance explained by these random effects resulted in issues with model convergence. Explanatory variables in the full model included interactions between ALAN and the four different plant traits. There was limited correlation between the different plant traits (for blueberry, all Pearson's $|r| < 0.21$, for oak $|r| < 0.65$). Given the scale of the study area (the total forest edge length in which the rows with light posts are located is 1.6 km long), we assume continuous populations of insect herbivores. However, the resource availability (including quantity of leaves and flower, nutritional quality, seasonality) differs between the two forest types (mixed deciduous and coniferous) which, in turn, likely affects the species locally present at any time (Marques et al., 2000). Hence, we included Forest type in the full model, as a fixed effect and as an interaction term with ALAN. For each dependent variable (insect damage for blueberry and oak, and gall abundance for oak), the full model included the following independent variables: Relative growth rate (RGR) * ALAN + Leaf size * ALAN + Leaf density * ALAN + Leaf thickness * ALAN + Forest type * ALAN.

The beta-regression model naturally incorporates some variance in the response, but as proportional data are typically heteroscedastic, we tested whether additional heteroscedasticity was captured by Forest type or Treatment using the likelihood-ratio, lrtest in the LMTEST package (Zeileis & Hothorn, 2002). For blueberry we found dispersion depended on the main effects of Forest type, and for oak on the main effects of Treatment; this dispersion was added to the full model.

Full models were then simplified to minimum adequate final models containing only significant ($p < 0.05$) terms using backward model selection. The presence of an interaction between ALAN and a trait in the final model indicates a plant trait-mediated effect of ALAN on herbivory intensity, whereas an interaction between Forest type and ALAN indicates that plant trait-mediated effects of ALAN differ between forest types. Pseudo- R^2 was calculated as the squared correlation of linear predictor and link-transformed response using the BETAREG package (Cribari-Neto & Zeileis, 2010) for the herbivory damage models and using likelihood ratio-based pseudo r -square in the MuMIn package (Barton, 2020) for the gall (negative binomial) model respectively. Post-hoc tests for significant differences between slopes and means of ALAN treatments and Forest types were conducted using the EMMEANS package and Tukey method for p -value adjustment (Lenth, 2020).

3 | RESULTS

3.1 | Plant-mediated herbivory damage of blueberry

Insect damage of blueberry leaves was associated with Leaf thickness and the interaction of ALAN treatment and Forest type ($p < 0.001$; Table 1, Figure 2). Insect damage decreased with increasing Leaf density. Insect damage was higher ($p < 0.0001$), and more variable, in the conifer forest than at the mixed deciduous site. This was dominated by a strong difference under red light (estimated >10% of foliage lost in the conifer forest, compared with around 2% under all colours in the deciduous forest, Figure 2).

3.2 | Plant-mediated herbivory and gall abundance of oak

3.2.1 | Insect damage

Insect damage to oak leaves was best described by the interaction of ALAN treatment with two plant traits (RGR and Leaf thickness) and ALAN treatment and Forest type (Table 1, Figure 3a,b). Under green and red ALAN, RGR was positively associated with insect damage, whereas in the dark control or white ALAN, increased RGR resulted in reduced damage. Post-hoc tests showed slopes of RGR under green and red ALAN were significantly and marginally significantly (respectively) higher than under white ALAN ($p = 0.005$ and $p = 0.087$ respectively). Under white and red ALAN, increased Leaf thickness reduced insect damage, with no change under green or dark light. The slope differed significantly between white ALAN and green ALAN ($p = 0.002$) and white light and the dark control

($p = 0.030$). Overall, oaks in the conifer forest suffered greater insect damage (mean fraction of leaf area lost under the different colours between 3% and 10%) than those in the mixed deciduous forest (all colours around 3%, see Figure 3, $p = 0.034$). This pattern was driven by much higher insect damage under red ALAN compared with all the other treatments in the conifer forest (red-dark $p = 0.047$, red-green $p = 0.013$, red-white = 0.066).

3.3 | Gall abundance

The occurrence of galls on a plant was driven by the interaction of ALAN and Forest type (Figure S4). Gall abundance on oak foliage was best described by interactions of ALAN treatment with Leaf thickness and Forest type (Table 1, Figure 4a,b). Overall, more leaves had galls in the mixed deciduous forest than in the conifer forest ($p = 0.001$). While in the dark control, Leaf thickness decreased gall abundance, all coloured spectra resulted in a slightly positive association between Leaf thickness and gall abundance (only slopes between dark control and red ALAN differed significantly, $p = 0.02$).

While overall there was no significant linear association between mean gall abundance and insect damage, there was a visible trend of those plants with high gall infection being less likely to have also sustained insect damage (Figure 5).

4 | DISCUSSION

We assessed whether different colours of artificial light at night (ALAN) affect insect herbivory indirectly by changing plant traits for two plant species. We found evidence for plant trait-mediated ALAN effects on insect damage for oak, but not for blueberry saplings.

TABLE 1 Model summaries of the insect damage of blueberry and oak, and gall intensity on oak as a function of artificial light at night (ALAN) treatment, Forest type, plant traits and their interactions. For terms retained in the final models, the table details the degrees of freedom (*df*), associated χ^2 and *p*-values. RGR refers to relative growth rate. Variance explained is represented by pseudo- r^2 for the negative binomial insect damage, and adjusted r^2 for poisson gall intensity. Empty cells represent terms not retained in the final model

Terms	<i>df</i>	Blueberry–insect damage		Oak–insect damage		Oak–gall abundance	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
ALAN treatment	3	17.65	<0.001	6.48	0.090	20.72	0.0001
Forest type	1	29.62	<0.0001	4.62	0.032	4.42	0.035
RGR	1			0.11	0.735		
Leaf thickness	1			5.11	0.024	0.01	0.931
Leaf density	1	7.97	0.005	12.70	0.0004		
Leaf size							
ALAN * Forest type	3	37.02	<0.0001	17.62	0.0005	19.63	0.0002
ALAN * RGR	3			12.90	0.005		
ALAN * Leaf density							
ALAN * Leaf thickness	3			12.64	0.005	8.10	0.044
ALAN * Leaf size							
Variance explained		0.43		0.24		0.30	

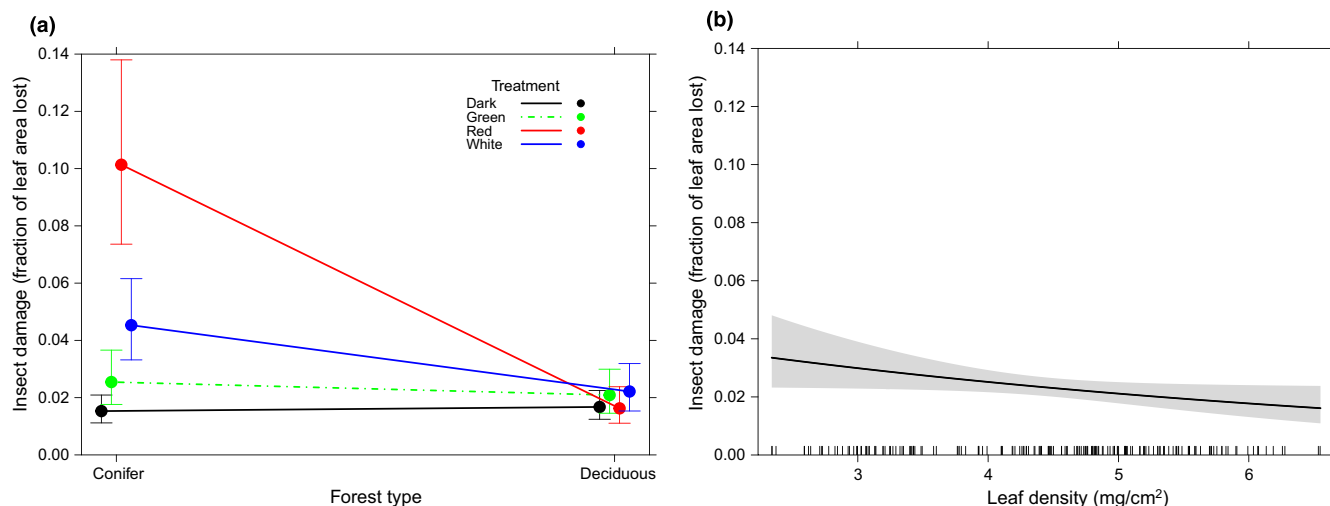


FIGURE 2 Graphical summary for the minimum adequate model for insect damage for blueberry saplings. Error bars (in a) and shaded area (in b) represent 95% confidence band for the fitted values. The rug plot (in b) shows the location of x-values. See Table 1 for model details and Figure S2 for a graphical summary with partial residuals.

Moreover, we found that the effects of ALAN (in particular, red light) on insect damage differed markedly between forest types within the same locale.

In oak, ALAN changed the relationship between insect damage and two plant traits: growth rate and leaf thickness. Such plant-mediated effects of ALAN seem in concordance with the growth-defence hypothesis (Huot et al., 2014), at least for oaks grown under red and green light. Plants grown under these night lights with enhanced growth showed increased foliar insect damage, presumably through a decrease in defensive capabilities. However, under white ALAN and the dark control, insect damage decreased with increasing growth rates—thus suggesting an increase in defence chemistry (e.g., metabolites or volatile compounds, rather than structure) with increased growth. Thicker leaves reduced insect damage, but only in the red and white treatment. For blueberry, denser leaves resulted in less damage (independent of ALAN), as would be expected if denser leaves are tougher and hence less palatable (Brunt et al., 2006).

We expected to find a stronger plant-mediated effect of ALAN on insect damage in more palatable species. Instead, we found no evidence of plant-mediated effects in blueberry, but we did in the less palatable oak. The lack of such effects in blueberry is somewhat surprising, as, at least during the day, an increase in light results in an increase in phenolics content (Martz et al., 2010), which would presumably result in a decrease in herbivory damage. The two species shared similar rates of insect damage overall, and similar responses to forest type and the ALAN spectrum. Rather than palatability, the differential plant-mediated effects of ALAN may be explained by any of many differences in ecology between the species, including tolerance of irradiance and shade, and the light environment of the adults (understory for blueberry and overstorey for oak). Further experiments with more species along such gradients will elucidate the mechanisms behind the different responses.

Insect damage was similar in the white, green and dark control treatment in both forest types. In contrast, there was a stark difference in insect damage between forest types under red light. There are multiple pathways that can explain such differences in insect damage under ALAN of different colours (see Figure 1), including effects of ALAN on insects (e.g. behaviour and community composition) and plant-mediated effects of ALAN on insects (i.e. affecting insect behaviour through ALAN impacts on plant traits).

Insect responses to ALAN of differing spectra include changes in behaviour like attraction to the armatures (Donners et al., 2018; Manfrin et al., 2017). We did not measure insect behaviour at our site. However, as many insects lack a receptor for red light (Alaasam et al., 2021; van der Kooi et al., 2021), we would not expect attraction to the light in this treatment. Such lack of attraction may have resulted in less distraction and more time spent feeding. Since we did not see a similarly elevated insect damage under the dark control, it is unlikely that this mechanism explains the high insect damage in the red treatment. If ALAN changed the insect community composition over time, for example due to differences in reproduction success and predator abundance (e.g. Manfrin et al., 2017; van Geffen et al., 2015), this may have resulted in different herbivory intensities between treatments. Five years after illumination started at our study site, macro-moth abundance reduced in the light treatments, compared to the dark control, but abundance did not differ between the three colour spectra (van Grunsven et al., 2020), suggesting that moth numbers are not driving the high insect damage under red light in our study.

When considering plant physiology, high insect damage under red light is counterintuitive. Based on studies of supplemental lighting of plants during the daytime, this is opposite to what we would expect. These studies show that low red: far red ratio light results in a decrease in foliar defences, and thinner leaves, which are more attractive to herbivores (Ballare, 2014; Lazzarin et al., 2021; Meijer et al., 2022). If similar processes are at play at night, one may expect

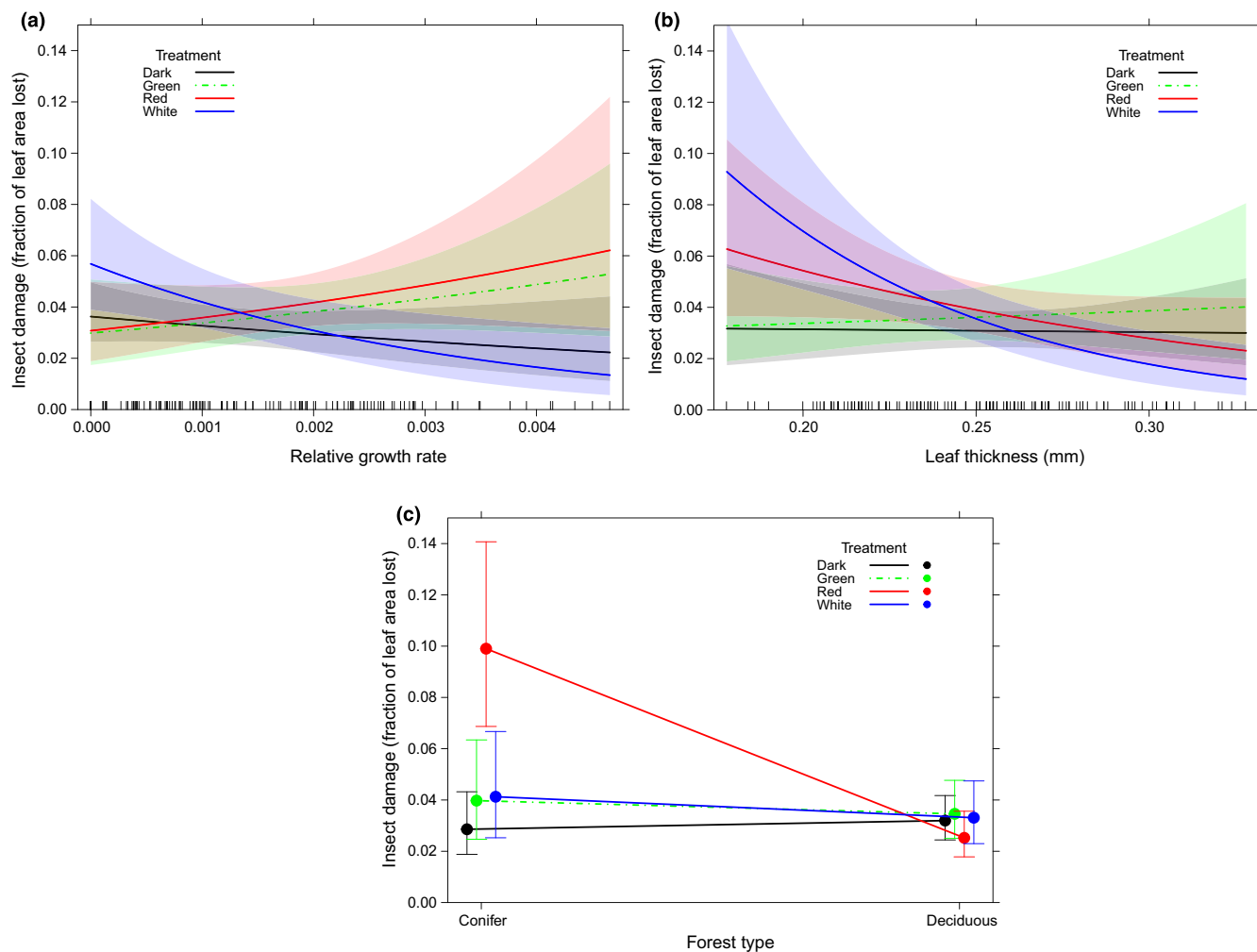


FIGURE 3 Graphical summary for the minimum adequate model for insect damage for oak. The shaded area (in a and b) and error bars (in c) represent 95% confidence band for the fitted values. The rug plot (in a and b) shows the location of x-values. See Table 1 for model details, and Figure S3 for a graphical summary with partial residuals.

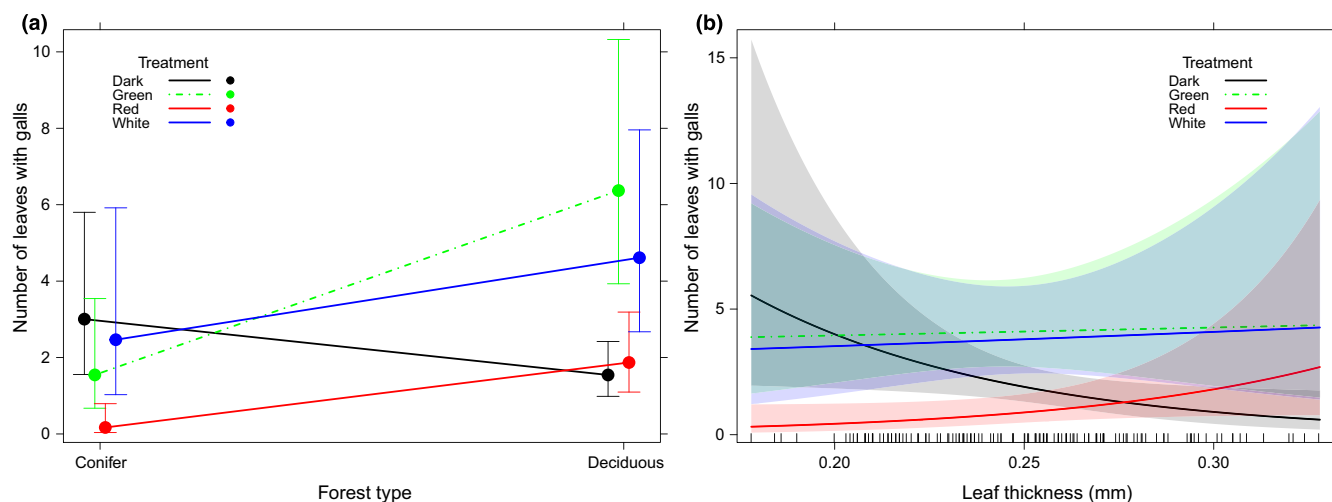


FIGURE 4 Graphical summary for the minimum adequate model for gall abundance on oak. The error bars (in a) and the shaded area (in b) represent 95% confidence band for the fitted values. The rug plot shows the location of x-values. See Table 1 for model details and Figure S4 for a graphical summary with partial residuals.

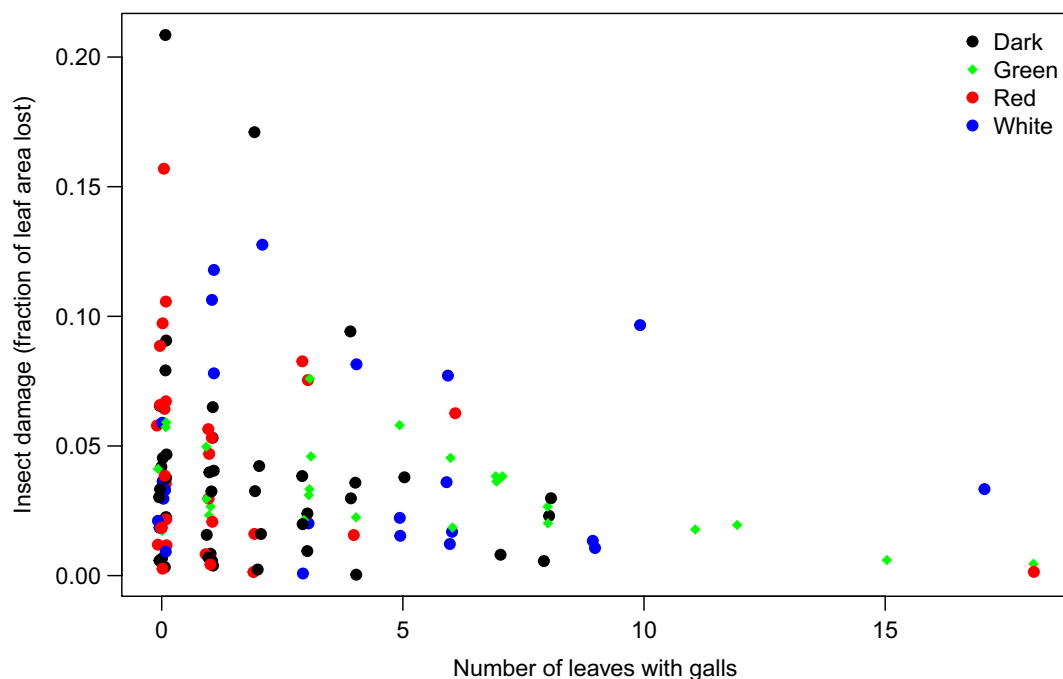


FIGURE 5 Number of leaves infected with galls versus the amount of insect damage. X-values are jittered to enable viewing of all data points. Each circle represents one oak seedling; the colour indicates the ALAN treatment.

foliage developed under high red: far red night-time light (i.e. our red treatment) should be least attractive to herbivores. Our current understanding, largely drawn from daytime processes, hence fails to explain the high damage under night-time red light. Potentially, these results are driven by physiological processes. For example, the strong positive association between RGR and herbivory damage under red light, at least for oak, may suggest that increased photosynthetic gain at night could be interfering with metabolic recovery normally taking place at night-time, which could render plants more susceptible to insect damage. This reinforces the dearth of knowledge and need for further investigation on the effects of ALAN of different spectra on plants and their interactions. Only then will we be able to understand and mitigate cascading effects of light pollution through the food web.

Interestingly, gall abundance showed an opposite effect of forest type compared to insect damage: oak leaves in mixed deciduous forest showed had more galls (except for the dark control, where levels were similar between forest types). The response of forest type (and its resident insect community) to ALAN determined whether or not galls are present and how many, but the effect of ALAN on gall abundance was also mediated by plants (leaf thickness). More speculatively, there may also be an interaction between the gall-forming phloem feeders and chewing herbivores. While we did not find an association between mean herbivory damage and gall abundance, there was a lack of co-occurrence of high gall numbers and high insect damage (Figure 5). Through their manipulation of their plant host, gall-forming insects may change the physical and chemical properties of their host, and this may subsequently result in a reduction in chewing insects (Kurzfeld-Zexer & Inbar, 2021). We did not find an increase in galls on more vigorous, faster growing

plants, failing to support the plant vigour hypothesis (Eliason & Potter, 2000).

We observed the integrated herbivory damage to our study plants as incurred by the combined insect community (rather than individual insect species) under different spectra of ALAN at one location, in two forest types, at the end of the growing season. The results hence encompass a myriad of light effects on insect behaviour, physiology and changes in insect community. The degree of host plant specialisation may also affect the extent to which insect species respond to downregulation of defence mechanisms due to light quality (Lazzarin et al., 2021). In addition, changes to foliar nutrient quality and chemistry may affect herbivory (Pérez-Harguindeguy et al., 2003) and these may be affected by ALAN. Similarly, ALAN may affect herbivore-induced defences (where plants induce defences, such as increased secondary metabolites or volatiles, in response to mechanical wounding by herbivores) (de Vries et al., 2017). While these additional foliar traits and defences were not directly included in the study, any changes imposed by ALAN would have been captured in the foliar insect damage.

Our results confirm that artificial illumination affects interactions between primary producers and their insect herbivores. It warrants further investigation how such impacts cascade through the food web. With more than two thirds of Key Biodiversity Areas worldwide experiencing ALAN (Garrett et al., 2020), and strong indications that ALAN is at least partly driving insect declines around the world (Boyes et al., 2020; Owens et al., 2019), it is important to identify how we can best reduce ecological impacts of ALAN to protect natural communities. Simple mitigation methods include shielding lights to prevent spill over into the environment, reducing the light intensity, using adaptable and/or smart lighting (lighting only during times of

peak demand, or in the case of smart lighting, only during times of use) and changing the colour spectrum of the light used (Sordello et al., 2022). Using light levels comparable to conventional LED street lighting, our study suggests that continuous night-time light affects herbivory intensity and plant-herbivore interactions. Moreover, these effects appear to depend on forest type and the light spectrum employed, thus highlighting the context dependency of ALAN impacts. This suggests that caution is required when using the manipulation of the ALAN spectrum as a simple mitigation measure, as results may not be uniform between ecosystems. Overall, our results underscore the importance of ALAN-induced trophic cascading effects, thus highlighting the need to carefully develop light infrastructure with adaptable and spectrum dependent mitigation measures.

AUTHOR CONTRIBUTIONS

Ellen Cieraad conceived the ideas. Ellen Cieraad, Maarten Schrama and Kamiel Spoelstra designed the methodology; Ellen Cieraad collected the data; Melanie Flink carried out the image analyses and conducted initial data analyses and write up as part of her MSc student research project, which was supervised by Ellen Cieraad and Maarten Schrama; Ellen Cieraad, Emily Strange and Kamiel Spoelstra analysed the data and interpreted the results. All authors contributed to the manuscript and gave their final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The dataset used in this work is deposited in Dataverse <https://doi.org/10.34894/VD98DG> (Cieraad, 2022).

ORCID

Ellen Cieraad  <https://orcid.org/0000-0002-9813-9590>

Emily Strange  <https://orcid.org/0000-0001-8491-3912>

Maarten Schrama  <https://orcid.org/0000-0001-9803-6244>

Kamiel Spoelstra  <https://orcid.org/0000-0001-8614-4387>

REFERENCES

- Alaasam, V. J., Kernbach, M. E., Miller, C. R., & Ferguson, S. M. (2021). The diversity of photosensitivity and its implications for light pollution. *Integrative and Comparative Biology*, 61(3), 1170–1181. <https://doi.org/10.1093/icb/icab156>
- Andrew, N. R., Roberts, I. R., & Hill, S. J. (2012). Insect herbivory along environmental gradients. *Open Journal of Ecology*, 2(4), 24024. <https://doi.org/10.4236/oje.2012.24024>
- Ballare, C. L. (2014). Light regulation of plant defense. *Annual Review Plant Biology*, 65, 335–363. <https://doi.org/10.1146/annurev-arplant-050213-040145>
- Barton, K. (2020). MuMIn: Multi-model inference. (1.43.17). <https://CRAN.R-project.org/package=MuMIn>
- Bennie, J., Davies, T. W., Cruse, D., & Gaston, K. J. (2016). Ecological effects of artificial light at night on wild plants. *Journal of Ecology*, 104(3), 611–620. <https://doi.org/10.1111/1365-2745.12551>
- Bennie, J., Davies, T. W., Cruse, D., Inger, R., & Gaston, K. J. (2015). Cascading effects of artificial light at night: Resource-mediated control of herbivores in a grassland ecosystem. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 370(1667), 20140131. <https://doi.org/10.1098/rstb.2014.0131>
- Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2020). Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. *Insect Conservation and Diversity*, 14(2), 167–187. <https://doi.org/10.1111/icad.12447>
- Brunt, C., Read, J., & Sanson, G. D. (2006). Changes in resource concentration and defence during leaf development in a tough-leaved (*Nothofagus moorei*) and soft-leaved (*Toona ciliata*) species. *Oecologia*, 148(4), 583–592. <https://doi.org/10.1007/s00442-006-0369-4>
- Caldwell, E., Read, J., & Sanson, G. D. (2016). Which leaf mechanical traits correlate with insect herbivory among feeding guilds? *Annals of Botany*, 117, 349–361. <https://doi.org/10.1093/aob/mcv178>
- Cieraad, E. (2022). Data from: Artificial light at night affects plant-herbivore interactions. *Dataverse*. <https://doi.org/10.34894/VD98DG>
- Cribari-Neto, F., & Zeileis, A. (2010). Beta Regression in R. *Journal of Statistical Software*, 34, 1–24. <https://doi.org/10.18637/jss.v034.i02>
- Crump, M. C., Brown, C., Griffin-Nolan, R. J., Angeloni, L., Lemoine, N. P., & Seymoure, B. M. (2021). Effects of low-level artificial light at night on Kentucky bluegrass and an introduced herbivore. *Frontiers in Ecology and Evolution*, 9, 732959. <https://doi.org/10.3389/fevo.2021.732959>
- Davidson, A. (2011). Measuring leaf perimeter and leaf area. In *Prometheus wiki*. Prometheus. <http://prometheuswiki.org/tiki-index.php?page=Measuring+leaf+perimeter+and+leaf+area>
- de Vries, J., Evers, J. B., & Poelman, E. H. (2017). Dynamic plant-plant-herbivore interactions govern plant growth-defence integration. *Trends in Plant Science*, 22(4), 329–337. <https://doi.org/10.1016/j.tplants.2016.12.006>
- Donners, M., van Grunsven, R. H. A., Groenendijk, D., van Langevelde, F., Bikker, J. W., Longcore, T., & Veenendaal, E. (2018). Colors of attraction: Modeling insect flight to light behavior. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329(8–9), 434–440. <https://doi.org/10.1002/jez.2188>
- Eliason, E. A., & Potter, D. A. (2000). Budburst phenology, plant vigor, and host genotype effects on the leaf-galling generation of *Callirhytis cornigera* (Hymenoptera: Cynipidae) on pin oak. *Environmental Entomology*, 29(6), 1199–1207. <https://doi.org/10.1603/0046-225X-29.6.1199>
- ffrench-Constant, R. H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., & McGregor, P. K. (2016). Light pollution is associated with earlier tree budburst across the United Kingdom. *Proceedings of the Royal Society B - Biological Sciences*, 283, 20160813. <https://doi.org/10.1098/rspb.2016.0813>
- Garrett, J. K., Donald, P. F., & Gaston, K. J. (2020). Skyglow extends into the world's key biodiversity areas. *Animal Conservation*, 23(2), 153–159. <https://doi.org/10.1111/acv.12480>
- Gaston, K. J., Ackermann, S., Bennie, J., Cox, D. T. C., Phillips, B. B., Sánchez de Miguel, A., & Sanders, D. (2021). Pervasiveness of biological impacts of artificial light at night. *Integrative and*

- Comparative Biology*, 61(3), 1098–1110. <https://doi.org/10.1093/icb/icab145>
- Grenis, K., & Murphy, S. M. (2019). Direct and indirect effects of light pollution on the performance of an herbivorous insect. *Insect Science*, 26(4), 770–776. <https://doi.org/10.1111/1744-7917.12574>
- Heinen, R. (2021). A spotlight on the phytobiome: Plant-mediated interactions in an illuminated world. *Basic and Applied Ecology*, 57, 146–158. <https://doi.org/10.1016/j.baee.2021.10.007>
- Huot, B., Yao, J., Montgomery, B. L., & He, S. Y. (2014). Growth–defense tradeoffs in plants: A balancing act to optimize fitness. *Molecular Plant*, 7(8), 1267–1287. <https://doi.org/10.1093/mp/ssu049>
- Jackson, S. D. (2009). Plant responses to photoperiod. *New Phytologist*, 181(3), 517–531. <https://doi.org/10.1111/j.1469-8137.2008.02681.x>
- Knop, E., Zoller, L., Ryser, R., Gerpe, C., Horler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature*, 548(7666), 206–209. <https://doi.org/10.1038/nature23288>
- Kurzfeld-Zexer, L., & Inbar, M. (2021). Gall-forming aphids are protected (and benefit) from defoliating caterpillars: The role of plant-mediated mechanisms. *BMC Ecology and Evolution*, 21(1), 124. <https://doi.org/10.1186/s12862-021-01861-2>
- Lazzarin, M., Meisenburg, M., Meijer, D., van Ieperen, W., Marcelis, L. F. M., Kappers, I. F., van der Krol, A. R., van Loon, J. J. A., & Dicke, M. (2021). LEDs make it resilient: Effects on plant growth and defense. *Trends in Plant Science*, 26(5), 496–508. <https://doi.org/10.1016/j.tplants.2020.11.013>
- Lenth, R. (2020). *Emmeans: Estimated marginal means, aka least-squares means*. (R package version 1.5.2-1). <https://CRAN.R-project.org/package=emmeans>
- Manfrin, A., Singer, G., Larsen, S., Weiß, N., van Grunsven, R. H. A., Weiß, N.-S., Wohlfahrt, S., Monaghan, M. T., & Hölker, F. (2017). Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. *Frontiers in Environmental Science*, 5, 2017.00061. <https://doi.org/10.3389/fenvs.2017.00061>
- Marques, E. S. D. A., Price, P. W., & Cobb, N. S. (2000). Resource abundance and insect herbivore diversity on woody fabaceous desert plants. *Environmental Entomology*, 29(4), 696–703. <https://doi.org/10.1603/0046-225X.29.4.696>
- Martz, F., Jaakola, L., Julkunen-Tiitto, R., & Stark, S. (2010). Phenolic composition and antioxidant capacity of bilberry (*Vaccinium myrtillus*) leaves in northern Europe following foliar development and along environmental gradients. *Journal of Chemical Ecology*, 36(9), 1017–1028. <https://doi.org/10.1007/s10886-010-9836-9>
- Meijer, D., Meisenburg, M., van Loon, J. J. A., & Dicke, M. (2022). Effects of low and high red to far-red light ratio on tomato plant morphology and performance of four arthropod herbivores. *Scientia Horticulturae*, 292, 110645. <https://doi.org/10.1016/j.scientia.2021.110645>
- Moles, A. T., & Westoby, M. (2000). Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? *Oikos*, 90(3), 517–524. <https://doi.org/10.1034/j.1600-0706.2000.900310.x>
- Muiruri, E. W., Barantal, S., Iason, G. R., Salminen, J.-P., Perez-Fernandez, E., & Koricheva, J. (2019). Forest diversity effects on insect herbivores: Do leaf traits matter? *New Phytologist*, 221(4), 2250–2260. <https://doi.org/10.1111/nph.15558>
- Murphy, S. M., Vyas, D. K., Sher, A. A., & Grenis, K. (2022). Light pollution affects invasive and native plant traits important to plant competition and herbivorous insects. *Biological Invasions*, 24(3), 599–602. <https://doi.org/10.1007/s10530-021-02670-w>
- Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K., & Seymoure, B. (2019). Light pollution is a driver of insect declines. *Biological Conservation*, 241, 108259. <https://doi.org/10.1016/j.biocon.2019.108259>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167. <https://doi.org/10.1071/BT12225>
- Pérez-Harguindeguy, N., Díaz, S., Vendramini, F., Cornelissen, J. H. C., Gurvich, D. E., & Cabido, M. (2003). Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology*, 28(6), 642–650. <https://doi.org/10.1046/j.1442-9993.2003.01321.x>
- Price, P. W. (1991). The plant vigor hypothesis and herbivore attack. *Oikos*, 62(2), 244–251. <https://doi.org/10.2307/3545270>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing <https://www.R-project.org>
- Sanders, D., Frago, E., Kehoe, R., Patterson, C., & Gaston, K. J. (2021). A meta-analysis of biological impacts of artificial light at night. *Nature Ecology & Evolution*, 5(1), 74–81. <https://doi.org/10.1038/s41559-020-01322-x>
- Sanders, D., Kehoe, R., Cruse, D., van Veen, F. J. F., & Gaston, K. J. (2018). Low levels of artificial light at night strengthen top-down control in insect food web. *Current Biology*, 28(15), 2474–2478.e3. <https://doi.org/10.1016/j.cub.2018.05.078>
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., & Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. *Nature Methods*, 9(7), 676–682. <https://doi.org/10.1038/nmeth.2019>
- Shibuya, T., Komuro, J., Hirai, N., Sakamoto, Y., Endo, R., & Kitaya, Y. (2010). Preference of sweetpotato whitefly adults to cucumber seedlings grown under two different light sources. *HortTechnology*, 20(5), 873–876. <https://doi.org/10.21273/HORTTECH.20.5.873>
- Sordello, R., Busson, S., Cornuau, J. H., Deverchère, P., Faure, B., Guetté, A., Hölker, F., Kerbirou, C., Lengagne, T., Le Viol, I., Longcore, T., Moeschler, P., Ranzoni, J., Ray, N., Reyjol, Y., Roulet, Y., Schroer, S., Secondi, J., Valet, N., ... Vauclair, S. (2022). A plea for a worldwide development of dark infrastructure for biodiversity – Practical examples and ways to go forward. *Landscape and Urban Planning*, 219, 104332. <https://doi.org/10.1016/j.landurbplan.2021.104332>
- Spoelstra, K., van Grunsven, R. H. A., Donners, M., Gienapp, P., Huigens, M. E., Slaterus, R., Berendse, F., Visser, M. E., & Veenendaal, E. (2015). Experimental illumination of natural habitat—an experimental set-up to assess the direct and indirect ecological consequences of artificial light of different spectral composition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140129. <https://doi.org/10.1098/rstb.2014.0129>
- van der Kooij, C. J., Stavenga, D. G., Arikawa, K., Belušić, G., & Kelber, A. (2021). Evolution of insect color vision: From spectral sensitivity to visual ecology. *Annual Review of Entomology*, 66(1), 435–461. <https://doi.org/10.1146/annurev-ento-061720-071644>
- van Geffen, K. G., van Eck, E., de Boer, R. A., van Grunsven, R. H. A., Salis, L., Berendse, F., Veenendaal, E. M., Stewart, A., & Sait, S. (2015). Artificial light at night inhibits mating in a geometrid moth. *Insect Conservation and Diversity*, 8(3), 282–287. <https://doi.org/10.1111/icad.12116>
- van Grunsven, R. H. A., van Deijk, J. R., Donners, M., Berendse, F., Visser, M. E., Veenendaal, E., & Spoelstra, K. (2020). Experimental light at night has a negative long-term impact on macro-moth populations. *Current Biology*, 30(12), R694–R695. <https://doi.org/10.1016/j.cub.2020.04.083>
- van Langevelde, F., Ettema, J. A., Donners, M., WallisDeVries, M. F., & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144(9), 2274–2281. <https://doi.org/10.1016/j.biocon.2011.06.004>
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. Springer. <https://doi.org/10.1007/978-0-387-21706-2>

Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression. *R News*, 2(3), 7–10.

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