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Artificial light at night promotes bottom-up changes in a woodland food chain☆

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ABSTRACT

Artificial light at night (ALAN) is a recognised disruptor of biological function and ecological communities. Despite increasing research effort, we know little regarding the effect of ALAN on woody plants, including trees, or its indirect effects on their colonising invertebrates. These effects have the potential to disrupt woodland food webs by decreasing the productivity of invertebrates and their secretions, including honeydew and lerps, with cascading effects on other fauna. Here, we cultivated juvenile river red gums (*Eucalyptus camaldulensis*) for 40 weeks under experimentally manipulated light (ALAN) or naturally dark (control) conditions. To assess direct impacts on tree growth, we took multiple measures of growth at four time periods, and also measured physiological function, biomass and investment in semi-mature trees. To assess experimentally the direct and indirect (tree-mediated) impacts of ALAN on invertebrates, from 19 weeks onwards, we matched and mismatched trees with their original ALAN environments. We colonised trees with a common herbivore of *E. camaldulensis*, the red gum lerp psyllid (*Glycaspis* nr. *brimblecombei*) and then measured the effects of current and historic tree lighting treatment on the psyllid life cycle. Our data revealed direct effects of ALAN on tree morphology: *E. camaldulensis* trees exposed to ALAN shifted biomass allocation away from roots and into leaves and increased specific leaf area. However, while the intensity of ALAN was sufficient to promote photosynthesis (net carbon gain) at night, this did not translate into variation in tree water status or photosystem adaptation to dim night-time light for ALAN-exposed trees. We found some evidence that ALAN had broad-scale community effects—psyllid nymphs colonising ALAN trees produced more lerps—but we found no other direct or indirect impacts of ALAN on the psyllid life cycle. Our results suggest that trees exposed to ALAN may share morphological responses with trees under dim daylight conditions. Further, ALAN may have significant 'bottom-up' effects on *Eucalyptus* woodland food webs through both trees and herbivores, which may impact higher trophic levels including woodland birds, mammals and invertebrates.

1. Introduction

Artificial light at night (ALAN) has the potential to mask, disrupt or imitate natural light signals, and is widely recognised as a powerful disruptor of light-mediated ecological processes (Dominoni and Nelson, 2018; Longcore and Rich, 2004; Sanders et al., 2021). The number of identified impacts of ALAN on the behaviour and physiology of individual species and functional groups is increasing dramatically (Rich and Longcore, 2006; Sanders et al., 2021). Most recently, similar negative effects on communities and specific ecological interactions are reported, including predator-prey interactions (Minnaar et al., 2015; Rydell, 1992; Wakefield et al., 2016) and pollination processes (Knop et al., 2017; Macgregor et al., 2017; reviewed in: Sanders and Gaston, 2018). This accumulated evidence points to the potential for ongoing and historical ALAN exposure to have cascading effects on communities through multiple mechanisms, including (i) direct effects on animal behaviour and plant growth; (ii) impacts on pollinators and herbivores that indirectly impact plants; and (iii) impacts on plants (shifts in

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growth, morphology or investment) that indirectly impact herbivores.

Primary producers (plants, algae and bacteria) are fundamentally important for terrestrial and aquatic ecosystems and are inherently dependent upon variation in light levels. Yet, compared to animals, our understanding of how ALAN affects the growth and survival of primary producers is relatively poor (Bennie et al., 2016; Briggs, 2005; Sanders and Gaston, 2018). Studies of non-woody plants report ALAN-related increases in carbon gain and growth (Demers et al., 1998; Park et al., 2020; Speisser et al., 2021; Yao et al., 2021); changes in morphology and physiology consistent with plants in the shade (Segrestin et al., 2021); reduced leaf investment and downregulation of daytime photosynthesis (Park et al., 2020; Pettersen et al., 2010; van Gestel et al., 2005); and increased stomatal conductance and water loss (Kavanagh et al., 2007). Evidence from ornamental trees and shrubs indicates that ALAN may advance phenological changes in spring (Ffrench-Constant et al., 2016) and delay those in autumn (Bennie et al., 2016; Cathey and Campbell, 1975; Kramer, 1937; Matzke, 1936; Škvareninová et al., 2017; Sullivan et al., 2019). What is unclear is whether ALAN exposure will result in selection of morphological and physiological characteristics in trees that are optimized for exposure to low-level night lighting. Such knowledge is critical because, in urban environments, tree canopies frequently intersect with streetlights or building lighting (Bennie et al., 2016). A series of unanswered questions remain, including whether nocturnal photosynthesis can supplement daylight photosynthesis and thus increase growth in wild plants, as has been reported in grasses and forbs (Speisser et al., 2021); and whether ALAN promotes morphological or physiological changes in trees that have cascading impacts on associated faunal communities.

The effects of ALAN on invertebrate-to-plant interactions, including pollination (Knop et al., 2017), pollen transport (Macgregor et al., 2017) and herbivory (Grenis and Murphy, 2019; McMunn et al., 2019) are documented. Less is known about plant-mediated effects of ALAN on invertebrate herbivore life history traits such as reproduction, ontogeny and survival (but see: Bennie et al., 2015; Sanders et al., 2015). Any indirect plant-to-invertebrate effects may exacerbate the direct effects of ALAN on invertebrates, affecting key life history traits such as altered mating behaviour (McLay et al., 2018; van Geffen et al., 2015), reduced oviposition, survival and fecundity (McLay et al., 2017; Willmott et al., 2018) and disrupted hatching cues (White, 1968a).

The movement and trophic ecology of certain invertebrate species may also increase their vulnerability to direct and indirect ALAN impacts. For example, invertebrates with sessile habits or life-stages may have a limited ability to move away from ALAN-impacted feeding or reproductive sites. Similarly, herbivores of long-lived woody plants may suffer indirect plant-mediated impacts of both current, and historic, exposure to ALAN. For example, if ALAN exposure during vegetative growth impacts leaf thickness (Hay and Heide, 1983), this may affect future herbivory (Brennan and Weinbaum, 2001), even if ALAN is no longer present at a site. Cascading effects of ALAN may thus disrupt evolutionarily stable relationships between host plants and their specialised herbivores (Hopkins et al., 2018).

The river red gum (*Eucalyptus camaldulensis* subsp. *Camaldulensis* (Dehnh.)) is an evergreen tree that provides trophic and reproductive resources to a wide variety of birds, mammals and invertebrates (Hollis, 2004; Mac Nally et al., 2011). River red gums are common in urban streets and parks in southern Australia (City of Melbourne, 2020), where their canopies are directly exposed to ALAN from street and park lighting and vehicular traffic (authors pers. obs). As a long-lived species (CSIRO, 2004), river red gums may experience ALAN impacts on temporal scales from hours to decades. Extrapolating from studies of vascular plants (trees, forbs and grasses), short-term impacts of ALAN on river red gums might include nocturnal photosynthesis (Speisser et al., 2021) and increased transpiration (Phillips et al., 2010), potentially undermining tree water status (Kavanagh et al., 2007). Longer-term effects might include physiological and morphological adaptation to dim night-time lighting (Givnish, 1988; James and Bell, 2000), or shifts in overall growth and investment (Bennie et al., 2018; Bennie et al., 2015; Speisser et al., 2021). However, in practice the short- and long-term effects of ALAN on trees, and *Eucalyptus* in particular, along with any potential effects on the herbivores that feed upon them remain underexplored.

Lerp psyllids (Hemiptera: Aphalaridae (Löw) and Psyllidae (Latreille)) on *Eucalyptus* host-trees are particularly likely to be vulnerable to both direct and indirect ALAN impacts on life history and survival. Psyllids spend most of their life cycle as sessile nymphs under characteristic starchy shells (lerps) which they secrete on the surface of *Eucalyptus* leaves (Hollis, 2004). As such, they are highly exposed to their environment, including any nearby source of ALAN. The life-cycles of lerp psyllid species rely on multiple photic cues that may be muted or disrupted by ALAN, including hatching cues (White, 1968a), and selection of feeding/oviposition sites based on colour (Farnier et al., 2014; Farnier and Steinbauer, 2016) and shade (White, 1970a, b). As herbivores, they rely on leaf phloem sap as their sole food source as nymphs and adults (Douglas, 2006); females oviposit while feeding (Hollis, 2004), and eggs draw moisture from the leaf cuticle (White, 1968b). Accordingly, ALAN may have indirect effects on psyllids at multiple life stages through light-mediated shifts in the growth, morphology, moisture or nutrient content of *Eucalyptus* leaves (White, 1970b). Lerp psyllids and their *Eucalyptus* host-trees thus provide an excellent model for exploring the direct and indirect effects of ALAN in a plant-herbivore system.

Here, we experimentally tested the effects of artificial light at night on the growth, morphology and leaf function of the river red gum and simultaneously investigated ALAN's impact on the life cycle and productivity of the red gum lerp psyllid (*Glycaspis* nr. *brimblecombei*) (Fig. 1). We cultivated red gum saplings under ALAN (equivalent in spectrum and intensity experienced by tree canopies in close proximity to streetlight luminaires) and control (dark at night) conditions for 40 weeks and measured a range of key morphological and physiological traits. To explore whether the effect of ALAN either directly, or indirectly (through its effects on the red gums) disrupted psyllid life history traits we transplanted *G.* nr. *Brimblecombei* psyllids on ALAN-exposed and control (no ALAN) trees; those trees in turn had previously been exposed to either the same, or opposite, lighting treatment.

2. Methods

2.1. Experimental site

The experiment was conducted in a rural paddock in Kongwak, Victoria, Australia (−38.513677°, 145.708209°). The field site was surrounded on three sides by a minor waterway (Foster Creek) with native *Acacia* and *Eucalyptus* trees (various species) on both banks (Fig. S1). The site had no direct illumination and very low skyglow (radiance x 10^{-19} W/cm^2/sr: 2018 = 0.44; 2019 = 0.32 (NOAA Earth Observation Group, 2019; Stare, 2019).

We constructed 24 light-proof plots (each 2.5 m × 2.5 m) using generic temporary fencing panels (2.4 m wide x 1.95 m high) covered on both sides with woven plastic block-out fabric (Shade Australia, Ingleburn NSW; Fig. 2a and b). Plots were arranged in two rows of 12, running approximately north-south (alignment: −10° from true north; Fig. 2d). Plots were assigned to one of two artificial light at night treatments (control or ALAN), alternating in a checkerboard fashion to minimise positional and aspect effects (Fig. 2d).

Following an initial period of tree cultivation, lighting treatments began on September 14, 2018 (experimental week 1, Australian early spring), and experiments and surveys were conducted from then until June 19, 2019 (experimental week 40, early winter).

2.2. Cultivation and selection of experimental trees

To assess the effects of ALAN on tree growth and invertebrate

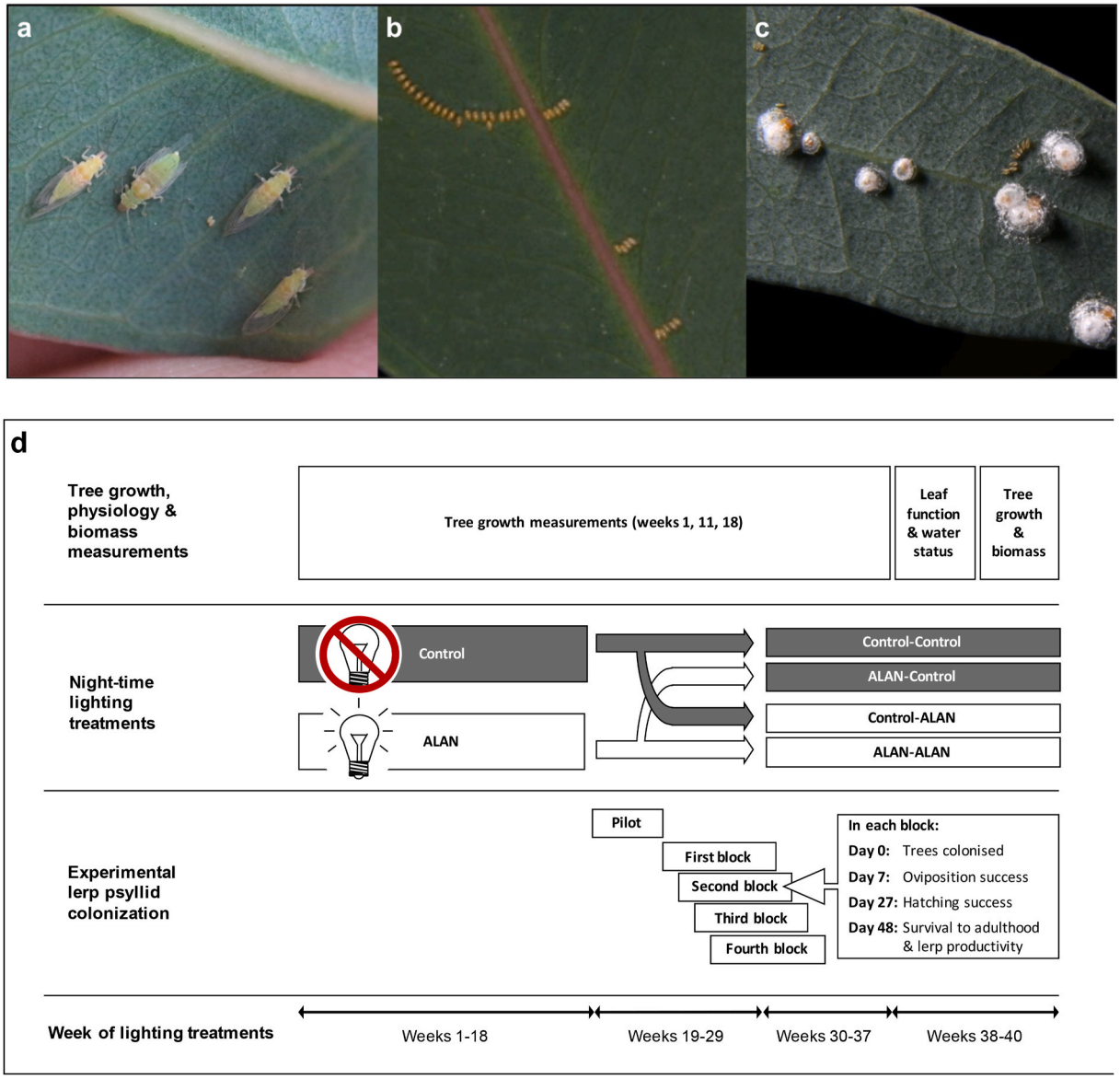

Fig. 1. The life cycle of the red gum lerp psyllid: (a) Adult *Glycaspis* nr *brimblecombei* psyllids with two eggs; (b) leaf with unhatched eggs; (c) leaf with hatched eggs, lerps, and early-instar nymphs (orange, visible through lerps) and (d) Timeline of experiments and measurements conducted. Lighting treatments: Weeks 1–18: Trees in original plots, 50% of trees exposed to ALAN, 50% exposed to Control conditions (designated First treatment: ALAN or Control). Between weeks 19–29: Each tree was either swapped to the opposite lighting treatment following experimental psyllid colonisation or swapped location but within the same lighting treatment. Between weeks 30–40: trees were fixed in their second lighting treatment (designated Second treatment): this created four cohorts of all combinations of First treatment and Second treatment treatments: 1. ALAN-ALAN; 2. Control-Control; 3. ALAN-Control; 4. Control-ALAN. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

colonisation we maintained 200 individually potted 10-month old river red gum seedlings (sourced from a naturally dark at night site: ERA Nurseries, Hamilton, Victoria where they had been cultivated under a natural day and naturally dark night light cycle and watered daily). Once transferred to the experimental site, we excluded visually diseased and morphologically unusual seedlings and transferred 144 (of the remaining 154) seedlings to 10 L planter bags before placing them into 15 L plastic tubs with *ad libitum* access to water. The allocated tub size allowed water to barely reach the soil surface, thus after rain trees could be inundated but not submerged in water. We assigned seedlings randomly (MS Excel, RAND function), in groups of six, to each of the 24 light-proof plots. Trees were exposed to natural rainfall, supplemented with irrigation in warmer weather. All tubs were filled/emptied to the same level, usually 7.5 cm (half-full), depending upon forecast weather conditions. Irrigation/equalisation took place weekly, or twice weekly in hot conditions (weeks 17–29; see Supplementary materials – Text Box 2 for more details of cultivation, watering and seedling selection).

To allow orientation effects to be tested, throughout the experiment, tree orientation (with respect to north) remained constant. However, to avoid within plot positional effects, the six trees were rotated by one position weekly resulting in all trees occupying all positions over a six-week period. One week after re-potting, all 144 seedlings were inspected visually to confirm the absence of visible invertebrate infestation/damage, and all surfaces treated with a broad-spectrum non-residual insecticide ('Yates' Pyrethrum Insect Pest Killer Concentrate, 4 g/L Pyrethrins, 16 g/L Piperonyl Butoxide, diluted 20 mL/Litre) to remove any pre-existing invertebrates. Insecticide was applied on a dry day with no rain predicted for at least the next 24 h post-application. Seedlings were then left for an additional three weeks under the natural day/night light cycle prior to the start of the lighting treatments.

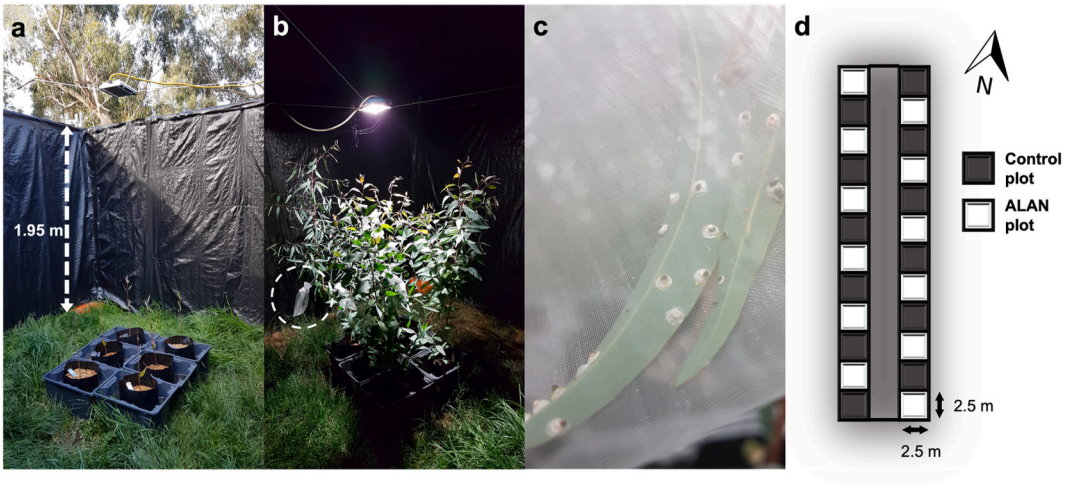

Fig. 2. Experimental field site in Kongwak, Victoria: (a) ALAN treatment plot showing 30W LED luminaire suspended above seedlings (week 1, daytime); (b) ALAN treatment plot (week 24, night time) with psyllid sample mesh bag attached to tree (circled); (c) Detail of mesh bag enclosing foliage and lerp psyllids; (d) plan of experimental site showing alternating arrangement of 'ALAN' and 'Control' treatment plots (additional site images in Supplementary materials, Fig. S1). Each plot was enclosed in non-permeable sheeting that did not permit light spill directly into neighbouring plots. Images: ML.

2.3. Lighting treatments: experimental weeks 1–40

From experimental week 1 onwards, 'ALAN' plots were artificially illuminated 1 h before sunset until 1 h after sunrise with a commercially available 30W LED outdoor light (Philips Essential SmartBright model BVP161, nominal CCT = 4000K, mean ± SE illuminance = 759 ± 22 Lux (150 cm below light); PAR = 20.2 ± 3.0 μmol $m^{-2}s^{-1}$ (average of measures taken 30, 90 and 150 cm below light); Fig. 2b, Table S1). These light levels were chosen to reflect the lighting intensity experienced by tree foliage in close proximity (≤1.5 m) to LED luminaires commonly installed on residential streets in Australia (e.g. Schréder, 2021). For most urban trees this may be the most intense constant night-time lighting experienced. As in a streetscape, foliage lower down on our trees, or on the side of the tree facing away from the luminaire, received less intense ALAN. The light was suspended 185 cm above the centre of the plot with four nylon guy ropes attached to each corner of the plot (Fig. 2a). 'Control' plots contained a dummy light of the same dimensions as the LED light, suspended in the same manner and casting an equivalent-sized shadow over the plot during the day (night-time illuminance 0.0 ± 0.0 Lux, Fig. 2a). Thus, all plots received natural daytime light levels but varied in night-time lighting (see Supplementary materials – Text Box 1 for details of lighting treatments). Lighting did not alter plot temperature (Table S1; mean temperature ± SE on a cool night: ALAN plots = 8.19 ± 0.03 °C; Control plots = 8.22 ± 0.03 °C).

2.4. Assessment of tree growth and condition: experimental weeks 1, 11, 18, 38

We recorded tree height, diameter, and condition immediately prior to the commencement of lighting treatments in week 1, and again in weeks 11, 18 and 38. Diameter was measured 300 mm above the soil surface (or 5 mm from tip where seedling was <305 mm high) with an electronic Vernier caliper (resolution: 0.01 mm, accuracy: 0.03 mm) (Gehring et al., 2008). If the 300 mm height coincided with a leaf or branch base, diameter was measured immediately above this area. To minimise the effects of stem asymmetry we took the average of two measurements at approximately 90°. Height was measured from the soil surface to the tip of the highest stem (excluding leaves, petioles) using a measuring tape (resolution: 1 mm). Inclined/curved stems were measured along the length of the stem (not in a vertical line from tip to soil). We also assessed tree condition as 'poor' (dried or miscoloured foliage, stunted growth, visibly impacted by invertebrates) or 'good' (not poor). Trees assessed as 'poor' (n = 17 (12%); Table S2) were retained in plots to maintain a consistent light and shade environment but were excluded from experiments.

2.5. Manipulation of psyllid colonisation: experimental weeks 19–35

To assess the relative direct (i.e. on the insect) and indirect (i.e. on the host plant the insect feeds upon) effects of ALAN for growth, reproduction and survival of red gum lerp psyllids (*Glycaspis* nr. *Brimblecombei;* Fig. 1a–c) we transplanted psyllids from their natural environment to our experimental trees. We collected psyllids from *E. camaldulensis* trees at three sites in suburban Melbourne, Australia (Wilson Reserve: −37.7785°, 145.0475°; Brunswick −37.7760°, 144.9691° and −37.7727°, 144.9705°) using a sweep net and manual aspirator. Due to widespread collapse of psyllid populations following extreme heat events in January 2019 (a previously recorded phenomenon: see Hall et al. (2015); Moore (1961); temperature records: Australian Government (2019)), these were the only sites with viable psyllid populations that could be found after an extensive search. Due to their urban location, each of these sites was exposed to some level of ALAN (mean ± SE illuminance = 0.91 ± 0.67 lux; skyglow radiance = 17.5 ± 5.62 x 10^{-19} W/cm^2/sr; Table S5) (NOAA Earth Observation Group, 2019; Stare, 2019).

Psyllids were transported in ventilated 70 mL vials containing a strip of moist filter paper within a cooled icebox. Prior to placement on trees, we grouped psyllids from the same site and transferred them to white organza bags (150 mm × 240 mm, Ontheinternet Products, Taree, NSW), with four males and four females per bag to reflect natural 1:1 sex ratios (Hodkinson, 2009). Each bag was attached to a randomly selected experimental tree stratified across all plots (n = 2 bags per tree, one on the north and one on the south side of each tree; total samples placed = 232 experimental + 30 pilot samples; detailed protocol in Supplementary materials – Text Box 3). The time taken between collection and placement of psyllids on trees was less than 8 h. Psyllids were placed on trees in one pilot (January 24, 2019) and four experimental blocks (February 20, February 25, March 8 and March 22, 2019) resulting in varied climatic conditions and tree age across the blocks. We estimated optimal times to monitor each stage of the psyllid life-cycle based on previous life history studies of *G. brimblecombei* (Firmino-Winckler et al., 2009; Hollis, 2004; Huerta et al., 2010; Messoudi et al., 2017; see Supplementary materials – Text Box 4) and observations of the pilot block. Between pilot and experimental samples, all 'good' trees used in

Table 1
Percentage variance explained and variable loadings for the first two principal components from a principal components analysis of morphological and physiological attributes of *Eucalyptus camaldulensis* trees (n = 21). Trees with missing results in any single attribute (n = 2) were excluded. Light saturated photosynthesis and diurnal transpiration use only measurements at 150 cm height. Additional attributes (photosynthesis and transpiration at 30 cm height, light compensation point) were excluded to avoid further reducing the sample size. Data were scaled and centred before modelling. Mean ± SE values are reported on original scale.

	PC1	PC2	Mean (±SE)
Percentage variance explained:	33.1%	18.1%	
Morphological variable loadings			
Specific Leaf Area	0.120	0.591	10.30 ± 0.40 (ALAN) 9.46 ± 0.60 (Control)
Root Mass Fraction	−0.264	−0.402	0.16 ± .013 (ALAN) 0.17 ± .007 (Control)
Leaf Mass fraction	−0.082	0.504	0.24 ± .011 (ALAN) 0.23 ± .008 (Control)
Physiological variable loadings			
Night-time photosynthesis (μmol/m^2/s)	0.431	−0.252	1.49 ± 0.17 (ALAN) 1.56 ± 0.10 (Control)
Night-time transpiration mmol $H_2O/m^{2/}s$	0.412	0.333	0.36 ± 0.06 (ALAN) 0.23 ± 0.04 (Control)
Light-saturated photosynthesis (μmol/m^2/s)	0.470	−0.135	16.23 ± 0.67 (ALAN) 15.90 ± 1.40 (Control)
Diurnal transpiration mmol $H_2O/m^{2/}s$	0.490	−0.097	3.59 ± 0.31 (ALAN) 3.51 ± 0.26 (Control)
Water potential (pre-dawn)	0.030	−0.059	0.93 ± 0.15 (ALAN) 0.96 ± 0.13 (Control)
Water potential (midday)	0.303	−0.171	13.71 ± 0.96 (ALAN) 13.53 ± 1.27 (Control)

the study were colonised with exactly two psyllid samples (thus we did not need to use psyllid colonisation as a covariate in tree analyses). Pilot block samples were excluded from psyllid analyses due to differences in handling (more frequent bag removal).

2.5.1. Psyllid life history

To assess oviposition success & parental mortality, at day 7 (or earlier, if all adults were observed to be dead at an earlier check) we removed the bag and all adult psyllids, counted the number of surviving adult psyllids, and checked for eggs on both sides of all bagged leaves. Due to the difficulty in distinguishing male and female psyllids under field conditions we did not separately record male and female mortality. If eggs were present we photographed all leaves with eggs (Canon 7Dii, Canon 18–135 mm IS STM Lens, Vivitar Series 1 67 mm close-up lens (+1), Kenko 36 mm DG extension tube; Yongnuo YN24EX-C Macro Ring Light Flash) and re-enclosed the foliage in a clean mesh bag. In this way all eggs in a given sample were laid within a known 7-day window, starting at day zero. Samples with no eggs after 7 days were deemed 'failed' and excluded from all post-oviposition analyses. At day 27, each sample bag was removed carefully from the tree, opened, and the leaves photographed (as above) to record the number of hatched eggs, unhatched eggs and lerps established, after which the bag was replaced and closed. At day 48, experimental bags and contents were removed along with their holding branch and then frozen at −80 °C until processing.

We counted the number of adult and juvenile psyllids, total lerps, and remains of hatched eggs using dissecting microscopes (Olympus® SZX-16, 11.2–184× magnification; SZX-7 16–112× magnification). For each sample, we recorded the number of adult psyllids, psyllid nymphs, lerps, and hatched eggs. Photographs taken at days 7 and 27 were reviewed on a 27-inch LED monitor (Dell P2717H, Dell Inc., Round Rock, Tx, USA) to count eggs laid, eggs hatched and lerps. From field observations, processed samples and review of photographs, we derived six measures of psyllid survival and productivity (adapted from White, 2016): parental mortality, oviposition, hatching success, lerp establishment, survival to adulthood, and lerp production (Table S4).

2.5.2. Direct and indirect impacts of ALAN

To distinguish the relative importance of direct (variation in ALAN during juvenile development) and indirect effects of ALAN (variation in ALAN not present during juvenile development, but the tree had previously been exposed to ALAN), at day 7, trees containing experimental bags with eggs ('colonised trees') were transferred to another experimental plot that had either the same or alternate lighting treatment. This resulted in four treatment groups that varied in pre- and post-oviposition lighting treatments ('First treatment', 'Second treatment'): 1. ALAN-ALAN; 2. Control-Control; 3. ALAN-Control; 4. Control-ALAN (Fig. 1d). To reduce plot biases, all colonised trees were switched to another plot regardless of whether their new allocated lighting treatment was the same as their current (see Supplementary materials – Text Box 3).

2.6. Assessment of leaf function and water relations: experimental weeks 38–40

2.6.1. Night-time and daytime leaf function

To explore whether ALAN exposure could promote net photosynthesis and increase nocturnal water loss, we measured night-time photosynthesis and transpiration. Measurements were made under multiple conditions (see below) in one tree from each plot that had been exposed to the same lighting treatment throughout the experiment (as per 'Lighting treatments' above; ALAN-ALAN: n = 12; Control - Control: n = 11; sample size reduced as one plot contained no suitable trees). Measurements were conducted over four sunny days and one night between experimental weeks 38 and 39, using an infrared gas analyser ('IRGA'; Li-Cor® Li6400, Li-Cor Inc, Lincoln, NE, USA)). Daytime measurements were conducted between 9:30 a.m. and 1:00 p.m. Night-time measurements were conducted over 3 h starting half an hour after the end of astronomical twilight. For each measurement we selected a fully expanded and undamaged leaf from the north side of each tree. The same 23 trees were used for all measurements; after each measurement we marked the leaf with permanent marker to ensure that we used a different leaf for each measurement.

We measured light response curves (LRCs) with nominal

Table 2
Model estimates, 95% confidence intervals and means for the effect of lighting treatment, time (where applicable), height (where applicable) and interactions on key physiological traits in *Eucalyptus camaldulensis*. In this table, the final set of models (ΔAICc ≤6) comprised a single model in each case. Effects for which 95% CI does not straddle zero are in bold. Estimates and confidence intervals are reported on the scale modelled (Ln, √ or neither, as indicated); mean ± SE values are untransformed.

	Estimates (±SE)	95% Conf. Interval (lower & upper bounds)		
a. Light compensation point (Ln(μmol/m^{2}s)) *n: ALAN = 9; Control = 9*				
Intercept	2.63 ± 0.05	2.53, 2.73		
Lighting	0.08 ± 0.07	−0.06, 0.22	15.21 ± 0.80 (ALAN)	13.94 ± 0.52 (Control)
b. Night-time photosynthesis (μmol/m^2/s under 40 μmol/m^2/s PAR) *n: ALAN = 12; Control = 11*				
Intercept	1.55 ± 0.21	1.14, 1.95		
Lighting	−0.06 ± 0.23	−0.50, 0.39	1.49 ± 0.17 (ALAN)	1.56 ± 0.10 (Control)
c. Night-time transpiration (mmol H_2O/m^2/s under 40 μmol/m^2/s PAR) *n: ALAN = 12; Control = 11*				
Intercept	0.24 ± 0.07	0.11, 0.37		
Lighting	0.11 ± 0.09	−0.06, 0.30	0.36 ± 0.06 (ALAN)	0.23 ± 0.04 (Control)
d. Light-saturated photosynthesis: A_{sat} (Ln(μmol/m^2/s) under 1800 μmol/m^2/s PAR)) *n: High: ALAN = 12; Control = 9; Low: ALAN = 12; Control = 8*				
Intercept	2.74 ± 0.08	2.56, 2.91		
Height	**−0.73 ± 0.08**	**−0.90, -0.57**	**8.12 ± 0.79 (30 cm)**	**16.1 ± 0.74 (150 cm)**
e. Diurnal transpiration (Ln(mmol H_2O/m^2/s) under 1800 μmol/m^2/s PAR)) *n: High: ALAN = 12; Control = 9; Low: ALAN = 12; Control = 8*				
Intercept	1.22 ± 0.08	1.05, 1.39		
Height	**−0.48 ± 0.09**	**−0.67, -0.30**	**2.23 ± 0.18 (30 cm)**	**3.55 ± 0.21 (150 cm)**
f. Water potential (√(MPa)) *n: ALAN = 12; Control = 11*				
Intercept	−0.73 ± 0.02	−0.78, −0.68		
Time	**−0.61 ± 0.03**	**−0.66, -0.56**	**−0.09 ± .010 (Pre-dawn)**	**−1.36 ± .077 (Midday)**

photosynthetic photon flux intensity (PPFD) of 0, 5, 10, 20, 40, 70, 100 and 150 μmol/m^2/s, using one leaf per tree at 150 cm from the tree base. We then calculated the light compensation point (LCP) for each tree (Marshall and Biscoe, 1980; Tu and Fisher, 2019). We measured daytime light-saturated photosynthesis (A_{sat}) and transpiration (PPFD = 1800 μmol/m^2/s, temperature = 20 °C) using one leaf sampled at 30 cm ('low') and one at 150 cm ('high'). Night-time photosynthesis was measured on one 'high' leaf (PPFD = 40 μmol/m^2/s, temperature = 20 °C). This approximated the average available night-time photosynthetically active radiation (PAR) at 150 cm height inside the ALAN-treated plots (Table S1) and was more than double the average light compensation point for *E. camaldulensis* (mean LCP ± SE = 14.58 ± 0.47 – see Results, Table 2a). To identify whether prolonged ALAN exposure resulted in adaptation of the photosystem, all measurements (LRCs, A_{sat}, night-time photosynthesis) were made on both ALAN and control trees.

2.6.2. Water potential

To explore the effects of ALAN on tree water status, at week 38, we measured pre-dawn (5:30 a.m.) and midday (12:00 p.m.) water potential in the same 23 trees used for leaf function tests. At each time period, we selected a fully expanded leaf from the top half of the canopy of each tree and removed at the base of the petiole using a razor blade. All 23 leaves were collected within a 15-min window, transferred to press-seal bags with all air squeezed out, then placed in an icebox containing a single freezer brick. Samples were mixed by hand within the icebox then removed haphazardly one at a time for measurement in a portable pressure chamber (Model 1000, PMS Instrument Company, Albany, OR, USA). Measurements were carried out by MTL within 90 min of removal from the tree and within 3 min of removal from the icebox.

2.6.3. Assessment of tree biomass, allometry specific leaf area: experimental week 40

To assess tree biomass, investment and leaf morphology, we harvested the 23 trees used for leaf function and water status measurements in week 40. Trees were separated into leaves, stems and roots, with roots hand-washed to remove all soil. To provide an estimation of leaf area, we measured the surface area of approximately 20 leaves from each tree with a LI-3100 Area Meter (Li-Cor Inc, Lincoln, NE, USA), then dried and weighed these separately. All samples were dried (D500 drying cabinets, Steridium, Brendale, Qld) at 80 °C and weighed twice daily until no weight change was observed. Dried samples were then weighed to the nearest 0.01g using a GF-3000 Precision Scale (A&D Weighing, Tokyo, Japan). We calculated total biomass (dry mass of whole tree; grams); leaf mass fraction (leaf mass/total biomass); root mass fraction (root mass/total biomass) and specific leaf area (leaf area/leaf mass; m^2kg^{-1}).

3. Analysis

All statistical analyses were carried out in R version 3.6.1 (R Core Team, 2019). To explore broad patterns in the effects of ALAN on tree morphology (specific leaf area, root and leaf mass fraction) and physiology (day- and night-time photosynthesis and transpiration, and pre-dawn and midday water potential), we conducted a principle components analysis ('PCA'; *prcomp* function, *stats* package), and created a PCA biplot of the first two principle components (*ggplot_pca* function, *AMR* package: Berends et al., 2021; *geom_mark_ellipse* function, *ggforce* package: Pedersen, 2021). Due to differences in samples size, light compensation point, photosynthesis at 30 cm height and tree growth were excluded from the PCA. We used linear mixed-effect models (*lmer* function, *lme4* package: Bates et al., 2015) to analyse tree growth, specific leaf area, light compensation point, photosynthesis (night-time and A_{sat}), transpiration (night-time and daytime), water potential, and number of psyllid eggs laid. Response variables were natural log- or square root-transformed where necessary to meet normality assumptions. We used binomial generalised linear mixed models (*glmer* function, *lme4* package) to analyse root and leaf mass fraction (as a proportion of total biomass), psyllid parental mortality (proportion dead/alive), oviposition success (proportion with eggs/no eggs), hatching success (proportion hatched), lerp establishment (proportion of hatched nymphs establishing lerps), survival to adulthood (proportion established lerp surviving), and lerp productivity (number of lerps per established nymph).

Lighting treatment(s) (First and, where relevant, Second treatment) were introduced as main effects in all models. Where relevant we added climate variables (average daily rainfall (mm), average daily solar exposure (kWh/m^2)), side of tree (north, south, indeterminate), psyllid bag height (cm), measurement leaf height (30/150 cm), measurement time (pre-dawn, midday), measurement week (1-40) and biologically relevant interactions. Rainfall during oviposition was strongly bimodal and was treated as a categorical variable (high (≥5.1 mm), low (≤2.8 mm)). Preliminary analyses (Table S6) showed that the site where parental generation psyllids were sourced did not impact response to ALAN (no *treatment* × *source* interaction) but did have marginal impacts on most life stages thus, source was used as a random effect. Other random effects comprised tree ID (for repeated measures), week (when not a main effect) and the following plot position variables: 'East-West' (plot in the eastern or western row) and 'Northness' (southernmost plot

= 1; northernmost = 12) where relevant. In the psyllid experiment, block number, tree age, temperature and climate variables (rainfall, solar exposure) were entirely confounded; thus we used only the climate variables in models as these had the added advantage of distinguishing effects of rain and sunshine, and reflected the intensity of natural light signal available to psyllids. Given the potential for biologically relevant interactions between artificial and natural light levels, and between First and Second lighting treatments, main models included two- or three-way interactions between (i) solar exposure and relevant lighting treatment(s); and (ii) side of tree and relevant lighting treatment(s).

We generated a 95% confidence interval for each fixed effect (*confint* function, *stats* package). Effects where the transformed 95% CIdid not include zero were considered supported, and we report estimates ± standard error (SE) for all effects. Models with >1 main effect were refined using model averaging (*MuMIn* package; Bartoń, 2018). The initial model set comprised main models and all possible subset models. Resulting models were ranked by AICc. For each analysis, model averaging was applied to a 'final set' of models with ΔAICc ≤6, excluding any model where a simpler (nested) version of the model with lower AICc existed (Richards et al., 2011). Predictors in averaged models were standardised (mean = 0, SD = 1) to improve interpretation of averaged effects. Estimates ± SE are reported from the full average. Predicted values for plotting were generated from the final averaged models (*predict* function, *stats* package).

3.1. Tree growth

After analysing total biomass in models containing diameter, height and combinations of both as predictors, we identified that the model containing tree diameter as the sole main effect was the best predictor of total biomass (see Supplementary materials - Text Box 3, Table S2). We therefore used diameter alone as our measure of tree growth. Tree growth was analysed as baseline diameter (week 1); change in diameter since week 1 under constant lighting treatments (ALAN-ALAN and Control-Control; weeks 11, 18 and 38), and change in diameter since week 1 under all four lighting treatment groups (week 38 only).

3.2. Psyllid survival and productivity

Parental mortality was analysed as the proportion of adults alive at day 7. We separately analysed the effects of ALAN on psyllid oviposition success (eggs/no eggs) and then number of eggs laid in successful clutches. Subsequent life stages were analysed as the proportion of successful individuals, weighted by total number of individuals (so that hatching success comprised the proportion of eggs hatched, weighted by total number of eggs laid, and so on). Lerp productivity was analysed as weighted proportion of lerps produced per established nymph. Prior to modelling, all proportions were standardised to the range 0–1. 'Side of tree' was dropped from models where confidence intervals for effects of 'Side of tree = North' and 'Side of tree = South' overlapped.

4. Results

4.1. Tree physiology, morphology and growth

Visual inspection of the principal components analysis biplot indicated that the control and ALAN treatments were largely undifferentiated by PC1, which loaded heavily on physiological attributes (photosynthesis and transpiration, both day- and night-time; Table 1, Fig. 3). The two treatment groups were more strongly differentiated by

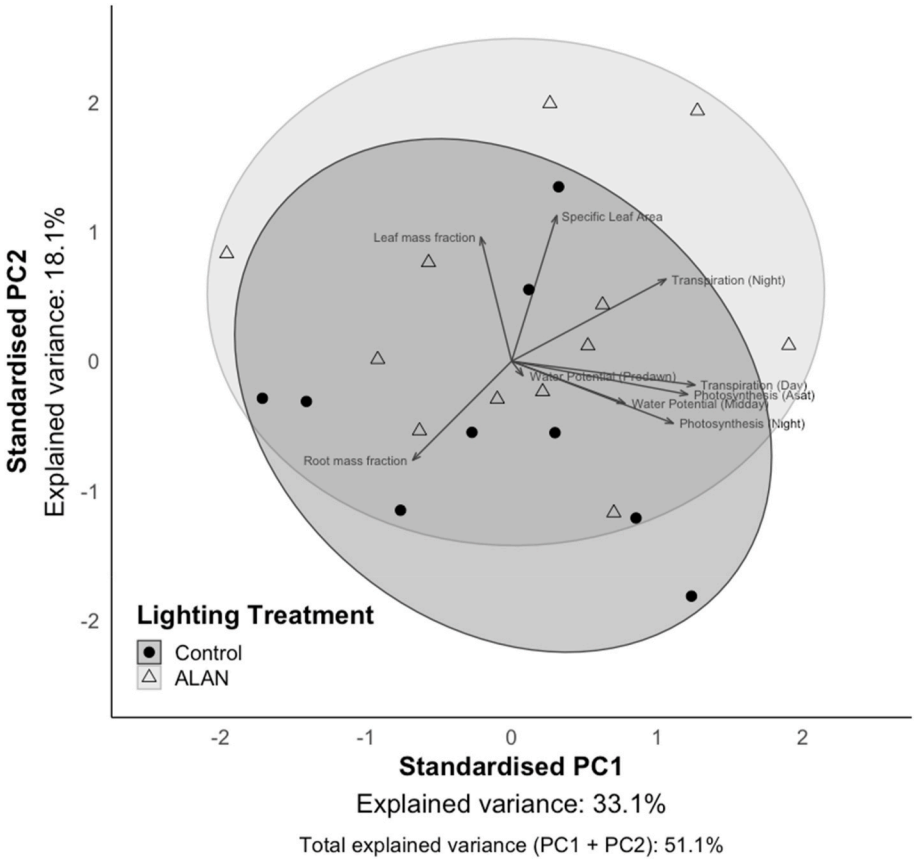

Fig. 3. Principal components analysis (PCA) biplot for the main morphological and physiological responses of *Eucalyptus camaldulensis* saplings grown under artificial light at night (ALAN; n = 12) or unlit (control; n = 9) conditions. Arrows = loading vectors for morphological and physiological responses (longer arrow = more variance explained). Ellipses = Khachiyan optimized ellipses enclosing observations within each treatment group.

Table 3
Model estimates with 95% confidence intervals, and treatment means with standard error, for the effect of lighting treatment (ALAN/Control), week (where relevant) and their interaction on tree growth and key morphological traits in *Eucalyptus camaldulensis*. a-e: the final set of models (ΔAICc ≤6) comprised a single model; f: model averaged results for final set are presented. Effects for which the 95% CI does not straddle zero are in bold. Estimates and confidence intervals are reported on the scale modelled (Ln, logit or neither, as indicated); mean ± SE values are untransformed.

	Estimates (±SE)	95% Conf. Interval (lower & upper bounds)	Mean (±SE)	
a. Specific leaf area (m^2kg^{-1}) – week 40, constant lighting treatment (Log scale) *n: ALAN = 12; Control: 11*				
Intercept	2.21 ± 0.07	2.06, 2.36		
Lighting	**0.14 ± 0.05**	**.0003, 0.25**	**10.37 ± 0.39 (ALAN)**	**9.40 ± 0.60 (Control)**
b. Root mass fraction – week 40, constant lighting treatment (Logit scale) *n: ALAN = 12; Control: 11*				
Intercept	−1.51 ± 0.07	−1.64, −1.38		
Lighting	**−0.21 ± .003**	**−0.22, -0.21**	**0.16 ± 0.01 (ALAN)**	**0.18 ± 0.01 (Control)**
c. Leaf mass fraction – week 40, constant lighting treatment (Logit scale) *n: ALAN = 12; Control: 11*				
Intercept	−1.26 ± 0.05	−1.41, −1.12		
Lighting	**0.13 ± .003**	**0.13, 0.14**	**0.24 ± .011 (ALAN)**	**0.23 ± 0.01(Control)**
d. Diameter – week 1 (mm) *n: ALAN = 71; Control = 67*				
Intercept	1.51 ± 0.08	1.32, 1.69		
Lighting	−0.05 ± 0.07	−0.18, 0.08	1.46 ± 0.04 (ALAN)	1.50 ± 0.05 (Control)
e. Change in diameter from week 1 to weeks 11, 18, 38 under constant lighting treatment (Log scale) *n: ALAN = 27, Control = 27*				
Intercept	1.36 ± 0.06	1.24, 1.50		
Week	**1.34 ± 0.04**	**1.26, 1.42**	**1.58 ± 0.06 (Week 11)** **4.07 ± 0.20 (Week 18)**	**10.53 ± 0.46 (Week 38)**
f. Change in diameter from week 1 to week 38 under swapped lighting treatments (Log scale) *n: ALAN-ALAN = 27; Control-Control = 27; ALAN-Control = 27; Control-ALAN = 25*				
Intercept	0.00 ± 0.00	0.00, 0.00		
Lighting (First treatment)	0.01 ± 0.03	−0.04, 0.07	11.80 ± 0.62 (ALAN)	10.67 ± 0.49 (Control)
Lighting (Second treatment)	−0.01 ± 0.02	−0.04, 0.03	10.82 ± 0.51 (ALAN)	11.64 ± 0.62 (Control)

PC2, which loaded heavily on morphological attributes (specific leaf area, leaf mass fraction and root mass fraction; Table 1, Fig. 3), suggesting that ALAN affected tree morphology more strongly than physiology.

When tested with streetlight-level ALAN (40 μmol $m^{-2}s^{-1}$) at night all trees (regardless of lighting treatment) produced a net photosynthetic response (Table 2), albeit at a level an order of magnitude lower than under daylight (1800 μmol/m^2/s) (mean ± SE photosynthesis: night = 1.52 ± 0.10 μmol $m^{-2}s^{-1}$; day = 16.1 ± 0.74 μmol $m^{-2}s^{-1}$). Thus, trees in the ALAN treatment were likely photosynthesising nightly over the duration of the study (whereas presumably control trees were not). However, this did not translate into clear variation between ALAN and control trees in any of the measured tree physiological parameters (Table 2). Light saturated photosynthesis (A_{sat}) and diurnal transpiration were higher in leaves at 150 cm versus 30 cm height and water potential was lower at midday than dawn (Table 2).

We found some support for a direct impact of ALAN on tree investment: in harvested trees (taken at week 40), leaf mass fraction and specific leaf area were higher for ALAN trees compared to control trees, while root mass fraction was lower (Table 3a–c, Fig. 4a–c). In contrast, while there was a clear positive relationship between tree age and diameter, this was consistently unrelated to ALAN treatment (Table 3 d-f) or the timing of ALAN exposure (no interaction between current and previous ALAN treatments; Table 3 d-f).

4.2. Psyllid colonisation

There was no effect of ALAN treatment (current or historic) on parental adult psyllid mortality (Table 4). However, current exposure to ALAN increased the number of lerps produced by each established nymph by approximately 8.4% (mean ± SE lerps per nymph: Control = 1.06 ± 0.02; ALAN = 1.15 ± 0.03; Table 4, Fig. 3d). Hatching success was positively associated with total rainfall during the egg development period (Table 4). There was no other effect of lighting treatment or climate variables on other psyllid life-history parameters in the F1 generation (Table 4).

5. Discussion

Here, using a novel tree-based mesocosm we demonstrated experimentally that ALAN at street light intensity promoted nocturnal photosynthesis and distorted the biomass allocation and leaf morphology of river red gum saplings. ALAN also increased the productivity of a colonising herbivore, the red gum lerp psyllid, but did not affect key life history events including adult survival, oviposition, hatching success, nymph establishment or development. Despite this species' dependence on *Eucalyptus* foliage for nutrition, shelter and reproduction, we found no clear evidence that ALAN-mediated shifts in leaf investment and morphology resulted in cascading impacts on the life cycle of psyllids.

5.1. Photosynthesis and growth

ALAN-mediated photosynthesis did not increase overall carbon assimilation by trees exposed to ALAN compared to control trees (Table 3e; no difference in growth). It is unlikely that ALAN trees were compensating by downregulating daytime photosynthesis (Park et al., 2020; Pettersen et al., 2010; van Gestel et al., 2005) as we found no significant difference in daytime photosynthetic capacity (Table 2d; no effect of ALAN treatment), and no evidence that the photosystem of ALAN trees adapted to take advantage of dim light (Table 2b; no difference in night-time photosynthetic capacity). However, we did find

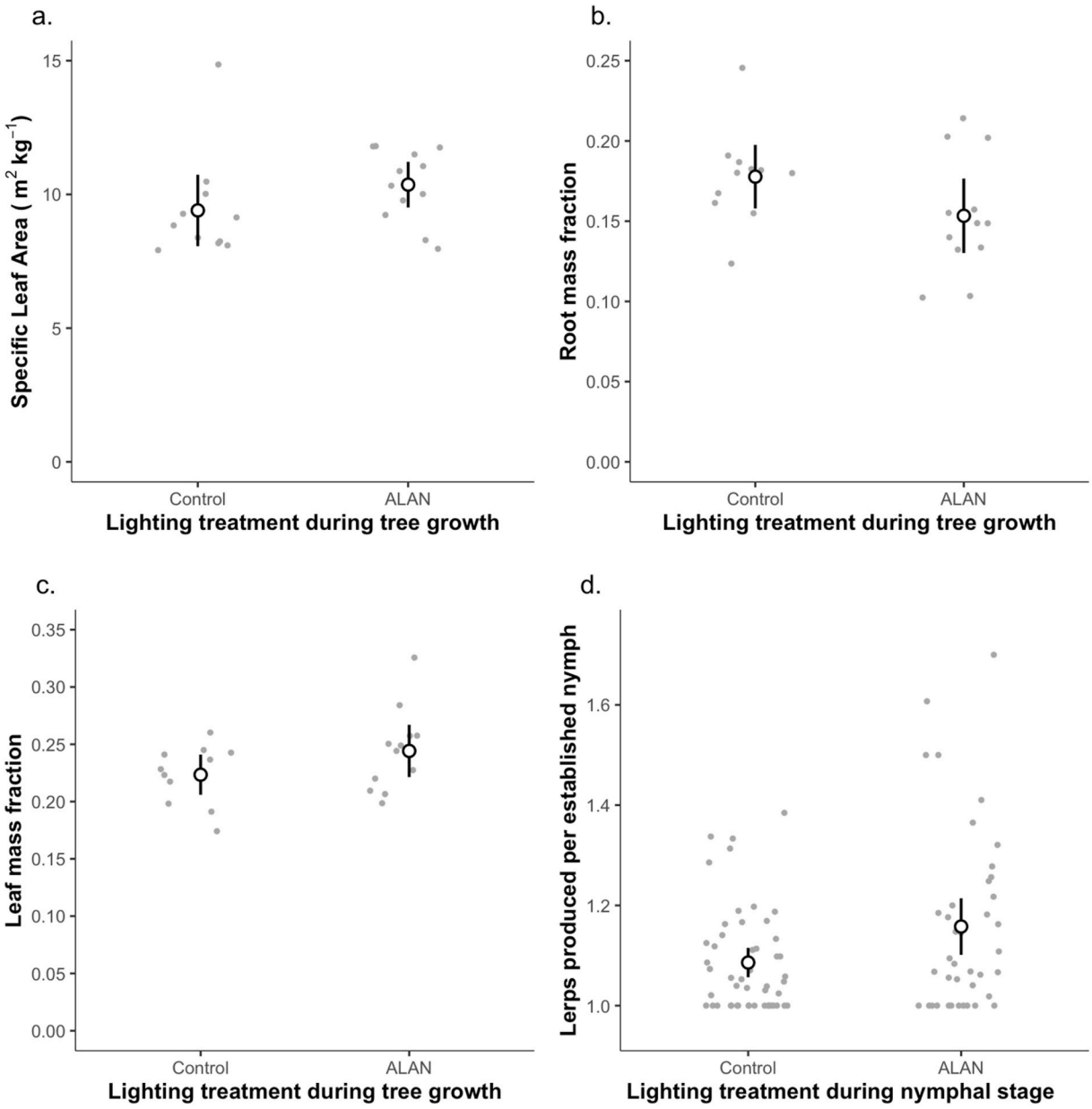

Fig. 4. Impact of lighting treatment during oviposition (first treatment) on (a) number of eggs laid in samples with >0 eggs and (b) number of parental adults surviving after 7 days. (c) Impact of lighting treatments (first treatment, second treatment) on proportion of individuals reaching key life stages: hatching success, lerp establishment, survival to adulthood. (d) Impact of lighting treatment during the psyllid life cycle (second treatment) on lerp productivity. Points = observed data; Circle and error bars = mean and 95% confidence interval; Box = Interquartile range; Bar = Median; Whiskers = minimium and maximum values. Asterisk = supported effect (95% CI does not included zero).

evidence for substantial developmental plasticity in the photosystem of *E. camaldulensis* (sufficient to produce differentiated 'sun' and 'shade' leaves in the upper and lower canopy; Table 2d). Since photosynthetic activity was measured towards the end of our experimental period, the absence of increased growth over the length of the experiment may suggest that night-time photosynthesis is age-dependent or seasonal. Alternatively, there may be subtle differences in daytime photosynthesis between ALAN and control trees (for example, daily duration of peak photosynthesis) not captured by our study. Previous studies have reported ALAN-mediated increases in above-ground plant biomass (Bennie et al., 2018; Speisser et al., 2021). These changes may have resulted from shifts in resource allocation from roots to leaves (see 'Morphological adaptation' below), particularly since ALAN levels employed in the studies were unlikely to have exceeded the light compensation point for most plants (Speisser et al.: 28.05 ± 1.25 lux at ground level; Bennie 29.6 ± 1.2 lux at ground level in the brightest treatment). If so, our results are consistent with these studies, and there remains no clear evidence that night-time photosynthesis under ALAN results in overall biomass gains.

5.2. Morphological adaptation

ALAN produced substantial changes in leaf morphology and leaf/root investment that are broadly consistent with shifts observed in plants growing under dim daylight (Table 3a, b, c). Plants acclimated to reduced daytime irradiance (due to latitude or shade) may maximise light-gathering by shifting investment from roots to leaves, and by producing 'shade leaves' characterised by higher specific leaf area, reduced photosynthetic response under light-saturated conditions, and reduced nitrogen/protein content (Givnish, 1988). The strength of these

Table 4
Model estimates with 95% confidence intervals for the effect of lighting treatment during oviposition (First treatment) and hatching and development (Second treatment), solar exposure, rain, side of tree, psyllid bag height and interactions on key psyllid life stages and lerp productivity. a-c: model averaged results for final set (ΔAICc ≤6) are presented; d-g: the final model set comprised a single model. Effects for which 95% CI does not straddle zero are in bold. Results are reported on the scale modelled. See Supplementary Fig. S3 for mean values.

	Estimates (±SE)	95% Confidence interval (lower and upper bounds)
a. Parental mortality – proportion of adults surviving (Logit scale)		
n: ALAN = 83; Control = 67		
Intercept	−1.92 ± 0.22	−2.35, −1.49
Lighting (First treatment)	−0.01 ± 0.17	−0.34, 0.32
Solar exposure	−0.31 ± 0.18	−0.66, 0.04
Lighting x Solar exposure	−0.27 ± 0.31	−0.87, 0.33
b. Oviposition success – proportion of samples with >0 eggs (Logit scale)		
n: ALAN = 85; Control = 78		
Intercept	−8.81 ± 1.0e+3	−2.0e+3, 2.0e+3
Lighting (First treatment)	0.08 ± 0.30	−0.50, 0.67
Side of tree	−0.12 ± 0.30	−0.71, 0.48
Rain	−13.5 ± 1.4e+3	−2.9e+3, 2.8e+3
Solar exposure	0.01 ± 0.09	−0.17, 0.20
c. Number of eggs laid – where >0 (Square root scale)		
n: ALAN = 54; Control = 51		
Intercept	4.60 ± 0.15	4.30, 4.89
Rain	0.37 ± 0.30	−0.21, 0.96
Solar exposure	0.30 ± 0.16	−0.02, 0.62
d. Hatching success – proportion of eggs hatched (Logit scale)		
n: ALAN-ALAN = 29; Control-Control = 32; ALAN-Control = 35; Control-ALAN = 32		
Intercept	−0.84 ± 0.46	−1.81, 0.06
Rain	**1.41 ± 0.28**	**0.85, 1.98**
e. Lerp establishment – proportion of nymphs establishing lerp (Logit scale)		
n: ALAN-ALAN = 23; Control-Control = 29; ALAN-Control = 33; Control-ALAN = 29		
Intercept	−0.35 ± 0.59	−1.52, 0.82
Solar exposure	0.30 ± 0.19	−0.08, 0.67
f. Survival to adulthood – proportion of nymphs surviving to adult (Logit scale)		
n: ALAN-ALAN = 12; Control-Control = 17; ALAN-Control = 17; Control-ALAN = 16		
Intercept	−0.91 ± 0.40	−2.12, 0.50
g. Lerp productivity – lerps produced per established nymph (Logit scale)		
n: ALAN-ALAN = 19; Control-Control = 23; ALAN-Control = 27; Control-ALAN = 22		
Intercept	0.53 ± 0.06	0.00, 0.00
Lighting (Second treatment)	**0.21 ± 0.11**	**3.53e-3, 0.42**

responses to dim natural light vary between taxa (Bebre et al., 2020), including among *Eucalyptus* species (Coble et al., 2014; James and Bell, 2000). In *E. camaldulensis,* dim-light adaptations in response to ALAN may be maladaptive, as this species relies on a deep root system to avoid desiccation (CSIRO, 2004). Any reduction in root investment may compromise the capacity of ALAN-exposed individuals to endure drought conditions. While ALAN had no impact on water status in our (albeit well-watered) saplings (Table 2f), further experimentation combining ALAN and drought stress may identify the physiological costs of ALAN-mediated reductions in root investment.

ALAN mediated shifts in leaf morphology could also have indirect impacts on related faunal communities, by disrupting herbivory or reproduction. We were surprised to find that the broader, thinner leaves produced under ALAN did not undermine the subsequent hatching success, development or survival of psyllid nymphs (Table 4d, e, f), since eggs and nymphs rely on access to leaf water and sap respectively (Hollis, 2004), and changes in leaf morphology may hinder attempts to locate vascular bundles (Brennan and Weinbaum, 2001). However, *G. brimblecombei* is associated with at least 10 *Eucalyptus* hosts (Hollis, 2004), and may thus exhibit greater plasticity in feeding behaviour than more host-specialised herbivores.

5.3. Lerp productivity & life history

The significant increase in the number of lerps created by ALAN-exposed nymphs, suggests that ALAN may have promoted increased feeding site shifts during the nymphal phase (Table 4g). Psyllid species across multiple families including *Glycapsis brimblecombei* (Aphalaridae) and *Cardiaspina densitexta* (Psyllidae) use colour or shade cues to select adult feeding (and thus oviposition) sites (Farnier et al., 2014; Farnier and Steinbauer, 2016; White, 1970a, b). Further experimentation may confirm whether initial nymphal feeding sites were made untenable by direct ALAN disturbance (e.g. shifting light/shade patterns at night), poor initial site choice (due to ALAN-muted colour cues) or poor nutrition (arising from ALAN impacts on leaf nutrient content). Poor nutrition may be less likely, as we found no evidence of cascading impacts on survival (White, 1970a, b). We also found no evidence of ALAN impacts on adult feeding (such as might be inferred from reduced adult survival or oviposition, neither of which was observed here).

More broadly, changes to lerp productivity could impact a wide variety of fauna in *Eucalyptus* woodlands; lerps provide a vital year-round food resource for birds (Barker and Vestjens, 1989; Paton, 1980), arboreal mammals (Dierenfeld, 2009), fruit bats (Law and Lean, 1992), invertebrates (Martínez et al., 2018) and humans (Faast et al., 2020). The direction of those impacts may depend upon whether the increase in number of lerps produced (here 8.4%; Table 4g) reflects an increase in the total weight of lerps produced (i.e. an increased food resource) or the same weight divided between more lerps (i.e. increase foraging effort per unit weight). Due to the effects of rain and dew partly dissolving (and thus reducing the weight of) lerps it was not possible to compare lerp weights in this study. Repeated experimental removal of lerps under laboratory conditions may clarify the relationship between the number and weight of lerps produced.

The general lack of response of red gum lerp psyllids to the presence of light at night (Table 4a–f) was perhaps surprising given that light is fundamental to multiple life history traits in this taxon and its relatives. Laboratory experiments on *Cardiaspina densitexta* found that hatching time was triggered by temperature and dawn light (White, 1968a) but was desychronised under constant light or constant darkness (i.e. with a complete loss of dawn cue) (White, 1968a). Moreover, in other invertebrates, the physiological and behavioural impacts of ALAN have been demonstrated at even lower light intensities than those used here (Durrant et al., 2020; Durrant et al., 2015; McLay et al., 2018; Thompson et al., 2019; Willmott et al., 2019). Instead, it appears that muting (but not wholly eliminating) the dawn cue may be insufficient to disrupt psyllid hatching cues (assuming these are similar for *G. brimblecombei* as for *C. densitexta*). Alternatively, a difference in experimental approaches may explain our results. Previous experiments with psyllids were laboratory based, with insects raised on harvested leaf discs that were fully hydrated at all times (White, 1968a); in contrast we raised psyllids on living trees exposed to the elements, where they may have benefited from non-photic timing cues, including the trees' fundamental daily water and nutrient cycles (which themselves respond to the availability of sunlight). These additional cues may have compensated for muted natural light signals.

6. Conclusion

Our study demonstrates that ALAN has direct species-level impacts on both a host tree and its colonising herbivore. This resulted in whole-tree shifts in resource allocation and leaf morphology, and increased lerp productivity. These findings add to the increasing body of evidence that ALAN may have significant 'bottom-up' impacts on ecological communities, mediated primarily through host plants (Bennie et al., 2015), now including trees. ALAN-mediated shifts in leaf investment have the potential to impact both trees and herbivores and promote cascading impacts on woodland food webs. Our study design standardised the number of leaves within each bag (although not leaf area or thickness), and this may have reduced the capacity for ALAN-mediated increases in leaf investment to impact the psyllid life cycle; for example, individual's choices of feeding and oviposition sites were more restricted than would otherwise be the case. However, at an ecosystem level, and over multiple generations, ALAN-mediated increases in foliage may expand the trophic and oviposition sites available to psyllids, potentially increasing the psyllid/lerp resource. This effect may be exacerbated by shifts in the number and weight of lerps produced under ALAN. Over the longer term, ALAN-impacted red gums may be more vulnerable to psyllid attack, increasing the risk of dieback and tree mortality (Hall et al., 2015; White, 1969). Given the link between drought stress and herbivore outbreaks in the psyllid-*Eucalyptus* system (Paine and Hanlon, 2010; White, 1969), the shift in leaf/root investment under ALAN may have synergistic effects on *E. camaldulensis* trees when exposed to drought. This is of concern across much of the river red gum's native and introduced range where hotter, drier conditions are forecast due to climate change. Broadening our understanding of how ALAN and other anthropogenic stressors (including human-induced rising temperatures) intersect will be critical if we are to mitigate their future impacts for potentially vulnerable tree species and the communities that live within them.

Author contributions statement

Martin T Lockett: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Vizualisation, Project administration, Funding acquisition. Rebecca Rasmussen: Investigation, Writing – review & editing. Stefan K Arndt: Conceptualization, Methodology, Supervision, Writing – review & editing. Gareth R Hopkins: Methodology, Supervision, Writing – review & editing. Therésa M Jones: Methodology, Resources, Supervision, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available from the Mendeley Data digital repository at: https://doi.org/10.17632/6brvzktzhj.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2022.119803.

References

Australian Government (Bureau of Meteorology), 2019. Daily maximum temperature - Melbourne (olympic park). In: Australian Government (Bureau of Meteorology). Melbourne, Victoria, Australia.
Barker, R.D., Vestjens, W.J.M., 1989. The Food of Australian BIrds (2 Volumes). CSIRO Australia, Melbourne.
Bartoń, K., 2018. MuMIn: Multi-Model Inference. R Package Version 1.40.4. The Comprehensive R Archive Network (CRAN).
Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48.
Bebre, I., Annighöfer, P., Ammer, C., Seidel, D., 2020. Growth, morphology, and biomass allocation of recently planted seedlings of seven European tree species along a light gradient. iForest 13, 261–269.
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. Philos. Trans. Royal Soc. B 370, 1–9.
Bennie, J., Davies, T.W., Cruse, D., Gaston, K.J., 2016. Ecological effects of artificial light at night on wild plants. J. Ecol. 104, 611–620.
Bennie, J., Davies, T.W., Cruse, D., Bell, F., Gaston, K.J., 2018. Artificial light at night alters grassland vegetation species composition and phenology. J. Appl. Ecol. 55, 442–450.
Berends, M.S., Luz, C.F., Friedrich, A.W., Sinha, B.N.M., Albers, C.J., C, G., 2021. Amr - an R package for working with antimicrobial resistance data. J. Stat. Software (accepted for publication).
Brennan, E.B., Weinbaum, S.A., 2001. Stylet penetration and survival of three psyllid species on adult leaves and 'waxy' and 'de-waxed' juvenile leaves of Eucalyptus globulus. Entomol. Exp. Appl. 100, 355–363.
Briggs, W.R., 2005. Physiology of plant responses to artificial lighting. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington, DC.
Cathey, H.M., Campbell, L.E., 1975. Security lighting and its impact on the landscape. J. Arboric. 1, 181–187.
City of Melbourne, 2020. In: Melbourne, C.o. (Ed.), Trees, with Species and Dimensions (Urban Forest. Melbourne.
Coble, A.P., Autio, A., Cavaleri, M.A., Binkley, D., Ryan, M.G., 2014. Converging patterns of vertical variability in leaf morphology and nitrogen across seven Eucalyptus plantations in Brazil and Hawaii, USA. Trees 28, 1–15.
R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
CSIRO, 2004. *Eucalyptus camaldulensis* Taxon Attribute File.
Demers, D.-A., Doraisa, M., Wien, C.H., Gosselin, A., 1998. Effects of supplemental light duration on greenhouse tomato (Lycopersicon esculentum Mill.) plants and fruit yields. Sci. Hortic. 74, 295–306.
Dierenfeld, E.S., 2009. Feeding behavior and nutrition of the sugar glider (Petaurus breviceps). Vet. Clin.: Exot. Anim. Pract. 12, 209–215.
Dominoni, D.M., Nelson, R.J., 2018. Artificial light at night as an environmental pollutant: an integrative approach across taxa, biological functions, and scientific disciplines. J. Exp. Zool. 329, 387–393.
Douglas, A.E., 2006. Phloem-sap feeding by animals: problems and solutions. J. Exp. Bot. 57, 747–754.
Durrant, J., Michaelides, E.B., Rupasinghe, T., Tull, D., Green, M.P., Jones, T.M., 2015. Constant illumination reduces circulating melatonin and impairs immune function in the cricket *Teleogryllus commodus*. PeerJ 3, e1075, 1-23.
Durrant, J., Green, M.P., Jones, T.M., 2020. Dim artificial light at night reduces the cellular immune response of the black field cricket, Teleogryllus commodus. Insect Sci. 27, 571–582.
Faast, R., Clarke, P.A., Taylor, G.S., Salagaras, R.L., Weinstein, P., 2020. Indigenous use of lerps in Australia: so much more than a sweet treat. J. Ethnobiol. 40, 328–347.
Farnier, K., Steinbauer, M.J., 2016. Elevated anthocyanins protect young Eucalyptus leaves from high irradiance but also indicate foliar nutritional quality to visually attuned psyllids. Ecol. Entomol. 41, 168–181.
Farnier, K., Dyer, A.G., Steinbauer, M.J., 2014. Related but not alike: not all Hemiptera are attracted to yellow. Front. Ecol. Evolut. 2, 1–12.
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. Proc. Biol. Sci. 283, 20160813.
Firmino-Winckler, D.C., Wilcken, C.F., de Oliveira, N.C., Oliveira de Matos, C.A., 2009. Biologia do psilídeo-de-concha *Glycaspis brimblecombei* Moore (Hemiptera, Psyllidae) em Eucalyptus spp. Rev. Bras. Entomol. 53, 144–146.
Gehring, C., Park, S., Denich, M., 2008. Close relationship between diameters at 30cm height and at breast height (DBH). Acta Amazonica 38, 71–76.
Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol. 15, 63–92.
Grenis, K., Murphy, S.M., 2019. Direct and indirect effects of light pollution on the performance of an herbivorous insect. Insect Sci. 26, 770–776.
Hall, A.A.G., Gherlenda, A.N., Hasegawa, S., Johnson, S.N., Cook, J.M., Riegler, M., 2015. Anatomy of an outbreak: the biology and population dynamics of a

Cardiaspina psyllid species in an endangered woodland ecosystem. Agric. For. Entomol. 17, 292–301.
Hay, R.K.M., Heide, O.M., 1983. Specific photoperiodic stimulation of dry matter production in a high-latitude cultivar of Poa pratensis. Physiol. Plantarum 57, 135–142.
Hodkinson, I.D., 2009. Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: psylloidea): a global synthesis. J. Nat. Hist. 43, 65–179.
Hollis, D., 2004. Australian Psylloidea: Jumping Plantlice and Lerp Insects. Australian Biological Resources Study (ABRS), Canberra, Australia.
Hopkins, G.R., Gaston, K.J., Visser, M.E., Elgar, M.A., Jones, T.M., 2018. Artificial light at night as a driver of evolution across urban–rural landscapes. Front. Ecol. Environ. 16, 472–479.
Huerta, A., Faúndez, M., Araya, J.E., 2010. Susceptibility of *Eucalyptus* spp. to an induced infestation of red gum lerp psyllid *Glycaspis brimblecombei* Moore (Hemiptera: Psyllidae) in Santiago, Chile. Cienc. Investig. Agrar. 37, 27–33.
James, S.A., Bell, D.T., 2000. Influence of light availability on leaf structure and growth of two Eucalyptus globulus ssp. globulus provenances. Tree Physiol. 20, 1007–1018.
Kavanagh, K.L., Pangle, R., Schotzko, A.D., 2007. Nocturnal transpiration causing disequilibrium between soil and stem predawn water potential in mixed conifer forests of Idaho. Tree Physiol. 27, 612–629.
Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., Fontaine, C., 2017. Artificial light at night as a new threat to pollination. Nature 548, 206–210.
Kramer, P.J., 1937. Photoperiodic stimulation of growth by artificial light as a cause of winter killing. Plant Physiol. 12, 881–883.
Law, B.S., Lean, M., 1992. An observation of little red flying-foxes (Pteropus scapulatus) feeding on lerps. Australian Mammology 15, 143–145.
Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2, 191–198.
Mac Nally, R., Cunningham, S.C., Baker, P.J., Horner, G.J., Thomson, J.R., 2011. Dynamics of Murray-Darling floodplain forests under multiple water stressors – the past, present and future of an Australian icon. Water Resour. Res. 47, 1–11.
Macgregor, C.J., Evans, D.M., Fox, R., Pocock, M.J.O., 2017. The Dark Side of Street Lighting: Impacts on Moths and Evidence for the Disruption of Nocturnal Pollen Transport.
Marshall, B., Biscoe, P.V., 1980. A Model for C3 Leaves Describing the Dependence of Net Photosynthesis on Irradiance: I. Derivation. Journal of Experimental Botany 31, 29–39.
Martínez, G., González, A., Dicke, M., 2018. Effect of the eucalypt lerp psyllid Glycaspis brimblecombei on adult feeding, oviposition-site selection, and offspring performance of the bronze bug, Thaumastocoris peregrinus. Entomol. Exp. Appl. 166, 395–401.
Matzke, E.B., 1936. The effect of street lights in delaying leaf-fall in certain trees. Am. J. Bot. 23, 446–452.
McLay, L.K., Green, M.P., Jones, T.M., 2017. Chronic exposure to dim artificial light at night decreases fecundity and adult survival in Drosophila melanogaster. J. Insect Physiol. 100, 15–20.
McLay, L.K., Nagarajan-Radha, V., Green, M.P., Jones, T.M., 2018. Dim artificial light at night affects mating, reproductive output and reactive oxygen species in Drosophila melanogaster. J. Exp. Zool. Part A 329, 419–428.
McMunn, M.S., Yang, L.H., Ansalmo, A., Bucknam, K., Claret, M., Clay, C., Cox, K., Dungey, D.R., Jones, A., Kim, A.Y., Kubacki, R., Le, R., Martinez, D., Reynolds, B., Schroder, J., Wood, E., 2019. Artificial light increases local predator abundance, predation rates, and herbivory. Environ. Entomol. 48, 1331–1339.
Messoudi, L., Maatouf, N., Rohi, L., 2017. Biology and development cycle of *Glycaspis brimblecombei* Moore, 1964 (Hemiptera: Psyllidae) on 2 species of Eucalyptus: *Eucalyptus camaldulensis* and *Eucalyptus grandis*. Int. J. Acad. Stud. 3, 129–141.
Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L., McKechnie, A.E., 2015. Stacking the odds: light pollution may shift the balance in an ancient predator–prey arms race. J. Appl. Ecol. 52, 522–531.
Moore, K.M., 1961. Observations on some Australian forest insects: 8. The biology and occurrece of *Glycaspis baileyi* Moore in New South Wales. 86:185–200. Proc. Linn. Soc. NSW 86, 185–200.
NOAA Earth Observation Group, 2019. Visible infrared imaging radiometer suite (VIIRS) data. In: Earth Observation Group, N.O.a.A.A. National Geophysical Data Center. Accessed at: www.lightpollutionmap.info.
Paine, T.D., Hanlon, C.C., 2010. Integration of tactics for management of Eucalyptus herbivores: influence of moisture and nitrogen fertilization on red gum lerp psyllid colonization. Entomol. Exp. Appl. 137, 290–295.
Park, J., Lee, H.B., An, S.K., Lee, J.H., Kim, K.S., 2020. Increasing Duration and Intensity of Nighttime Supplemental Lighting Promotes Growth and Photosynthesis in Young Cymbidium Plants. Horticulture, Environment, and Biotechnology.
Paton, D.C., 1980. The importance of manna, honeydew and lerp in the diets of honeyeaters. Emu 80, 213–226.
Pedersen, T.L., 2021. Ggforce: Accelerating 'ggplot2', R package version 0.3.3.
Pettersen, R.I., Torre, S., Gislerød, H.R., 2010. Effects of leaf aging and light duration on photosynthetic characteristics in a cucumber canopy. Sci. Hortic. 125, 82–87.
Phillips, N.G., Lewis, J.D., Logan, B.A., Tissue, D.T., 2010. Inter- and intra-specific variation in nocturnal water transport in Eucalyptus. Tree Physiol. 30, 586–596.
Rich, C., Longcore, T., 2006. Ecological Consequences of Artificial Night Lighting. Island Press, Washington.
Richards, S.A., Whittingham, M.J., Stephens, P.A., 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. Behav. Ecol. Sociobiol. 65, 77–89.
Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. Funct. Ecol. 6, 744–750.
Sanders, D., Frago, E., Kehoe, R., Patterson, C., Gaston, K.J., 2021. A meta-analysis of biological impacts of artificial light at night. Nat. Ecol. Evolut. 5 (1), 74–81. https://doi.org/10.1038/s41559-020-01322-x.
Sanders, D., Gaston, K.J., 2018. How ecological communities respond to artificial light at night. J. Exp. Zool. Part A 1–7.
Sanders, D., Kehoe, R., Tiley, K., Bennie, J., Cruse, D., Davies, T.W., Veen, F.J.F.v., Gaston, K.J., 2015. Artificial nighttime light changes aphid-parasitoid population dynamics. Sci. Rep. 5.
Schréder, Sylvania, 2021. Sylvania StreetLED Mk II (Datasheet). Schréder SA. Online at: https://au.schreder.com/sites/default/files/2021-02/STREETLED%20MK%20II_product_sheet_March2021.pdf.
Segrestin, J., Mondy, N., Boisselet, C., Guigard, L., Lengagne, T., Poussineau, S., Secondi, J., Puijalon, S., 2021. Effects of artificial light at night on the leaf functional traits of freshwater plants. Freshw. Biol. 66, 2264–2271.
Škvareninová, J., Tuhárska, M., Škvarenina, J., Babálová, D., Slobodníková, L., Slobodník, B., Středová, H., Minďaš, J., 2017. Effects of light pollution on tree phenology in the urban environment. Morav. Geogr. Rep. 25, 282–290.
Speisser, B., Liu, Y., van Kleunen, M., 2021. Biomass responses of widely and less-widely naturalized alien plants to artificial light at night. J. Ecol. 109, 1819–1827.
Stare, J., 2019. Light Pollution Map (Website).
Sullivan, S.M.P., Hossler, K., Meyer, L.A., 2019. Artificial lighting at night alters aquatic-riparian invertebrate food webs. Ecol. Appl. 29, e01821.
Thompson, E.K., Cullinan, N.L., Jones, T.M., Hopkins, G.R., 2019. Effects of artificial light at night and male calling on movement patterns and mate location in field crickets. Anim. Behav. 158, 183–191.
Tu, K.P., Fisher, J.B., 2019. Photosynthetic Light Response Curve Fitting (Excel spreadsheet tool). Landflux.org downloaded at: https://landflux.org/tools.
van Geffen, K.G., van Eck, E., de Boer, R.A., van Grunsven, R.H.A., Salis, L., Berendse, F., Veenendaal, E.M., 2015. Artificial light at night inhibits mating in a Geometrid moth. Insect Conserv. Divers. 8, 282–287.
van Gestel, N.C., Nesbit, A.D., Gordon, E.P., Green, C., Pare, P.W., Thompson, L., Peffley, E.B., Tissue, D.T., 2005. Continuous light may induce photosynthetic downregulation in onion - consequences for growth and biomass partitioning. Physiol. Plantarum 125, 235–246.
Wakefield, A., Stone, E.L., Jones, G., Harris, S., 2016. Light-emitting Diode Street Lights Reduce Last-Ditch Evasive Manoeuvres by Moths to Bat Echolocation Calls. Royal Society Open Science, p. 2.
White, T.C.R., 1968a. Hatching of eggs of *Cardiaspina densitexta* (Homoptera, Psyllidae) in relation to light and temperature. J. Insect Physiol. 14, 1847–1859.
White, T.C.R., 1968b. Uptake of water by eggs of Cardiaspina densitexta (Homoptera: Psyllidae) from leaf of host plant. J. Insect Physiol. 14, 1669–1683.
White, T.C.R., 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology 50, 905–909.
White, T.C.R., 1970a. The nymphal stage of *Cardiaspina densitexta* (Homoptera : Psyllidae) on leaves of *Eucalyptus fasciculosa*. Aust. J. Zool. 18, 273–293.
White, T.C.R., 1970b. Some aspects of the life history, host selection, dispersal and ovipostion of adult Cardiaspina densitexta (Homoptera : Psyllidae). Aust. J. Zool. 18, 105–117.
Willmott, N.J., Henneken, J., Selleck, C.J., Jones, T.M., 2018. Artificial light at night alters life history in a nocturnal orb-web spider. PeerJ 6, e5599.
White, T.C.R., 2016. Lerp insect (*Cardiaspina densitexta*) outbreaks on pink gum (*Eucalyptus fasciculosa*) in the southeast of South Australia. Austral Ecology 41 (3), 339–341. https://doi.org/10.1111/aec.12313.
Willmott, N.J., Henneken, J., Elgar, M.A., Jones, T.M., 2019. Guiding lights: foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night. Ethology 125, 289–297.
Yao, X.C., Tu, H.Q., Wang, X.L., Wang, J., 2021. The effect of supplemental LED night lighting on the growth and physiology of the Para rubber tree. J. Rubber Res. 24 (3), 321–326. https://doi.org/10.1007/s42464-021-00095-7.