

Concepción, julio 2021.

Señora:
Carolina Schmidt
MINISTRA MEDIO AMBIENTE
Presente.

Ref. Observaciones Consulta Ciudadana Norma de emisión para la regulación de la contaminación Lumínica.

De nuestra consideración:

Junto con saludarle, le comento que se realizó una sesión extraordinaria para desarrollar un trabajo participativo con todas/os los integrantes del Consejo Consultivo de la Región del Biobío, con el objetivo de consensuar observaciones al anteproyecto de norma de emisión elaborado a partir de la revisión del decreto supremo Revisión N°43 de 2012, del Ministerio del Medio Ambiente, que establece la Norma de emisión para la regulación de la contaminación Lumínica.

De esta sesión se concluyen las siguientes observaciones:

1. La luz artificial en la noche tiene potencialmente efectos generalizados en los hábitats terrestres y costeros. Se requiere considerar en la norma numerosos estudios publicados al respecto, que informan de posibles amenazas para los sistemas naturales a través de la aniquilación de interacciones positivas a través de los niveles tróficos, potencialmente perjudicando la relación entre la biodiversidad y el funcionamiento de los ecosistemas e interactuando con otros factores estresantes globales y locales que actualmente afectan las áreas costeras. Se adjuntan 4 estudios de gran valor para enriquecer el anteproyecto de norma
2. Es importante resguardar las zonas urbanas definidas y no sólo las zonas que poseen planes de Recuperación, Conservación y Gestión de Especies (RECOGE) para aquellas especies clasificadas por el Reglamento para la Clasificación de Especies Silvestres, y que el Ministerio del Medio Ambiente facultades para ejecutar programas de investigación, protección y conservación de la biodiversidad, sino también otros ambientes en los que se pueden observar impactos negativos a los ecosistemas que son afectados por la contaminación lumínica.
3. Otro tema son los plazos que se establecen para el recambio de luminarias de hasta 5 años, la mayoría de las/os Consejeras/os propone reducirlo a 3 años para la inversión y cambio de las luminarias, considerando que existen experiencias anteriores que pueden servir de guía para el desarrollo de esta acción de forma más rápida y eficiente
4. Se debe regular la iluminación en las zonas industriales que están cerca de áreas de protección natural, considerando que pueden afectar la biodiversidad existente del entorno natural.
5. Otro tema es el impacto es el crecimiento urbano que es un fenómeno muy intenso en el país con relación a las distintas áreas naturales. Saber si esta norma va a ser considerada en este aspecto.

Nota: Se adjuntan los estudios, según lo indicado en el punto 1.

En representación de las/os Integrantes del Consejo Consultivo:

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Mario Delannays Araya. Seremi de Medio Ambiente. Región del Biobío

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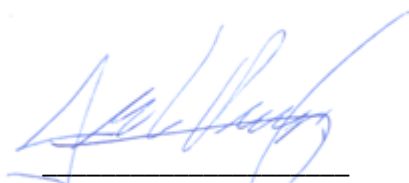
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Ronald Ruf Wilkomirsky Cámara de la Producción y del Comercio CPC Biobío

Esperando una buena acogida y atento a novedades, le saluda atentamente a usted.



Luciano Pérez Fuentealba
Presidente Consejo Consultivo,
Seremi Medio Ambiente,
Región del Biobío.

Artificial light at night alters trophic interactions of intertidal invertebrates

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Summary

1. Despite being globally widespread in coastal regions, the impacts of light pollution on intertidal ecosystems has received little attention. Intertidal species exhibit many night-time-dependent ecological strategies, including feeding, reproduction, orientation and predator avoidance, which are likely negatively affected by shifting light regimes, as has been observed in terrestrial and aquatic taxa.

2. Coastal lighting may shape intertidal communities through its influence on the nocturnal foraging activity of dogwhelks (*Nucella lapillus*), a widespread predatory mollusc that structures biodiversity in temperate rocky shores. In the laboratory, we investigated whether the basal and foraging activity of this predator was affected by exposure to night-time lighting both in the presence and absence of olfactory predator cues (*Carcinus maenas*, common shore crab).

3. Assessments of dogwhelks' behavioural responses to night-time white LED lighting were performed on individuals that had been acclimated to night-time white LED lighting conditions for 16 days and individuals that had not previously been exposed to artificial light at night.

4. Dogwhelks acclimated to night-time lighting exhibited natural refuge-seeking behaviour less often compared to control animals, but were more likely to respond to and handle prey irrespective of whether olfactory predator cues were present. These responses suggest night-time lighting likely increased the energetic demand of dogwhelks through stress, encouraging foraging whenever food was available, regardless of potential danger. Contrastingly, whelks not acclimated under night-time lighting were more likely to respond to the presence of prey under artificial light at night when olfactory predator cues were present, indicating an opportunistic shift towards the use of visual instead of olfactory cues in risk evaluation.

5. These results demonstrate that artificial night-time lighting influences the behaviour of intertidal fauna such that the balance of interspecific interactions involved in community structuring may be affected.

Key-words: artificial light at night, intertidal ecosystems, LEDs, light pollution, predation, rocky shores, species interactions

Introduction

Artificial light at night is pervasive across the globe with sky brightness resulting from light pollution continuing to spread at an estimated rate of 6% per year (Holker *et al.* 2010). From buildings, vehicles and streetlights, to oil rigs, ships and underwater vessels, artificial illumination is

found even in remote locations away from urban centres (Davies *et al.* 2014; Falchi *et al.* 2016). Yet the environmental threat associated with human-induced changes to natural light regimes has been poorly understood until recently, despite their importance for guiding biological processes in a variety of taxa (Gaston *et al.* 2013).

Natural light regimes determine when individuals are most active (Bradshaw & Holzapfel 2010), are used for orientation and navigation (Pardi & Papi 1953), and enable effective intraspecific communication (Haddock,

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Moline & Case 2009; Mäthger *et al.* 2009; Siebeck *et al.* 2010). The natural rhythm of celestial bodies guides synchronised reproductive events (Lessios 1991; Bentley, Olive & Last 1999; Gorbunov & Falkowski 2002), and migratory behaviour (Berge *et al.* 2009; Cohen & Forward 2009; Last *et al.* 2016) across otherwise disparate populations. The intensity and spectra of light also influence predator detection and avoidance (Troschianko *et al.* 2009), and influence species distributions through habitat selection (Thorson 1964; Mundy & Babcock 1998; Kiyofuji & Saitoh 2004). In the past decade, a dramatic increase in the number of light-sensitive taxa and biological processes impacted by night-time lighting has been revealed. The variety of known impacts include those on movement and behaviour (Bird, Branch & Miller 2004; Rotics, Davan & Kronfeld-Schor 2011; Becker *et al.* 2013), disorientation (Tuxbury & Salmon 2005; Merkel 2010), sexual maturation (Oppedal, Dempster & Stien 2011; Dominoni, Quetting & Partecke 2013) and predator–prey dynamics (Rydell 1992; Yurk & Trites 2000; Dwyer *et al.* 2013). Yet, while our understanding of the ecological implications of light pollution has grown, there has been little research into its potential impacts on the many taxa that utilise natural light regimes in marine ecosystems (Thorson 1964; Naylor 2010). Previous studies have highlighted detrimental effects on the movement, habitat selection and foraging patterns of marine vertebrates, including fish (Oppedal, Dempster & Stien 2011; Becker *et al.* 2013), wading birds (Santos *et al.* 2010; Dwyer *et al.* 2013) and sea turtles (Witherington & Bjørndal 1991; Kamrowski *et al.* 2012; Mazar *et al.* 2013). Light pollution is, however, likely altering the structure and functioning of marine ecosystems in many other ways that have yet to be explored (Davies *et al.* 2014). Approximately 22% of coastlines (Davies *et al.* 2014) and 35% (20% across their entire area) of marine-protected areas (Davies *et al.* 2016) around the world experience artificial light at night, suggesting that many intertidal ecosystems are exposed. The potential impacts of altering natural day–night cycles that inform the behaviour of many intertidal species nonetheless remains unexplored.

The distribution and foraging of predatory species is commonly influenced by artificial light at night in terrestrial ecosystems (Stone, Jones & Harris 2009; Davies, Bennie & Gaston 2012). On temperate rocky shores, the dogwhelk *Nucella lapillus* (Linnaeus 1758) exerts strong top-down controls on biodiversity by preying on limpets, barnacles and mussels, releasing canopy-forming algae from space competition and indirectly facilitating the establishment of canopy-affiliated taxa as a result (Crothers 1985; Hughes & Burrows 1993). Dogwhelks are widely distributed across the North Atlantic, often in close proximity to urban centres (Crothers 1985), indicating that many populations are likely exposed to artificial light at night year-round (Gaston & Bennie 2014). Dogwhelks have well-developed lens eyes (Richter *et al.* 2010) which – alongside olfactory cues (Morgan 1972) – are

used to navigate their environment and detect predators and prey. As dogwhelks are typically most active from dusk onwards (Crothers 1985), chronic exposure to artificial night-time lighting is expected to have significant impacts on their predatory activity and predator avoidance. Furthermore, dogwhelks have proven a useful model species for investigating the impacts of other global anthropogenic stressors, such as ocean acidification and warming, on animal behaviour, interspecific interactions and species distributions (Queirós *et al.* 2015).

The objective of this study was to determine whether night-time lighting influenced the nocturnal activity, foraging behaviour and risk aversion of *N. lapillus*. Specifically, we asked (i) whether chronic exposure to night-time lighting influenced the nocturnal activity and foraging behaviour of dogwhelks; (ii) whether exposing previously artificial light naïve dogwhelks to night-time lighting influenced their nocturnal activity and foraging behaviour; and (iii) whether the responses of dogwhelks observed in (i) and (ii) were dependent on risk of predation as perceived via olfactory cues.

Materials and methods

OVERVIEW

Two consecutive laboratory experiments were undertaken to investigate the impact of artificial light at night on the activity and foraging of dogwhelks. The first assessed the behaviour of individuals previously exposed to artificial night-time lighting for 16 days (hereafter referred to as acclimated, in that they were acclimated to an artificial light regime followed by assessments under artificial light at night). The second assessed individuals that had not previously been exposed to artificial light at night (hereafter referred to as non-acclimated, in that they were acclimated to a natural light regime followed by assessment under artificial night light). In both experiments, the treatment individuals were compared to control individuals that had been acclimated to a simulated natural day–night cycle of light followed by assessment without artificial light at night. Using non-acclimated individuals and those allowed short-term acclimation under artificial night-time lighting granted a first insight into the plasticity of dogwhelk behaviour in response to this stressor. Each behavioural trial was undertaken both in the presence and absence of predation risk in the form of olfactory cues from *Carcinus maenas* (Leach 1814) in order to quantify whether measured responses to night-time lighting were modulated by risk perception. *Carcinus maenas* is a cathemeral predator of dogwhelks on rocky shores that is most active during nocturnal high tides (Crothers 1985; Trussell, Ewanchuk & Bertness 2003; Naylor 2010). The experimental set up in this study closely followed that in Queirós *et al.* (2015), which effectively identified the impacts of well-established global stressors such as ocean acidification and warming on dogwhelk predation.

EXPERIMENTAL SETUP

Adult dogwhelks were carefully hand-picked at low tide from Mount Batten, Plymouth Sound, United Kingdom (N 50°21'

30.29", E -4°70' 50.07") between April and June 2015 and then immediately transported to Plymouth Marine Laboratory's intertidal mesocosm system (Findlay *et al.* 2008). In summary, the laboratory is a controlled environment room where seawater temperature and tidal conditions are maintained to follow the natural variability of Plymouth Sound (Queirós *et al.* 2015, Supporting Information). In the lab, all animals were randomly allocated between two 1-m³ indoor mesocosm tanks which were supplied with re-circulating 1-µm filtered and aerated locally sourced seawater. All individuals were allowed to acclimate to mesocosm conditions for 16 days, during which they were allowed to feed *ad libitum* on blue mussels, *Mytilus edulis* (Linnaeus 1758), made available for 65 h between Friday and Monday every week.

The experimental setup for the mesocosms is illustrated in Fig. S1a, Supporting Information. In both mesocosms, A TMC GroBeam 1500 Ultima Natural Daylight LED tile light (illuminance 4430 lux at 400 mm in air) was used to simulate natural daylight conditions, with a day–night cycle adjusted weekly to simulate changes in the timing of sunrise and sunset at their source habitat (Table S1). Dogwhelks in the naturally lit mesocosm tank (mesocosm 1, Fig. S1) remained in darkness (0 lux) throughout the night-time period, as this best approximated natural nocturnal lighting conditions in rocky shores and other habitats unexposed to light pollution (Gaston *et al.* 2013). Those in the mesocosm with artificial light at night (mesocosm 2, Fig. S1) were illuminated with an LED aquarium light (Interpet LED Bright White Light Single Row 36 cm) to simulate artificially lit conditions of 22.3 ± 3.2 SE lux across the water's surface, comparable to upper light levels measured at the surface of waters adjacent to illuminated structures in the built marine environment (piers, port and harbour walls, offshore infrastructure installations) (GHD 2012; Davies *et al.* 2015). Light trespass between treatments and the surrounding laboratory environment was avoided by covering each mesocosm tank with 0.12-mm-thick rubberised blackout fabric. All other environmental conditions (temperature, tidal regime, aeration, timing and quantity of food supply) were consistent across mesocosm tanks. Water temperature and salinity were monitored daily and maintained at 12.4 ± 0.4 °C and 33.1 ± 0.2 ppt, respectively, in both tanks. While LED lights do emit heat, it is relatively little and thus had no impact on the temperature within the mesocosms.

BEHAVIOURAL TRIALS

After 16 days of acclimation to the mesocosm conditions, 12 dogwhelks were randomly selected from the mesocosm tanks and divided between four 12 × 12 × 40 cm glass assessment tanks (three individuals per tank), within which a range of behavioural trials were performed after sunset. Two assessment tanks per light treatment were individually placed at one end of two light secure imaging boxes (n assessment tanks_{total} = 4) within which the light regime was manipulated to reflect each of the two mesocosm conditions. Digital SLR cameras (Canon EOS 500 D, 15 MP) were placed at the opposing end of both imaging boxes. One box (imaging box 1, Fig. S1b) contained red LED lights (max. 10 lux) to provide as close to natural darkness as was feasible, while providing sufficient light to adequately capture the animals' behaviour via the cameras. Aquatic gastropods typically possess a single visual pigment with a peak spectral sensitivity between 470–505 nm (Hughes 1970; Gillary 1974; Zhukov *et al.* 2006), thus the red LEDs provided sufficient light to capture images

while minimising the amount of light at wavelengths that dogwhelks were able to detect and respond to. The other box (imaging box 2, Fig. S1b) was internally illuminated by an Interpet Bright White LED light (21.16 ± 3.05 lux) to simulate the artificially lit night-time conditions. The two tanks within each box were individually supplied via a peristaltic pump system (Watson-Marlow, flow 20 mL min⁻¹) with re-circulating filtered seawater (as before). Olfactory cues from *C. maenas* were introduced to the predator treatment by circulating seawater through an adjacent tank (outside of the imaging box and not visible to the dogwhelks) containing shore crabs (*C. maenas*). This allowed us to assess the impact of night lighting on dogwhelk behaviour both in the presence and absence of a perceived predation risk simultaneously. Crabs were also collected on a weekly basis, from the same collection site.

Dogwhelks were gently lowered into the assessment tanks (n total = 12, n per imaging box = 6, n per assessment tank = 3), the enclosures sealed and time-lapse photography initiated immediately. In summary, 6 h assessments were divided into two sections of 3 h each: the first section was used to assess individual basal activity; the second section was used to assess response to a prey mimic. Images were recorded every 5 min (n images per trial = 288; n images per tank = 72; n images per section = 36) using remote control of the digital SLR cameras within each imaging box via a PC and the time-lapse software EOS GB Timelapse 3 Pro. In total, five response variables were assessed. The basal activity of individuals was measured via assessment of the expected behaviour exhibited by dogwhelks in these conditions, which is to travel from the bottom of the assessment tanks to the waterline (as per Vadas, Burrows & Hughes 1994; Queirós *et al.* 2015). The speed at which they did so was also measured as this behaviour is tightly linked to individual basal metabolic rate (Queirós *et al.* 2015). Individual response to prey was measured as: whether or not dogwhelks moved towards an introduced prey mimic; whether or not they handled the prey mimic; the distance travelled before handling the prey; or, if they did not make contact, the total distance travelled during the 3-h assessment. The prey mimic consisted of 10 g of fresh, crushed blue mussels (*Mytilus edulis*, Linnaeus 1758) within a sealed mesh bag, which was gently lowered to the bottom of the assessment tanks near the diffusing air stone to allow adequate distribution of the prey odour cue (*sensu* Queirós *et al.* 2015). Blue mussels are one of the key prey items for dogwhelks in natural systems. The dogwhelks were starved throughout the behavioural trials to maximise the response to prey. We did not assess potential within-gender differences between treatments or during the assessments.

ACCLIMATED EXPERIMENT

To assess the responses of dogwhelks acclimated to the artificial light regime in mesocosm 2, 12 individuals were randomly selected from both mesocosms ($n_{\text{mesocosm 1}} = 6$; $n_{\text{mesocosm 2}} = 6$) and divided between the assessment tanks within the imaging boxes that reflected their acclimation conditions. The procedure for this experiment is illustrated in Fig. S1. Behavioural assessments as outlined above were repeated two to four times per week over 4 weeks using new individuals (mussels, dogwhelks and crabs) until a total of 12 assessments per treatment were completed (n per night = 4; n per treatment = 12; n total = 48).

NON-ACCLIMATED EXPERIMENT

To assess non-acclimated responses to artificial light at night, a second experiment was conducted following completion of the first. Twelve individuals were randomly selected from mesocosm 1 and divided between the four assessment tanks within both imaging boxes. The procedure for this experiment is illustrated in Fig. S2. Behavioural assessments as outlined above were repeated three to four times per week over 2 weeks using new individuals (mussels, dogwhelks and crabs) until a total of seven assessments per treatment were completed (n per night = 4; n per treatment = 7; n total = 28).

IMAGE ANALYSIS

Images were analysed using the open source image analysis software Image J (1.45S; National Institutes of Health, Bethesda, MD, USA). The trajectory of each of the three individual dogwhelks in each image set was tracked using the 'Manual tracking' plugin and custom-built scripts, considering both length of trajectory and time (used to calculate speed).

STATISTICAL ANALYSIS

In each experiment, we tested whether night-time light treatment (Light treatment) had a significant impact on the measured behavioural responses, and whether this impact was dependent on the presence or absence of predator cues (Light treatment : Predator cue interaction). The effects of Light treatment and Predator cue were tested by comparing a model containing both main effects, with models where each was dropped. The effect of the interaction between Light treatment and Predator cue was tested by comparing the full model with one containing only the first terms for Light treatment and Predator cue.

Each behavioural response was analysed using either a generalised linear model or generalised linear mixed effects model (CRAN: lme4) fitted using appropriate error distributions (Gaussian for 'basal speed' and 'foraging distance'; binomial for the remaining logistic responses), following transformation if required (log in the case of 'foraging distance').

Mixed effects models were used where the inclusion of a random effects term describing the influence of interactions between individual dogwhelks in each assessment tank, improved model parsimony (Tables S2 and S3). Such interactions were considered likely to have a measurable impact on the behavioural responses, since decisions regarding, for example, whether to feed in the presence of a predator, may well depend on whether or not other individuals (competitors) are moving towards or handling a prey item (Queirós *et al.* 2015). To control for the influence of these competitive interactions, each individual was ranked (1–3) according to the order in which they were observed performing the measured behavioural responses, and these rankings were included as random effects in mixed effects models if they significantly improved model parsimony [decreased the value of Akaike's Information Criterion (AIC) by a value of two or more (Burnham & Anderson 2002); Tables S2 and S3].

Dogwhelks were ranked in the order in which they reached the waterline following introduction to the assay tanks when analysing the response variables 'Reached waterline' and 'Speed to waterline'. Dogwhelks were ranked in the order in which they moved in response to the introduction of the prey item when

analysing the response variables 'Response to prey', 'Foraging distance' and 'Prey handled'. Four alternative random effects models were compared for each measured behavioural response, one in which Rank was assumed to influence the response independently of other treatment variables (c. 1|Rank), one in which the influence of Rank was assumed to be dependent on the night-time lighting treatment (c. Treatment|Rank), one in which the influence of Rank was assumed to be dependent on whether or not olfactory predator cues were present (c. Predator|Rank), and one in which Rank was assumed to be dependent on both the Predator and the Light treatments. In cases where including Rank as a random effect improved model fit c. 1|Rank was found to be the most parsimonious random effects model structure (see Tables S2 and S3). The inclusion of random effects improved model parsimony only for the responses 'whether or not dogwhelks reached the waterline', and 'whether or not dogwhelks responded to the introduction of prey' (Tables S2 and S3).

To avoid zero inflated models, 46 and 51 values of zero were removed from the foraging distance models as they indicated either a lack of response or that the prey landed directly on top of the dogwhelk. These zero responses are, however, implicit in the probability of response models (binary response models). Where significant interactions between light and predator treatments were detected (See Table S4), Tukey's pairwise comparisons were performed (without correcting for false discovery rate) in order to quantify the nature of the interaction. (CRAN: lsmeans). All analyses were conducted using the statistical software R (R Core Team, 2013).

Results

Dogwhelks acclimated to the night-time light were significantly less likely to seek refuge at the waterline of the assessment tanks than those kept under the control conditions (Table 1a Light treatment, Fig. 1a), regardless of the presence of a predator cue (Table 1a Light treatment : Predator cue). The speed at which those dogwhelks that reached the waterline did so was, however, unaffected by the light treatments (Table 1b Light treatment). For non-acclimated dogwhelks, the light treatments did not alter the probability that they sought the waterline (Table 2a, Light treatment), nor did it influence the speed of those that did so (Table 2b, Light treatment).

In the acclimated experiment, a higher proportion of dogwhelks exposed to the night-time lighting regime responded to the introduction of the prey mimic (blue mussel tissue) compared to dogwhelks that were not exposed to artificial light at night (Table 1c Light treatment, Fig. 1b). Of those dogwhelks that responded to the introduction of prey, a higher proportion also handled the prey in the night-time lighting treatment compared to those in the simulated natural light regime (Table 1e, Fig. 1c).

The foraging distance covered by dogwhelks that responded to the introduction of prey was, however, not influenced by the light treatments (Table 1d Light treatment). No significant effects of light treatment on prey handling or foraging distances were detected in the

Table 1. The impact of night-time artificial lighting on the basal activity and predatory behaviour of acclimated dogwhelks (*Nucella lapillus*) in the presence and absence of olfactory predator (*Carcinus maenas*) cues. Results are presented for either generalised linear models or generalised linear mixed effects models comparing dogwhelks exposed to simulated natural daylight regimes vs. artificially lit night-time conditions (Light treatment), fully crossed with the presence or absence of olfactory cues from *C. maenas* (Predator cue). The choice of whether or not to include a random effect to control for interactions between individuals, and the specification of the random effects term were selected by comparison of Akaike's Information Criterion (see Table S2). In cases where the inclusion of a random effect improved model parsimony, c. 1|rank was always the most parsimonious random effects specification (Table S2). Results that are significant at the 95% or greater confidence level are underlined.

Behavioural response	Predictor	χ^2 or F^*	<i>P</i>
(a) Reached waterline (Yes/No) [†]	Light treatment	16.27 _(4,140)	<0.001
	Predator cue	4.76 _(4,140)	0.029
	Light treatment : Predator cue	1.60 _(5,139)	0.205
(b) Speed to waterline [‡]	Light treatment	0.03 _(2,85)	0.859
	Predator cue	<0.01 _(2,85)	0.976
	Light treatment : Predator cue	0.06 _(3,84)	0.814
(c) Response (Yes/No) [†]	Light treatment	6.19 _(4,140)	0.013
	Predator cue	1.79 _(4,140)	0.181
	Light treatment : Predator cue	0.16 _(5,139)	0.691
(d) log (Foraging distance) [‡]	Light treatment	1.23 _(2,96)	0.271
	Predator cue	3.03 _(2,96)	0.085
	Light treatment : Predator cue	0.22 _(3,95)	0.637
(e) Handled (Yes/No) [§]	Light treatment	186.7 _(2,142)	0.007
	Predator cue	165.2 _(2,142)	0.088
	Light treatment : Predator cue	141.4 _(3,141)	0.505

*Degrees of freedom are given in parentheses.

[†]Generalised Linear Mixed Effects Model with binomial error distribution (c. 1|rank as a random effect).

[‡]Generalised Linear Model with Gaussian error distribution.

[§]Generalised Liner Model with binomial error distribution.

non-acclimated experiment (Table 2d and e), but a significantly higher proportion did respond to the introduction of prey under artificially lit night-time conditions when predator cues were present compared to the control light treatment (Table 2c Light treatment : Predator cue, Fig. 1d, see Table S4 for pairwise comparisons).

Discussion

Rocky shore organisms including dogwhelks will be increasingly exposed to a range of anthropogenic stressors throughout the 21st century (including ocean acidification, climate change and noise pollution) that have demonstrated impacts on their distribution, behaviour and morphology (Jueterbock *et al.* 2013; Queirós *et al.* 2015; Roberts *et al.* 2015). Here, we have demonstrated that artificial night-time lighting – a globally widespread, rapidly expanding and yet understudied source of anthropogenic change – has effects on the behaviour of dogwhelks that are comparable with those observed in response to ocean acidification and climate change in similar laboratory studies (Queirós *et al.* 2015).

The effects reported here are in response to the upper levels of artificial light exposure encountered in the built marine environment. As such while they evidence the potential for night-time lighting to impact dogwhelk behaviour in directly illuminated marine habitats (port and harbour walls, sea defences, pier pilings, offshore infrastructure installations and urbanised shorelines) the extent

to which more widespread, and lower intensity artificial sky glow influences the behaviour of this common predator in temperate intertidal ecosystems remains unclear. Given that we used a red light to illuminate the control tanks in which behavioural assays were performed (but not in the control tanks during the acclimation phase), any impact of this red light on dogwhelk behaviour would be expected to reduce the effects size difference between our white LED illuminated and control organisms. Hence, while we nonetheless detected significant effects size differences in this study, and the spectral sensitivity of intertidal gastropod eyes (470–505 nm; Hughes 1970; Gillary 1974; Zhukov *et al.* 2006) suggests that our red LEDs would have remained largely imperceptible to control organisms, our study may underestimate the true effect of white LED lighting on dogwhelk behaviour.

Night-time lighting affected the basal and foraging activity of dogwhelks, regardless of the presence of a predator. Dogwhelks acclimated under the artificial night-time light regime were less likely to seek refuge at the water–air interface, yet were more likely to respond to, and handle prey (blue mussels) when it was introduced. Furthermore, we found that non-acclimated dogwhelks had higher response rates to prey under night-time lighting when predator cues were present. These results raise the prospect that both temporary and long-term coastal lighting installations could already be altering trophic interactions within rocky shore communities, a relatively understudied system with regard to light pollution.

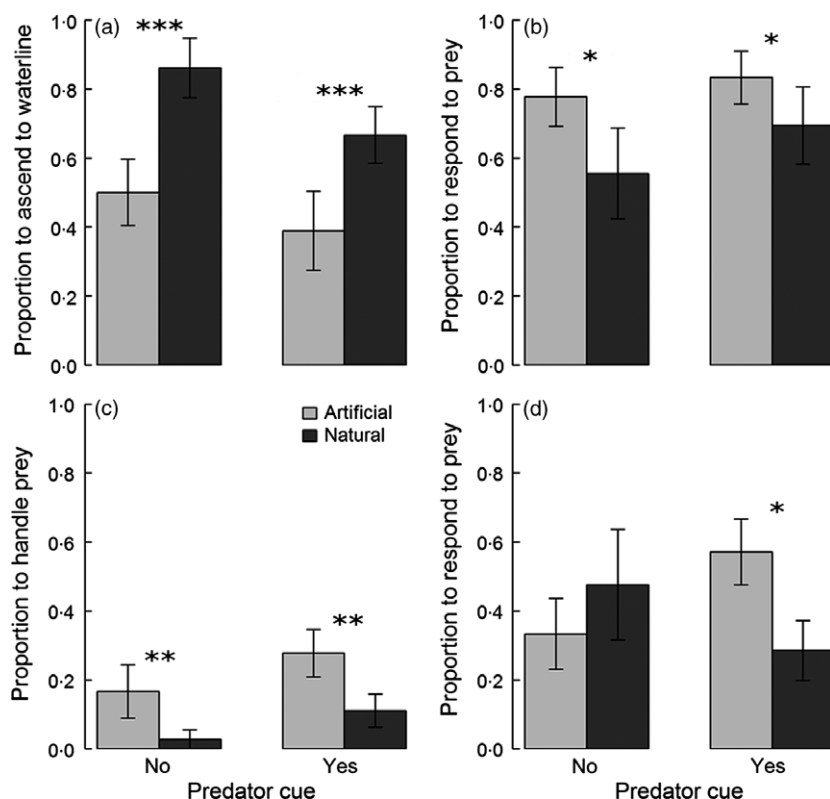


Fig. 1. The effects of night-time lighting and predation risk on basal activity (a–b) and foraging behaviour (c–d) of dogwhelks, *Nucella lapillus*. Light grey bars represent the responses of *Nucella* in the imaging box containing artificial lighting. Dark grey bars represent those in the imaging box with darkened, ‘natural’ conditions. ‘No’ and ‘Yes’ indicate whether the olfactory predator cue was present in the assessment tank. (a–c) show responses for individuals following 2 weeks acclimation under night-time artificially lit and naturally lit regimes; (d) shows responses for individuals not previously exposed to artificial light at night. Bar heights represent mean response; error bars represent standard errors. Stars denote differences between adjacent bars that are significant at the 95% (*), 99% (**) and 99.9% (***) confidence levels. (a–c) n trials = 12; n individuals = 144; (d) n trials = 7; n individuals = 84.

Acclimated dogwhelks displayed a pattern of basal activity previously observed in starved whelks (Vadas, Burrows & Hughes 1994), in that they did not reposition themselves at the waterline when introduced to the assessment tanks. This behaviour is consistent with energy preservation through metabolic depression, also previously observed in this species in response to global stressor simulations such as ocean acidification (Queirós *et al.* 2015). In the present study, stress could be caused by a disruption of the dogwhelks’ circadian rhythms after prolonged exposure to artificial light at night. Increased foraging activity when food was available could therefore be seen as a compensatory change in behaviour to support higher energy expenditure, as has been observed in dogwhelks with raised metabolic rates resulting from simulated ocean warming (Queirós *et al.* 2015). Light pollution has already been associated with chronic stress in European blackbirds and several species of rodent, leading to irregular reproductive activity (Dominoni, Quetting & Partecke 2013), impaired cognitive skills (Van der Meer, Van Loo & Baumans 2004) and increased rates of aggression (Fonken *et al.* 2012). The behavioural changes observed in this study could carry significant consequences for individual fitness as they interfere with known predator avoidance techniques in dogwhelks and other species, which are most exposed to predators during foraging excursions, outside of their otherwise occupied refuge.

Non-acclimated dogwhelks were more likely to respond to the introduction of prey under artificial compared to

natural light regimes only when predator cues were present. Given that dogwhelks could detect the presence of crabs using olfactory cues, it is likely that they established none were present in the given environment visually. This opportunistic shift towards using visual cues for detecting predation risk at night under artificial light suggests that coastal lighting could have an effect on predatory strategy that alters the balance of interspecific interactions within temperate intertidal communities. Night-time lighting would also, however, increase the visibility of dogwhelks to predators such as crabs and may have unforeseen effects on the settlement and anti-predator defences of prey species, so that the observed increases in foraging in the laboratory may not necessarily confer increased fitness in a real community setting, as noted previously with regard to other stressors (Queirós *et al.* 2015). Sensory pollutants such as noise and light affect predator detection and avoidance in a range of taxa including moths (Wakefield *et al.* 2015), birds (Meillère, Brischoux & Angelier 2015) and hermit crabs (Chan *et al.* 2010), but there is currently little information on the compounding effects of simultaneous disturbances to multiple sensory modalities (Halfwerk & Slabbekoorn 2015). The responses we observed in both acclimated and non-acclimated dogwhelks indicate that artificial light from coastal developments may similarly impair dogwhelks ability to assess predation risk.

Anthropogenic lighting is linked to changes in the foraging habits of bats (Rydell 1992), harbour seals (Yurk & Trites 2000) and wading birds (Santos *et al.* 2010; Dwyer

Table 2. The impact of night-time artificial lighting on the basal activity and predatory behaviour of non-acclimated dogwhelks (*Nucella lapillus*) in the presence and absence of olfactory predator (*Carcinus maenas*) cues. Results are presented for either generalised linear models or generalised linear mixed effects models comparing dogwhelks exposed to simulated natural daylight regimes vs. artificially lit night-time conditions (Light treatment), fully crossed with the presence or absence of olfactory cues from *C. maenas* (Predator cue). The choice of whether or not to include a random effect to control for interactions between individuals, and the specification of the random effects term were selected by comparison of Akaike's Information Criterion (see Table S3). In cases where the inclusion of a random effect improved model parsimony, (c. 1|rank) was always the most parsimonious random effects specification (Table S3). Results that are significant at the 95% or greater confidence level are underlined. Post hoc comparisons of significant interactions are given in Table S4

Behavioural response	Predictor	χ^2 or F^*	P
(a) Reached waterline (Yes/No) [†]	Light treatment	1.23 _(4,80)	0.267
	Predator cue	0.00 _(4,80)	1.000
	Light treatment : Predator cue	0.32 _(5,79)	0.575
(b) Speed to waterline [‡]	Light treatment	0.05 _(2,60)	0.820
	Predator cue	0.86 _(2,60)	0.357
	Light treatment : Predator cue	0.26 _(3,59)	0.610
(c) Response to prey (Yes/No) [†]	Light treatment	0.60 _(4,80)	0.437
	Predator cue	0.07 _(4,80)	0.795
	Light treatment : Predator cue	5.61 _(5,79)	<u>0.018</u>
(d) log (Foraging distance) [‡]	Light treatment	0.84 _(2,31)	<u>0.366</u>
	Predator cue	2.54 _(2,31)	0.122
	Light treatment : Predator cue	0.60 _(3,30)	0.447
(e) Prey handled (Yes/No) [†]	Light treatment	0.25 _(4,80)	0.619
	Predator cue	0.25 _(4,80)	0.619
	Light treatment : Predator cue	0.18 _(5,79)	0.669

*Degrees of freedom are given in parentheses.

[†]Generalised Linear Mixed Effects Model with binomial error distribution (c. 1|rank as a random effect).

[‡]Generalised Linear Model with Gaussian error distribution.

et al. 2013); changes which will likely have cascading impacts on the structure and functioning of their respective communities. Given the potential of anthropogenic lighting to affect a wide range of taxa and habitats, it is necessary to understand the long-term ecological and evolutionary impacts of these changes (Swaddle *et al.* 2015). In marine systems, this is particularly true in the context of other ubiquitous environmental stressors impacting marine organisms, such as noise pollution, acidification and warming. To our knowledge, no studies have investigated how light pollution will interact with other global anthropogenic stressors that affect organism behaviour, fitness, survival and reproduction. Shifts to visual hunting under artificial light at night could potentially compensate for the limited chemosensory functioning observed in dogwhelks exposed to ocean acidification (Queirós *et al.* 2015). Furthermore, our findings do not take into account the plasticity of species-level processes such as behaviour over long periods of time, as has been shown in a number of taxa, including dogwhelks (Form & Riebesell 2012; Queirós *et al.* 2015; Rhul *et al.* 2016). More comprehensive, long-term studies incorporating light pollution alongside other anthropogenic stressors are therefore necessary to determine what individual-level trade-offs will arise for organisms exposed to an increasing diversity of global anthropogenic pressures shaping natural ecosystems, and how these may be carried across multiple generations.

There is currently a significant gap in knowledge regarding the diversity of taxa and habitats impacted by artificial night-time lighting in coastal regions. Our study

demonstrates that night-time lighting has the potential to change the trophic dynamics of rocky shore ecosystems by altering predator–prey interactions within these systems. The potential for widespread impacts of artificial light at night on a plethora of coastal organisms whose physiology and behaviour are guided by natural light cues is clear.

Authors' contributions

T.W.D. and A.M.Q. conceived of and secured funding for the study; C.U. conducted the experiment with advice from A.M.Q. and T.W.D.; C.U. conducted the analysis with advice from T.W.D. and A.M.Q.; C.U. wrote the first draft of the manuscript; all authors contributed to revisions.

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Data accessibility

Data associated with this manuscript are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.s0t00> (Underwood, Davies & Querós 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Diagram of set up for experimental mesocosm treatments and behavioural assessments for acclimated dogwhelks.

Fig. S2. Diagram of set up for experimental mesocosm treatments and behavioural assessments for non-acclimated dogwhelks.

Table S1. Day–night cycle for experimental mesocosms.

Table S2. Selection of random effects terms for inclusion in models used to analyse responses of acclimated dogwhelks.

Table S3. Selection of random effects terms for inclusion in models used to analyse responses of non-acclimated dogwhelks.

Table S4. Post hoc pairwise comparisons of the interacting effects of Light treatment and Predator cue on whether or not dogwhelks responded to the introduction of prey during the non-acclimated experiment (Table 2c).



Exposure to Artificial Light at Night and the Consequences for Flora, Fauna, and Ecosystems

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The present review draws together wide-ranging studies performed over the last decades that catalogue the effects of artificial-light-at-night (ALAN) upon living species and their environment. We provide an overview of the tremendous variety of light-detection strategies which have evolved in living organisms - unicellular, plants and animals, covering chloroplasts (plants), and the plethora of ocular and extra-ocular organs (animals). We describe the visual pigments which permit photo-detection, paying attention to their spectral characteristics, which extend from the ultraviolet into infrared. We discuss how organisms use light information in a way crucial for their development, growth and survival: phototropism, phototaxis, photoperiodism, and synchronization of circadian clocks. These aspects are treated in depth, as their perturbation underlies much of the disruptive effects of ALAN. The review goes into detail on circadian networks in living organisms, since these fundamental features are of critical importance in regulating the interface between environment and body. Especially, hormonal synthesis and secretion are often under circadian and circannual control, hence perturbation of the clock will lead to hormonal imbalance. The review addresses how the ubiquitous introduction of light-emitting diode technology may exacerbate, or in some cases reduce, the generalized ever-increasing light pollution. Numerous examples are given of how widespread exposure to ALAN is perturbing many aspects of plant and animal behaviour and survival: foraging, orientation, migration, seasonal reproduction, colonization and more. We examine the potential problems at the level of individual species and populations and extend the debate to the consequences for ecosystems. We stress, through a few examples, the synergistic harmful effects resulting from the impacts of ALAN combined with other anthropogenic pressures, which often impact the neuroendocrine loops in vertebrates. The article concludes by debating how these anthropogenic changes could be mitigated by more reasonable use of available technology – for example by restricting illumination to more essential areas

and hours, directing lighting to avoid wasteful radiation and selecting spectral emissions, to reduce impact on circadian clocks. We end by discussing how society should take into account the potentially major consequences that ALAN has on the natural world and the repercussions for ongoing human health and welfare.

Keywords: artificial-light-at-night, light-emitting-diodes, photoreception, biological clocks, ecosystems, anthropogenic impact

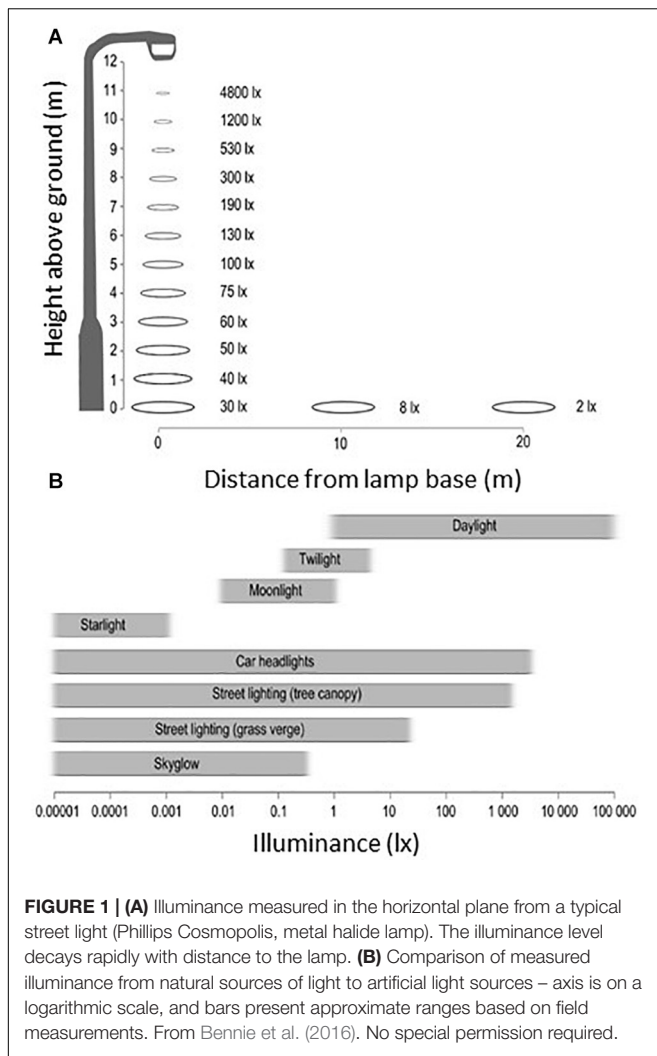
INTRODUCTION

Human activities are almost exclusively associated with brightly lit environments. The last century has seen an unprecedented increase in the use of Artificial Light at Night (ALAN), with a current ongoing global increase rate of more than 6% per year (Höller et al., 2010). This is dramatically affecting land as well as aquatic and open sea areas. Mediterranean and temperate zones, mangroves and forest regions in proximity to agricultural areas are particularly affected (Votsi et al., 2017). Today, more than 80% of the world's population lives under a "lit sky" at night (Falchi et al., 2016), actually affecting up to 99% in Europe and North America and on the increase in the Middle East (Tamir et al., 2017) and Asia (Jiang et al., 2017). ALAN acts both directly and indirectly (through sky glow) upon organisms. The illuminance at ground level can equal that of the full moon ($0.01 < < 1$ lx) (Bennie et al., 2015a, 2016; **Figure 1**) and can even be amplified by the cloud ceiling. ALAN was first intended to detect obstacles, increase road safety and secure potentially dangerous areas at night, but has now been extended to all aspects of human activities, including industrial, commercial, amenity spaces or tourist purposes. Illumination levels often exceed real needs; in some areas the aesthetic aspects (lighting of monuments) or advertising (lighting of commercial areas, shop windows, street signs and illuminated posters) have been given precedent. It follows that untouched natural areas - essential to the development of wildlife - are constantly decreasing. The consequences on biotopes and living organisms (including humans) are multiple. Basic responses and functions related to orientation in space (phototaxis, phototropism) and time (circadian rhythms) are affected by ALAN. These processes are the result of millions of years of evolution, while ALAN-induced changes are operating on a time scale of only a few decades. This is particularly evident when it comes to temporal events, which depend on the predictable alternation of light (L) and darkness (D) during the 24 h LD cycle, day after day and season after season. From the very earliest times of life on earth, organisms developed time-measurement systems - circadian clocks - which allowed them to forecast and anticipate these natural changes, essential for aligning physiological activity with the appropriate

time. As a result, most of the basic functions of living organisms are controlled by these internal, genetically determined, clocks. These clocks depend absolutely on the 24 h LD cycle to accurately synchronize their activity with solar time, and in turn they orchestrate a myriad of downstream biochemical, physiological and behavioural events so that the right process occurs at the right time. Thus, changing the natural LD cycle cannot be without consequences for biological organisms. In humans, perturbation of the circadian system results in major physiological impacts (Attia et al., 2019), for example in altered hormonal balance, including melatonin secretion. Melatonin is one key circadian clock output involved in the synchronization of many rhythmic functions; in addition it is suspected to possess powerful anti-oxidative properties (Reiter et al., 1997). In humans, a correlation between ALAN and the appearance of various disorders (activity/sleep rhythms, mental health disorders, energy metabolism, weight gain and obesity, sensitivity to some cancers [breast, prostate]) has been documented quite extensively (Dominoni et al., 2016; Attia et al., 2019) but the level of proof remains low because in most cases the light intensities used are far above the levels encountered in ALAN.

Here, we provide an overview of the tremendous variety of light-detection strategies which have evolved in unicellular organisms, plants and animals. We further give a comprehensive description of the different visual pigments which permit photo-detection in all living organisms from ultraviolet to infrared. The review then moves on to discuss how living organisms actually use light information in a meaningful way, crucial for their development, growth and survival: phototropism, phototaxis, photoperiodism, and synchronization of circadian clocks. These aspects are treated in depth, as their perturbation underlies much of the potentially disruptive effects of ALAN. The review goes into considerable detail on circadian networks in living organisms, since these fundamental features exist in virtually all life forms and are of critical importance in regulating the interface between environment and body. It is necessary to understand the diverse principles underlying their functioning across the different phyla in order to appreciate why ALAN can represent such a disruptive influence. Although much of the data reported in the literature necessarily comes from older lighting technology, the review addresses how the approaching ubiquitous introduction of light-emitting diode (LED) technology may exacerbate, or in some cases reduce, the generalized ever-increasing light pollution. A focus is put on the fundamental role of short wavelength emissions, since these are the most relevant wavelengths when considering signalling through vertebrate photoreceptive tissues and synchronization of central circadian clocks. Nevertheless the paper also stresses that due to the huge

Abbreviations: ALAN, Artificial Light at Night; ccg, clock-controlled gene; Cry, cryptochromes; D, darkness; DD, constant dark; FSH, folliculo-stimulating hormone; HPS, high pressure sodium; ipRGCs, intrinsically photosensitive retinal ganglion cells; JH, juvenile hormone; L, light; LD, alternation of light and darkness; LH, luteinizing hormone; LL, constant light; LED, light-emitting diode; LOV, light, oxygen or voltage; LPS, low-pressure sodium-vapour; LWS, long wavelength sensitive opsin; PCB, polychlorobiphenyl; PDF, pigment-dispersing factor; Rh, rhodopsin; SWS1, short wavelength sensitive opsin; THS, thyroid stimulating hormone.



range of light detection systems used by living organisms, other wavelengths may also be problematic. Numerous examples are given of how widespread exposure to ALAN is perturbing many aspects of plant and animal behaviour and survival. We examine the potential problems at the level of individual species and populations before extending the debate to the consequences for integrated ecosystems. It also emphasizes additive harmful effects resulting from the impacts of ALAN together with other anthropogenic pressures. The article concludes by debating how these anthropogenic changes could be easily mitigated by more reasonable use of available technology and how society should take into account the potentially major consequences that ALAN has on the natural world and the repercussions for ongoing human health and welfare.

THE INTEGRATION OF THE LIGHT SIGNAL IN LIVING ORGANISMS

Nothing in biology makes sense except in the light of evolution (Dobzhansky cited in Lamb, 2013).

The capture of light information goes back to ancestral cyanobacteria, the first known representatives of life on earth, which appeared ~3.8 billion years ago. It allows organisms to orientate in space (phototropism for animals, phototaxis for plants) and time (synchronization of the endogenous clocks that drive the daily, lunar and annual rhythms of metabolic, physiological and behavioural functions). Living beings have implemented a huge variety of systems and mechanisms in order to capture light, from simple photoreceptive organelles to highly complex structures such as the chloroplast of plants and the camera eyes of vertebrates, insects and cephalopods.

In unicellular organisms, photoreception is mediated by a photoreceptor organelle existing as either a single spot (cyanobacteria, euglena) or a more elaborated structure (dinoflagellates), containing all the elements found in a vertebrate eye, *i.e.*, pigment, a cornea-shaped surface, a lens and a lamellar structure (Gehring, 2005, 2011, 2014). It has been hypothesized that these organelles might correspond to chloroplasts incorporated by horizontal transmission, but having lost their photosynthetic activity (Gehring, 2012).

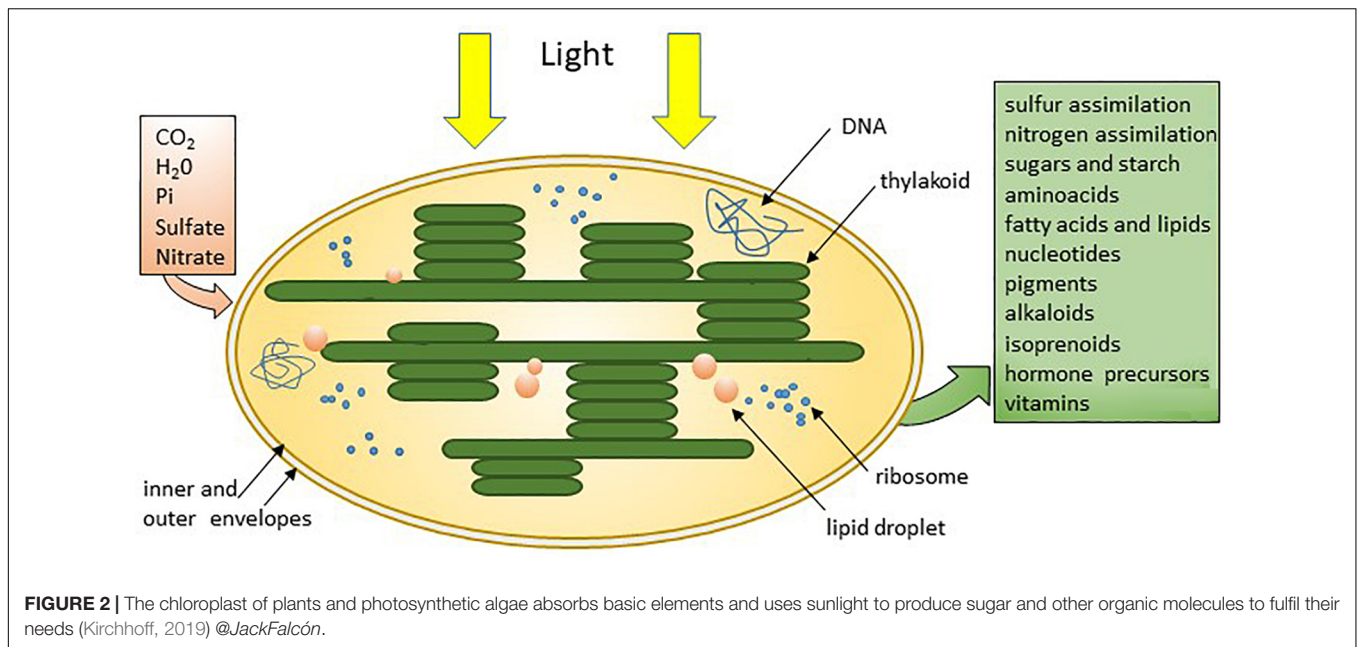
Cyanophyceae, the current representatives of the ancestral cyanobacteria are, like the original form, capable of capturing light and ensuring photosynthesis. They exist as single cell units or associated in filaments, and can fix carbon dioxide [CO₂] and release oxygen [O₂], but have no chloroplast. Phototaxis and photoperiodic synchronization of circadian clocks have been demonstrated in *Cyanobacteria* (Gehring, 2012), as in the terrestrial *Cyanobacterium Leptolyngbya* sp., which shows two maxima of absorption (λ_{max}) at 456 and 504 nm. Populations of *Cyanobacteria* are increasing worldwide, favoured by trophic and/or ecological imbalances (including eutrophication of water), and pose major physical (invasion, obstructions) and toxicological (production of dangerous or even deadly toxins) problems (Svrcek and Smith, 2004).

The Chloroplast of Plants

The ingestion of cyanobacteria by primitive eukaryotic cells ~1.5/1.6 billion years ago led to the formation of chloroplasts (Figure 2), found in the cytoplasm of eukaryotic photosynthetic cells (Kirchhoff, 2019). In the unicellular alga of the *Chlamydomonas* genus, there is one chloroplast per cell, while multicellular plants possess several tens of chloroplasts in one cell, with the leaves showing the highest density. The chloroplast allows photosynthesis, *i.e.*, it absorbs light energy to fix inorganic CO₂ and produces glucose and O₂ (the highest production of O₂ is from algae and marine phytoplankton, followed by forests). Moreover, it is involved, by interacting with photoreceptive molecules and circadian clock genes, in the response to light (Jaubert et al., 2017).

The Photoreceptive Cells and Organs of Animals

The rhabdomeric and ciliary photoreceptors are the two main types of photoreceptive cells found in the animal kingdom. Both show a highly segmented and polarized organization, with a photoreceptive pole made of folds or stacks of membrane, a cell



body and an opposing pole for neurotransmission (**Figure 3A**). Evolution of photoreceptor cells and organs runs in parallel, and studies have shown that eyes and other photoreceptive structures have a monophyletic origin that started with a single prototype (Fain et al., 2010; Gehring, 2012; Lamb, 2013; Gavelis et al., 2015). Evolution led to the appearance of a variety of complex ocular types (**Figure 3B**). Thus, while the camera-type eye containing ciliary photoreceptors characterizes the eyes of humans and other vertebrates, camera-type eyes are also found in jellyfish and cephalopods, which instead possess rhabdomeric photoreceptors as is the case in most invertebrates. However, coexistence of rhabdomeric and ciliary photoreceptors is not uncommon, as observed in the cephalochordate *Amphioxus*, the living proxy of all vertebrates (Zhang Q. L. et al., 2019). The retina of the hagfish eye, as well as the pineal gland of fish, frogs and sauropsids, is composed mainly of photoreceptor cells connected directly to ganglion cells. The first are of the ciliary type and the second are derived from rhabdomeric photoreceptors, as shown at least in the hagfish (Autrum et al., 2012; Lamb et al., 2007; Lamb, 2013). The retina of all other vertebrates has become more complex, with the appearance of bipolar, horizontal and amacrine cells in an intermediate position. The most recent data indicate that bipolar cells are derived from ciliary type photoreceptors, while the ganglion cells derive from the rhabdomeric line; amacrine and horizontal cells would also belong to the rhabdomeric line (Lamb, 2013).

Compound and Camera Type Eyes

A dozen different eye structures have been identified in animals, which developed through different evolutionary pathways (divergent, parallel, or convergent) (Shubin et al., 2009). Some are just scattered photoreceptors (alone or a few together) all along the body, found in small invertebrates and in larvae of insects and worms. They are designated as *primitive eyes* because

they are associated with a pigmented cell positioned on one side, permitting the perception of light directionality. These structures are simple dosimeters of the surrounding light intensity allowing negative or positive phototaxy (escape or attractive behaviour respectively). In tubular worms these groups of cells form wells or *pit* eyes; the pit eye forms a small hollow in which photoreceptor cells display different orientations, thus allowing spatial detection of light (**Figure 3Ba**). From these pit eyes appeared the *spherical* concave mirror eyes with a pupil, but without a crystalline lens, as seen bordering the mantle of the bivalves (clams, scallops) (**Figure 3Bb**). More elaborated camera eyes are found in vertebrates, molluscs (squid, octopus), jellyfish, some annelids, arthropods (including spiders), insect larvae and copepods (**Figure 3Bc**). Finally, the *compound eye*, the most widespread model, is characteristic of insects (75% of existing animal species), most crustaceans, myriapods, some bivalves and polychaetes (**Figure 3Bd,e**). Compound eyes are formed of identical units called ommatidia, which each contains a cluster of photoreceptor cells surrounded by supporting cells and pigmented cells. Each ommatidium possesses a cornea and a conical lens that focuses light towards the rhabdomeric photoreceptors. In the majority of diurnal species, each ommatidium is isolated from its neighbours by a pigment layer, which makes communication between them impossible (**Figure 3Bd**). In nocturnal species the absence of pigment allows the diffusion of light from one ommatidium to its close neighbours, conferring a gain of sensitivity (**Figure 3Be**).

The eye with its retina is not the only structure that allows light detection, as both invertebrates and vertebrates possess additional extra-retinal light sensitive structures.

Extraretinal Photoreception in Vertebrates

Aquatic vertebrates, amphibians and lizards possess a pineal complex formed by a pineal gland associated with either a

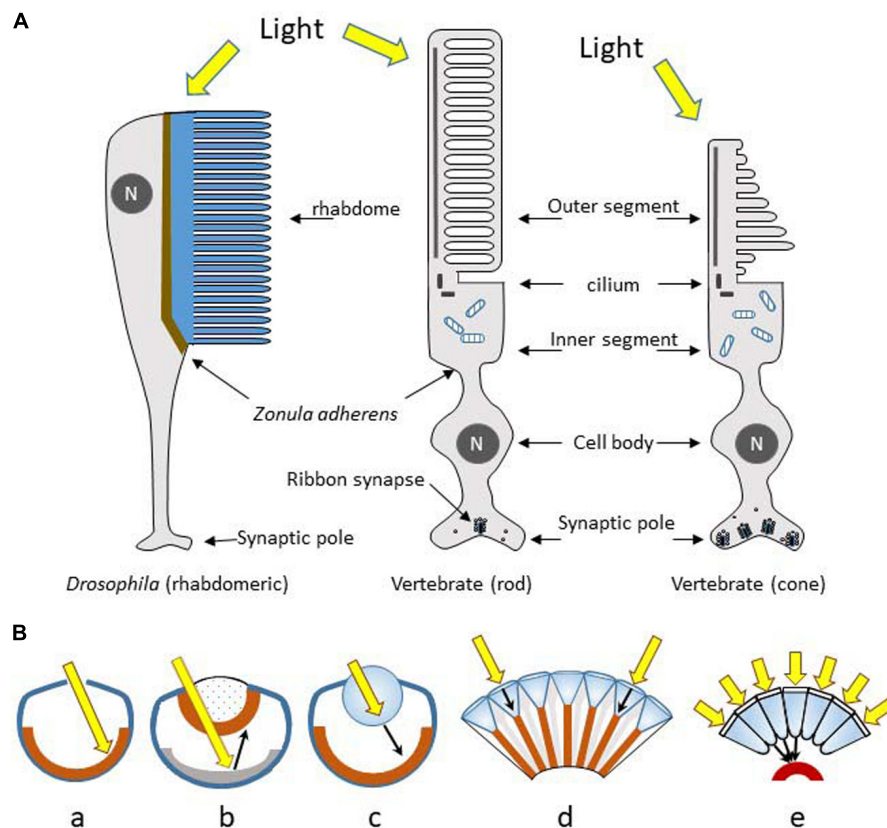


FIGURE 3 | (A) Rhabdomeric microvilli-based (invertebrates) and cilia-based (vertebrates) photoreceptors display conserved cell polarity and topology. They evolved most probably from a common ancestor in early Bilateria. The photosensory pole is made of stacks of plasma membrane separated from the baso-lateral membrane by a zonula adherens. N, nucleus. **(B)** The main optical designs of eyes: (a) The pinhole eye; light (yellow arrow) falls directly upon the photoreceptors (brown layer). (b) The concave-mirror eye; light crosses the retina, and is then focused back onto the retina upon reflection from a hemispheric reflective mirror (*tapetum*, grey zone). (c) The camera type eye; light is focused by the lens to form an image on the retina. (d and e) The compound eyes; light reaches the photoreceptors exclusively from the small corneal lens (d type) located directly above, or focused through a large number of corneal facets and cones to be directed towards single rhabdoms (e type). Redrawn from Warrant (2019).

parapineal organ or a parietal eye (depending on the species) (Collin et al., 1988; Falcón, 1999; **Figures 4A–J**). The gland appears as an evagination of the roof of the diencephalon, located at the surface of the brain. In the majority of cases (particularly in poikilothermic species) the skull directly above the pineal gland is thinner and translucent and the skin is less pigmented (**Figures 4A–D**). In large fish (e.g., the tuna) where the brain is located deep inside the head, a translucent cartilaginous tube directs light from the surface to the pineal gland (personal observations). All these anatomical characteristics allow better light penetration. In addition to the pineal gland, frogs and lizards possess a parietal eye (**Figures 4E–J**) located between the skull and the skin, which sends a nerve that crosses the skull to reach the brain. In addition, the parietal eye of lizards possesses a lens (**Figure 4J**). In birds, snakes and mammals these specializations have regressed: the pineal gland of adult mammals is often located more deeply in the brain and has lost its ability to detect light directly, even though they still express the proteins necessary for phototransduction (**Figures 4K,L**). Furthermore, during development mammalian pinealocytes display morphological

features characteristic of ciliary photoreceptor cells but which subsequently regress (Blackshaw and Snyder, 1997).

The pineal epithelium of non-mammalian vertebrates displays the characteristics of a simplified retina as it contains cone-type photoreceptors connected to ganglion cells, the latter sending their axons towards specific brain centres. It is of interest to note that retinal and pineal brain projections overlap in some areas, thus providing convergent light information (Ekström and Meissl, 2003). In contrast to the retina, the pineal organ is only a dosimeter of light intensity, albeit of great sensitivity. In addition to this nervous information pineal photoreceptors also produce the “time-keeping hormone” melatonin (see Localization of the Circadian System – Vertebrates) (Falcón, 1999). In the course of evolution snakes and mammals have lost the parapineal and parietal organs, as well as the direct photosensitivity of the pineal gland, and they no longer produce nervous information (Collin et al., 1988). In these species, the pineal cells (pinealocytes), receive light information *via* the retina and a complex nerve pathway; only the nocturnal production of melatonin persists

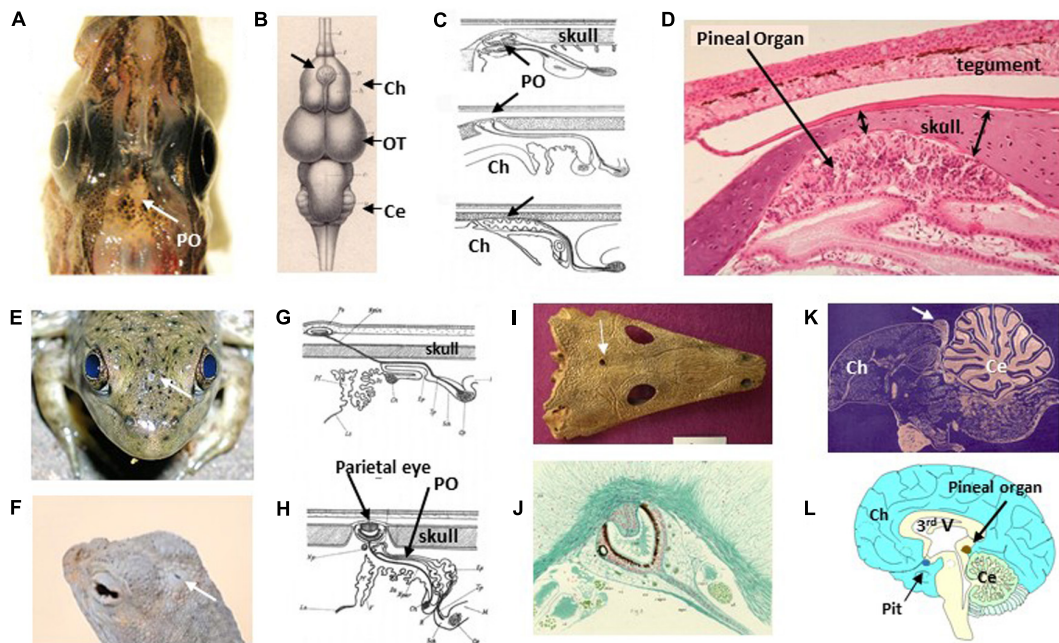


FIGURE 4 | Extraretinal photoreception in vertebrates. **(A)** Dorsal view of the head of the Polar Cod *Boreogadus saida*; the pineal organ (PO) is located in the sagittal axis just behind the eyes in an area with unpigmented meninges (@JackFalcón). **(B)** Dorsal view of the brains of the Red Mullet *Mullus surmulletus* showing the location of the pineal organ (thick arrow), located in between the two cerebral hemispheres (Ch); OT, optic tectum; Ce, cerebellum; from Baudelot (1883) (no permission required). **(C)** Schematic sagittal sections through the epithalamus area of, from top to bottom, lampreys, chondrichthyans and teleost fish; from Studnicka (1905). Note that the skull above the pineal organ is thinner, as also seen in panel **(D)** (no permission required). The histological sagittal section is from the Sea Bream *Sparus aurata*; the pineal is located in a kind of large pit below the skull (note that the tegument above also appears thinner) (gift from Professor J.A. Muñoz Cueto, Cadiz, Spain). **(E,F)** Head dorsal views showing the spot position of the frontal organ in the American Bullfrog *Rana catesbeiana* **(E)** and the parietal eye of the Zebra-tailed Lizard *Callisaurus draconoides* **(F)** (arrows) (@JackFalcón). **(G,H)** Schematic sagittal sections through the epithalamus areas of frogs **(G)** and lizards **(H)**; the pineal organs are located below the skull, while the frontal/parietal eyes are located in the skin connected to the brain by a stalk (Studnicka, 1905) (no permission required). **(I)** Dorsal fossil skull of the ancestral amphibian *Thoosuchus jakovlevi* showing the location of the frontal organ hole just equidistant from the eyes (with permission from https://commons.wikimedia.org/wiki/File:Thoosuchus_jakovlevi.JPG). **(J)** The pineal eye of the tuatara *Sphenodon punctatus* resembles a simplified retina with an eye cup and a lens-like structure; sagittal section from Dendy (1911) (no permission required). **(K)** In the avian brain the pineal organ form a gland in between the cerebral hemispheres and the cerebellum (gift from Professor J.P. Collin). **(L)** In humans the gland is located deep in the brain (@JackFalcón).

(Klein et al., 1997). Birds display features characteristic of both early and late vertebrates.

In addition to these organized photoreceptive organs, *intracerebral photoreceptors*, the existence of which had been postulated early in the last century (Von Frisch, 1911; Benoit and Assenmacher, 1954), have been found in fish, lizards and birds (Hang et al., 2016; Haas et al., 2017) (see also below **Figure 11**). Their role remains enigmatic; some may contribute to the annual control of reproduction (Benoit and Assenmacher, 1954).

Finally, ectothermic vertebrates (fish, amphibians, and lizards) possess photosensitive cells on the surface of their skin, which participate in the control of migration in lampreys (Binder and McDonald, 2008), the aggregation/dispersion of skin pigments in fish and frogs (Moriya et al., 1996; Chen et al., 2014), or basking in reptiles (Tosini and Avery, 1996).

Extra-Retinal Photosensitivity in Invertebrates

In addition to their rhabdomeric eyes, insects possess ocelli and eyelets, which may have various shapes and locations

(**Figures 5A-E**). The ocelli of insects are simple lens eyes consisting of a single, large aperture lens, followed by several hundreds of rhabdomeric photoreceptors which converge onto a few tens of interneurons (Berry et al., 2011). *Drosophila* eyelets contain 4 to 6 rhabdomeric photoreceptors and are derived from the larvae visual organs (Helfrich-Förster et al., 2002). Compound eyes and ocelli have a common ancestral origin (Friedrich, 2006), and these extra-retinal photoreceptors are likely to be involved in behaviour and synchronization of endogenous rhythms. Spiders do not have ocelli, but may possess from 1 to 4 pairs of eyes with different functions (**Figure 5F**)

Photopigments and Visual Perception Phytochromes

Phytochromes are found in plants, fungi, bacteria and cyanobacteria, unicellular algae and diatoms. They are covalently associated with a phytychromobilin as chromophore in plants and cyanobacteria, and biliverdin in other bacteria and fungi (Bhoo et al., 2001; Glukhova et al., 2014; Huche-Thelie et al., 2016). In plants, several forms of phytychromes may be present simultaneously (five in *Arabidopsis thaliana*, three

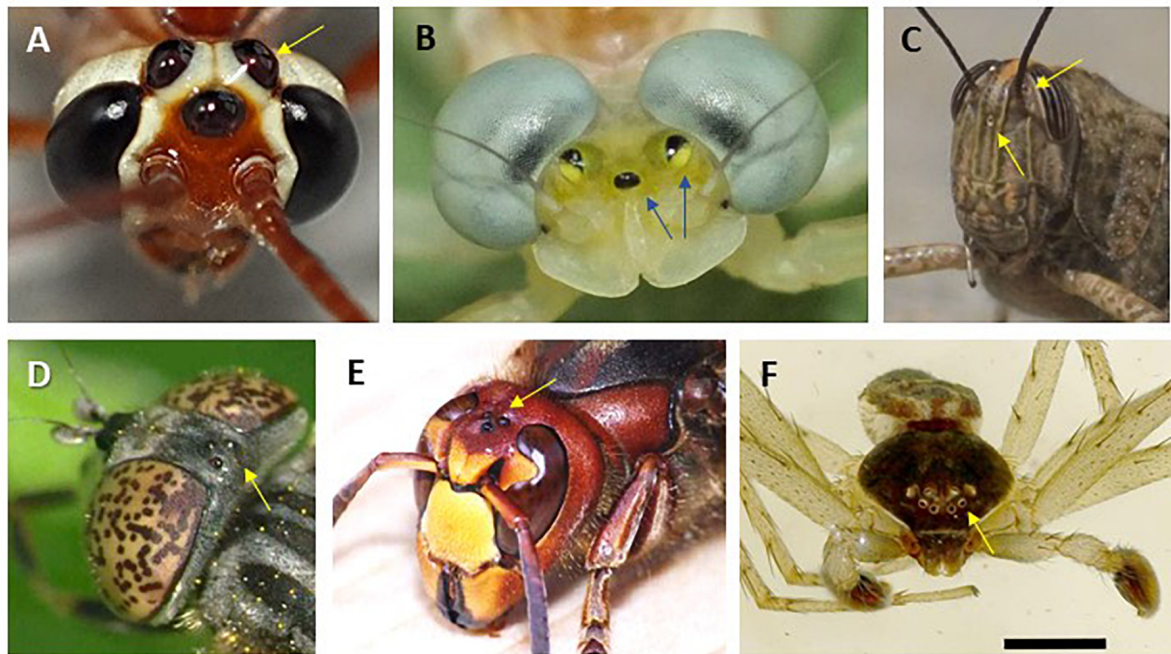


FIGURE 5 | Extra-ocular light perception in various insect species (A–E) and eyes of a spider (F). Arrows point to ocellar structures as found in *Netellia* sp. (A), *Heptagenia* sp. (B), grasshopper *Locusta migratoria* (C), *Eristalinus sepulchralis* (D), *Vespa cabro* (E), and *Philodromus dispar* (F). Photo credits: P. Falatico (A,B,D,E; @ <http://aramel.free.fr/>), J Falcón (C), D. Vaudoré (F; @<https://www.galerie-insecte.org/galerie/ref-183890.htm>). No special permissions required.

in sorghum, black cottonwood and rice, and two in pea) (Demotes-Mainard et al., 2016). They display maximal sensitivity in the red range of wavelengths, although response to other wavelengths is also observed but with much lower sensitivity (Figure 6A). Phytochromes exist in two states: the inactive state has a sensitivity maximum in the red ($580 < \lambda_{\max} < 660$), while the active state displays its maximum in the infrared ($690 < \lambda_{\max} < 720$). The final effects on downstream regulated processes in the plant depend on the red/infrared ratio (Bhoo et al., 2001; Demotes-Mainard et al., 2016). Light induces bilin photoisomerization and triggers photoconversion from the red to infrared form, prompting activation of the phytochrome HIS-kinase activity and downstream cascades. Darkness induces the opposite and thus the plant needs a dark phase to regenerate the phytochrome from the infrared to red form. Consequently, a natural LD 24 h cycle is essential for the proper synchronization and regulation of physiological cycles in plants (see below).

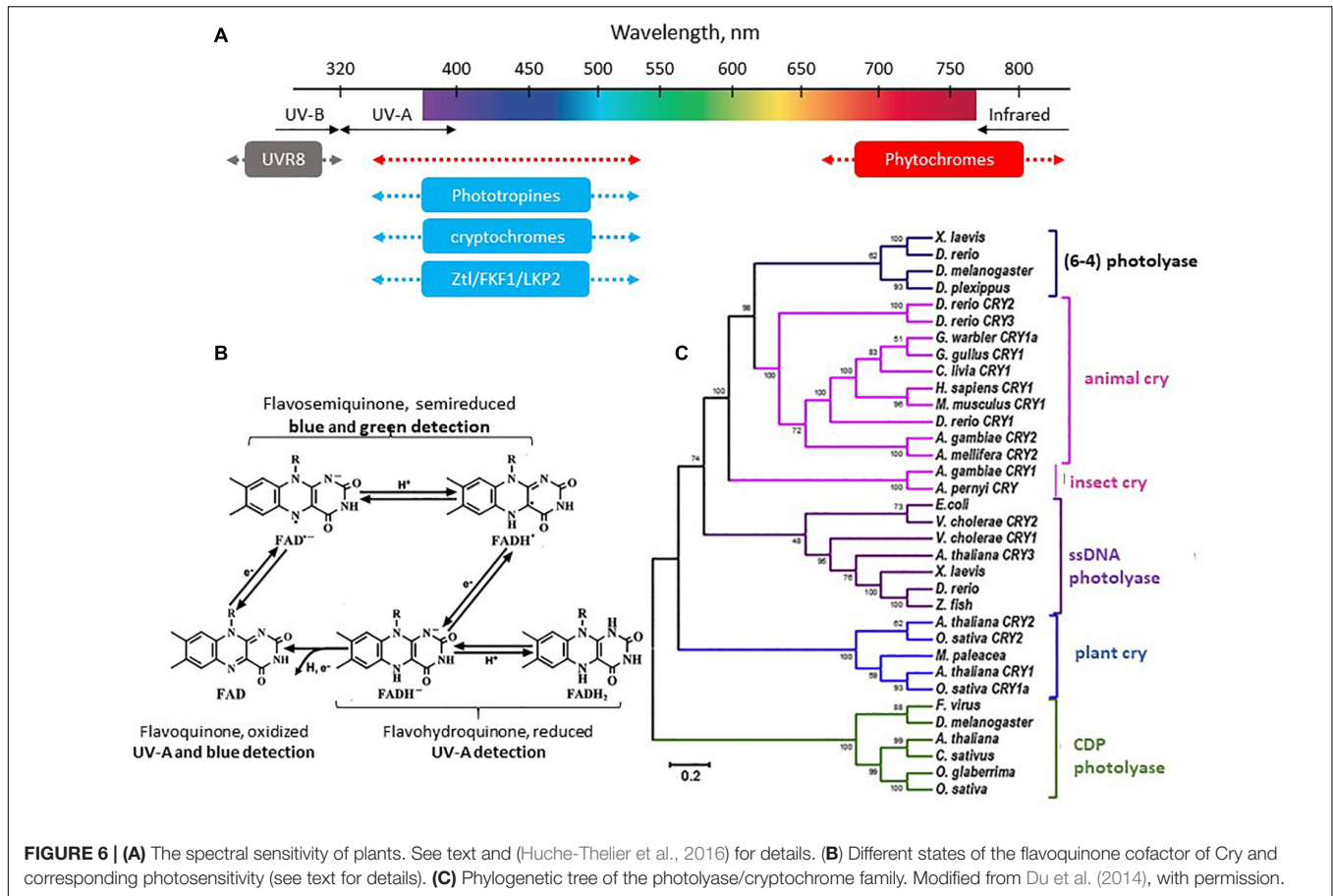
It is of interest to note that phytochromes also contribute to blue light-dependent regulation either redundantly or synergistically with cryptochromes (Cry; the blue light photoreceptors), and that physical interactions between Cry and phytochromes proteins have been demonstrated (Demotes-Mainard et al., 2016).

Cryptochromes

Cry are found in all living organisms (Chaves et al., 2011; Yu and Fischer, 2018). They belong to the photolyase family of proteins and use flavin adenine dinucleotide (FAD) as a

cofactor (Figures 6B,C). Photolyases and Cry from the DASH (for *Drosophila*, *Arabidopsis*, *Synechocystis*, Human) family (Cry-DASH) are involved in DNA repair (Tagua et al., 2015), which operates between 350 and 530 nm. In plants and animals Cry1 and Cry2 have lost the DNA repairing property. UV-A ($\lambda_{\max}$ 370 nm) and blue ($\lambda_{\max}$ 450 nm) radiations activate an electron transfer and reduction of FAD (initially in an oxidized form) (Huche-Thelier et al., 2016; Liu et al., 2016; Figure 6C). In the animal kingdom Cry are also part of the circadian clock molecular machinery, i.e., they ensure both the capture of the light signal (input to the clock) and the function of the clock itself. However, this is not the case in vertebrates where they are no longer light sensitive (see section “Orientation in Time: The Circadian Clocks” below).

As mentioned above, Cry interact with phytochromes in plants, where they also regulate phototropin expression (see section “LOV (Light, Oxygen, or Voltage) Domain Proteins”). They are also involved in the mechanisms of orientation (insects) and magnetoreception (plants, insects, birds) (Chaves et al., 2011; Gehring, 2012). For example, strong magnetic fields reduce plant growth in blue light but not in red light. In Cry deficient (*Cry*^{−/−}) *Drosophila* (*Drosophila melanogaster*) and cockroaches (*Periplaneta americana*), magnetic field orientation function is lost while it is restored in transgenic animals expressing the human gene (*Cry2*^{+/+}) (Bazalova et al., 2016). Similarly, magnetic field orientation through retinal Cry has been demonstrated in migratory birds (particularly nocturnal migrants) and, under dim light intensity, orientation remains correct only at wavelengths under 530 nm



(Mouritsen et al., 2004a,b; Solov'yov et al., 2010; Niessner et al., 2011; Fusani et al., 2014).

LOV (Light, Oxygen, or Voltage) Domain Proteins

Light, oxygen, or voltage domain containing proteins are a family of blue light receptor proteins that include phototropins, ZTL/FKF1/LKP2 and aureochromes (Suetsugu and Wada, 2013). Phototropins are specific to green plants (land plants and green algae) and ZTL/FKF1/LKP2 to land plants. Aureochromes are specific to photosynthetic stramenopiles, including yellow-green algae (*Xanthophyceae*), brown algae (*Phaeophyceae*), and diatoms (*Bacillariophyceae*).

Phototropins are serine/threonine kinase proteins, which are sensitive to blue and UV-A light (Figure 6A). They use mono-nucleotide flavin (FMN) as chromophore. Studies in *A. thaliana* have demonstrated that phototropin expression is regulated by phytochromes and Cry (Huche-Thelie et al., 2016). Phototropins are involved in the control of phototropic responses (hypocotyl and stem bending, and leaf positioning), the accumulation of chloroplasts and opening of the stomata (responsible for gaseous exchanges between the plant and its environment) (Huche-Thelie et al., 2016).

Like the phototropins, ZTL (Zeitlupe), FKF1 (Flavin-binding Kelch), and LKP2 (LOV Kelch Protein-2) are also associated

with FMN and responsive to blue and UV-A wavelengths (Figure 6A; Suetsugu and Wada, 2013). ZTL regulates the circadian clock either directly (through degradation of key clock proteins) but also can indirectly affect the flowering time. LKP2 and FKF1 predominantly control photoperiodic flowering (scent emission, corolla opening, and movements), the former through regulating the circadian clock, and the latter acting downstream of the clock; studies also suggest they contribute to controlling hypocotyl growth (Imaizumi et al., 2003; Dodd et al., 2015; Yon et al., 2016). In fungi, the blue photoreceptor proteins White Collar-1 (WC1) and Vivid (VVD), two LOV domain-containing photoreceptors, are part of the circadian clock machinery (Hurley et al., 2015; Yu and Fischer, 2018; Saini C. et al., 2019).

Opsins

Opsins are members of the G-protein-coupled 7 transmembrane domain receptor (GPCR) superfamily that are associated with the chromophore retinal. This feature is a fundamental distinction between opsins and phytochromes, Cry and LOV-domain containing proteins, which are cytosolic. Upon illumination, retinal isomerizes from the 11-*cis* to all-*trans* configuration (in vertebrates), or all-*trans* to 13-*cis* (in bacteriorhodopsin), triggering the cellular response to light (Shichida and Matsuyama, 2009). Opsins, evolved

from a common ancestral molecule ~ 700 million years ago (Figure 7), show enormous diversity in structure, tissue distribution and function (Porter et al., 2012); more than 1000 sequences are available (Shichida and Matsuyama, 2009).

The two categories, microbial (type I) and animal (type II) opsins, share a common architecture but with little sequence homology and have different functions (Kandori, 2015).

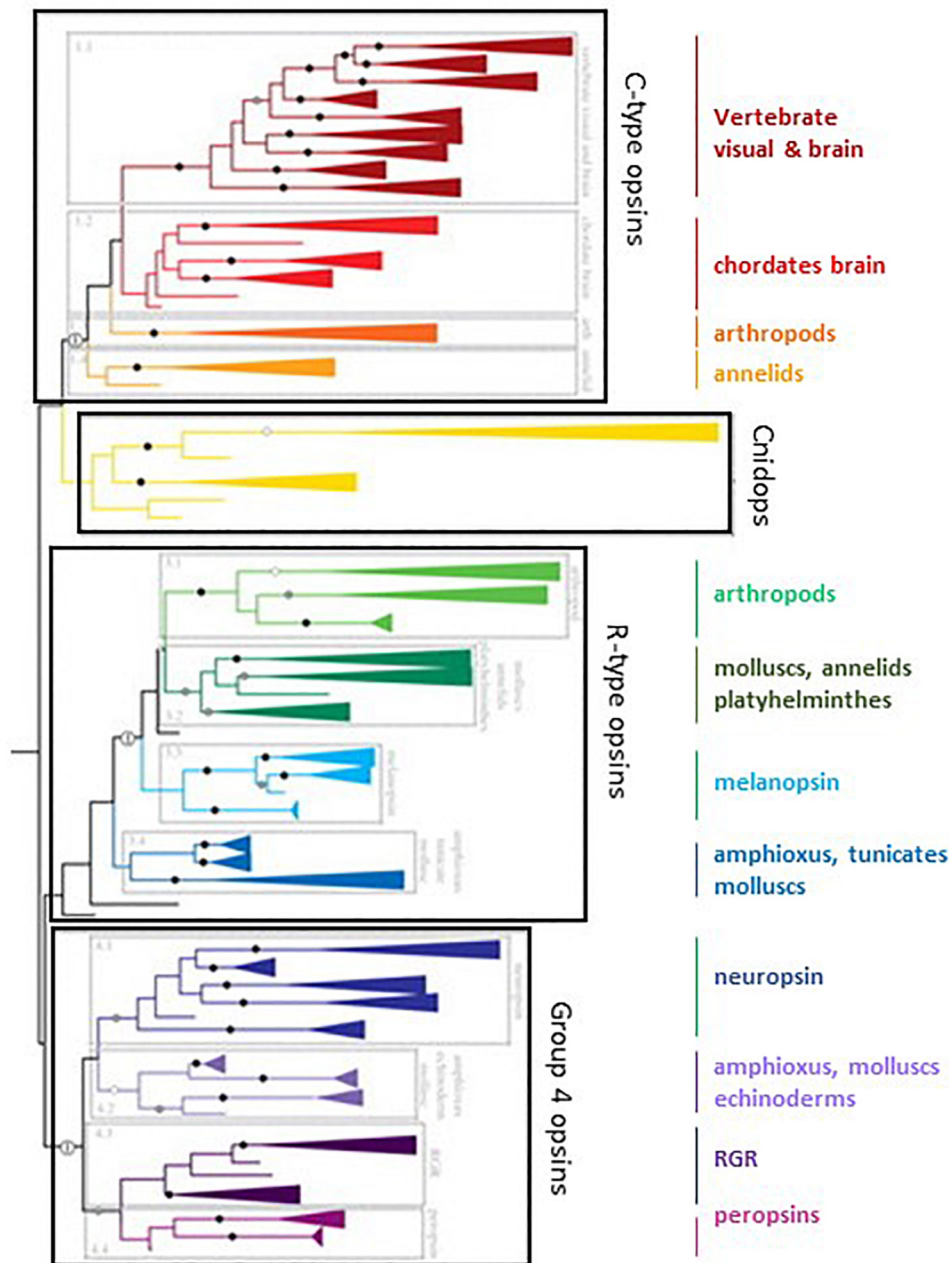


FIGURE 7 | The family of opsins in the tree of evolution. C-opsin family includes the vertebrates visual and brain opsins (Rh1, Rh2, SWS1, SWS2, M/LWS, pinopsins, parainopsins, vertebrate ancient and parietal opsins), the chordates' brain opsins (teleost multiple tissue opsins (TMTs), encephalopsins and uncharacterized amphioxus and urchin opsins), the arthropod opsins (honeybee pteropsin, and uncharacterized insect and *Daphnia pulex* opsins), and the annelids group (uncharacterized *Platynereis* brain and urchin opsins). Cnidops family includes ctenophore and cnidarian opsins. R-type opsins include the arthropod visual pigments (M, LWS, and SWS), the annelid, Platyhelminthes and mollusc visual pigments, the melanopsins (vertebrates' melanopsin 1 and 2, and amphioxus sequences) and uncharacterized tunicate, amphioxus and mollusc opsins. Group 4 Opsins include neuropsins (four separate clades), amphioxus, sea urchin and mollusc opsins, RGR (uncharacterized mollusc opsins) and peropsins (amphioxus and hemichordate opsins). See text and (Porter et al., 2012) for more details. Modified from Porter et al. (2012). No special permission required.

Type I or microbial rhodopsins

Microbial opsins display great diversity and heterogeneity, comprising archaeal light-activated ion pumps, sensory rhodopsins and halorhodopsins (in bacteria, fungi, cyanobacteria, and dinoflagellates), and rhodopsin channel in green algae. Type I rhodopsins are usually proton or chloride ion (Cl^-) pumps with green ($560 < \lambda < 590 \text{ nm}$) or blue ($\lambda_{\text{max}}: 490 \text{ nm}$) absorption maxima, the latter being particularly observed in deep-sea bacteria (Shichida and Matsuyama, 2009).

Type II or animal rhodopsins

Originally opsins were classified in two groups, the C-opsins and the R-opsins, based on the belief they were specific for ciliary photoreceptors (for the former), and rhabdomeric photoreceptors (for the latter). This was shown recently to be an oversimplification (Leung and Montell, 2017). Several animal opsin subfamilies are now recognized, classified as a function of the G-protein they are coupled to and the different intracellular pathways they activate (Porter et al., 2012; Oakley and Speiser, 2015; Terakita et al., 2015). These include the vertebrate visual and non-visual opsins (Gt-coupled), encephalopsin (opn3, Gi/Go-coupled), invertebrate opsin (Go-coupled), cnidarian opsin (Gs-coupled), neuropsin (opn5, Gi-coupled) and melanopsin (Gq-coupled). The function of the two others, peropsin and photoisomerase, is less well known. Type II rhodopsins share less than 20% identity between them. In each group there are some involved in light capture and others whose functions remain unknown. It is noteworthy that the melatonin receptor line appeared after the very first duplication of the ancestral opsin gene (Feuda et al., 2012; **Figure 7**).

Vertebrate opsins, encephalopsins, Go and Gs opsins are expressed in ciliary photoreceptor cells of the retina and pineal gland of vertebrates, while Gq opsins are expressed in rhabdomeric photoreceptor cells of invertebrates (Shichida and Matsuyama, 2009). In vertebrates, opsins are also expressed in the inner layers of the retina, as is the case for VA (vertebrate ancient) opsin in the inner nuclear layer of non-mammalian vertebrates, or melanopsin in a specific set of intrinsically photosensitive retinal ganglion cells (ipRGCs) in mammals (Jiang et al., 2018) (see also “Type II or animal rhodopsins”). Mammals possess a single melanopsin gene (Opn4m, for mammalian), whereas all other vertebrates have at least two (Opn4m and Opn4x [for *Xenopus*]). Chicken Opn4m is restricted to a subset of RGC while Opn4x is found in a different subset of RGC as well as horizontal cells (Verra et al., 2011). There are also long and short isoforms of both Opn4m and Opn4x, which also have differential distributions. In addition to the retina and pineal complex of non-mammalian vertebrates, non-visual light sensitive opsins are also expressed in several brain regions (Hang et al., 2016), scattered throughout the brain (fish) or restricted to the diencephalon (frogs, reptiles and birds) (Pérez et al., 2019). These opsins mediate non-visual light detection regulating many functions, including early development, locomotor activity, or annual control of reproduction, as suspected from very early studies in fish (Von Frisch, 1911) and birds (Benoit, 1935), and now unequivocally demonstrated (Nakane et al., 2010, 2013; Fernandes et al., 2012; Hang et al., 2014, 2016; Currie et al., 2016)

(see also **Figure 11**). Melanopsin (humans) and encephalopsin (rat) have also been detected in the mammalian brain (Nissilä et al., 2012a,b) but it is unknown whether they are linked to a direct sensitivity to light reported for the mammalian brain (Leung and Montell, 2017). A few studies also report the localization of opsins in the brain of a variety of invertebrates (larvae and adult) (Spaethe and Briscoe, 2005; Shiga and Numata, 2007; Donohue et al., 2018). In most of these cases this non-visual photoreception controls behaviour and daily rhythms.

Opsins have also been detected in the skin dermatophores and photophores of vertebrates and invertebrates (Tosini and Avery, 1996; Binder and McDonald, 2008; Pankey et al., 2010; Chen et al., 2014; Baker et al., 2015; Delroisse et al., 2018). These dermatophores participate in the control of pigment aggregation (fish, amphibians), positive (lizard), or negative (gastropod) phototaxis, and the migratory cycle (lamprey). In mice, OPN5 mediates photo-entrainment of clock genes in skin cells (Buhr et al., 2019), and OPN3 mediates blue-light activation of lipolysis in adipocytes (Nayak et al., 2020). Finally, in mammals melanopsin is expressed in blood vessels and iris muscle, being involved in the control of photo-relaxation and pupillary constriction respectively (Leung and Montell, 2017).

Wavelength discrimination of opsins

Evolution has led to a diversification of opsin genes, resulting from a succession of mutations and whole genome duplications, followed by gains of function or losses of one paralog. The spectral sensitivity peaks of opsins range from ~ 310 to $\sim 700 \text{ nm}$ in the animal kingdom (between ~ 400 and $\sim 650 \text{ nm}$ in vertebrates) (Rowe, 2002; **Figure 8**). It is not the purpose to discuss here the ways animals discriminate colours; this has been extensively reviewed elsewhere (Lamb, 2013; Olsson et al., 2017; Jacobs, 2018). Rather, we want to emphasize the wide variety of situations - from a single opsin up to several dozens - that can be found from one species to another.

In vertebrate rods, rhodopsin (Rh1) is responsible for the achromatic response (though amphibians and geckos are capable of colour discrimination under scotopic conditions due to two sub-populations of rods detecting light of different wavelengths). The chromatic response is provided by multiple cone sub-types, each expressing one type of opsin, although co-expression of different opsins in one single cone is not an exception (Isayama et al., 2014). Up to four groups of opsins are expressed in cones, maximally sensitive in the UV/blue (SWS1, SWS2), the green/yellow (Rh2) and the red (LWS) ranges (Jacobs, 2018). Whereas most mammals have only two cone pigments (SWS1 or SWS2, and Rh2), diurnal old-world primates have three (SWS2, Rh2, and LWS) (Rowe, 2002; Imamoto and Shichida, 2014). Many marine mammals and a few nocturnal rodents, carnivores, and primates have secondarily lost the S cone pigment and became monochromatic (**Figure 8**). Invertebrates often display higher diversity as they may possess from a few up to several dozens of visual opsin genes, depending on the species, covering from the UV to the far red wavelengths (Jacobs, 2018; Warrant, 2019; **Figure 8**). In both vertebrate and invertebrate eyes, photoreceptors and photopigments often display a non-uniform distribution within the retina,

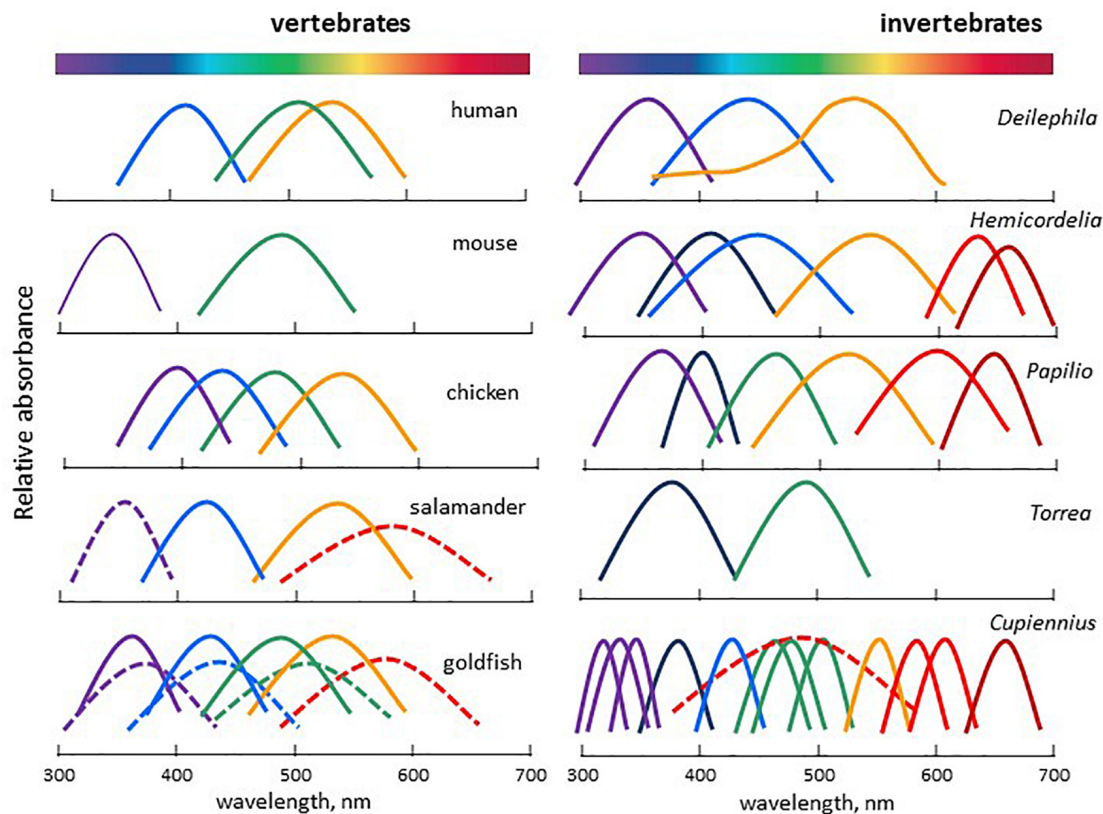


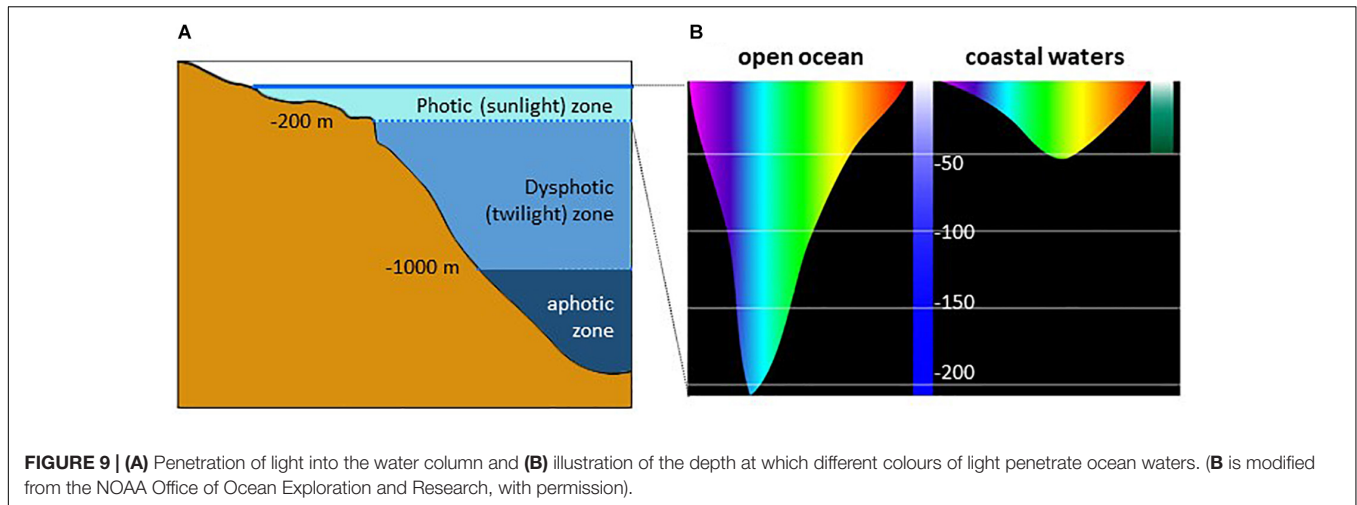
FIGURE 8 | Spectral sensitivity curves of selected vertebrate and invertebrate representatives, illustrating the wide variety of light detection systems encountered. **Vertebrates:** human *Homo sapiens*, mouse *Mus musculus*, chicken *Gallus domesticus*, Salamander *Salamandra*, goldfish *Carassius auratus*. **Invertebrates:** elephant hawk moth *Deilephila elpenor*, dragonfly *Hemicordulia tau*, butterfly *Papilio xuthus*, annelid worm *Torrea candida*, nocturnal spider *Cupiennius salei*. Adapted and modified from Imamoto and Shichida (2014), Warrant (2019).

in a stochastic/regionalized, regionalized, or ordered manner, providing specific adaptations to the ecological niche they occupy (Viets et al., 2016; Marshall, 2017; Stöckl and Kelber, 2019; Warrant, 2019). Specific adaptation to the local environment is often observed underwater where the composition of the available light depends on many factors, including depth, time of day and other physical parameters (Figure 9). To compensate for these changes, underwater animals have developed mechanisms that alter spectral sensitivity (Temple et al., 2008), including gain or loss of a photoreceptor class, changes in chromophore type [retinal (A1) or 3,4-dehydroretinal (A2)] and expression of different opsin classes or subtypes within a photoreceptor class. The changes may occur during development or depending on the species requirements in adulthood. Light-induced shifts in cone frequency and opsin expression occur in many aquatic species; the expression of opsins is modified by the population habitat and lighting conditions in the Bluefin Killifish, *Lucania goodie*, and during development in Coho Salmon, *Oncorhynchus kisutch*, in a manner that maximizes photonic capture (Fuller and Claricoates, 2011). Similarly, ontogenetic and sexual variations in the expression of opsins have also been described in insects (Temple et al., 2008; Arikawa et al., 2017; Lichtenstein et al., 2018).

ORIENTATION IN SPACE: PHOTOTAXIS, PHOTOTROPISM

Orientation in space, defined as phototaxis in animals and phototropism in plants, are movements in response to the lighting environment. Positive and negative phototaxis (*i.e.*, towards or away from the light stimulus) is most often triggered by blue light detection, but not only (Randel and Jekely, 2016). It may cover the whole spectrum, from UV/A up to near-infrared (Cyanobacteria, Chau et al., 2017; Wilde and Mullineaux, 2017) or just part of it (UV to green in the fruit fly *Drosophila melanogaster* larvae, Humberg and Sprecher, 2017); UV/blue in Hemiptera *Diaphorina citri* (Paris et al., 2017); near-infrared in the zebrafish *Danio rerio* larvae (Hartmann et al., 2018); and green in the bat *Pipistrellus nathusii* (Voigt et al., 2017). Animals (particularly aquatic larvae) may change their preferences during development.

Phototropism characterizes plants and fungi, which, as sedentary organisms, have evolved the ability to alter their growth to optimize light capture and photosynthesis (Goyal et al., 2013; Fankhauser and Christie, 2015; Schumacher, 2017). In most plants and fungi phototropism is triggered by both red and UV-A/blue light, while in flowering plants blue light



is the predominant signal. In *Botrytis cinerea*, a pathogenic fungus of plants, light stimulates germination of the conidia, while dark stimulates its growth. Also, germ tube growth is reduced by near-UV, blue and far-red light, which induce negative phototropism, while red light promotes germ tube elongation and induces positive phototropism (Schumacher, 2017). In fact, negative phototropism induced by near-UV/blue light increases pathogenicity, whereas positive phototropism induced by red light suppresses it.

ORIENTATION IN TIME: THE CIRCADIAN CLOCKS

Orientation in time is provided by the so-called circadian system. This system is made of circadian clocks, which function autonomously and rhythmically with a period of approximately 24 h (Bell-Pedersen et al., 2005). Circadian clocks are present in virtually all living organisms, including cyanobacteria, micro-green algae, plants, fungi and animals (Figure 10). The alternation of light and dark during the 24 h LD cycle is the main environmental input signal to the clocks (although there are others such as food intake, temperature or social interaction), synchronizing and entraining their autonomous activity with the natural world. In return, the clocks produce a number of rhythmic messages, either through direct gene regulation (so-called clock-controlled genes or ccg) or indirectly through activating second messenger cascades. Together, the rhythmic input to the clocks, the clocks themselves and their rhythmic outputs, constitute the circadian system. Such an organization governs myriad metabolic, physiological and behavioural processes, thereby synchronizing their activities with the natural periodicities (Reiter, 1991; Falcón et al., 2007b, 2010; Bloch et al., 2013; Table 1). It has been estimated that between 10 and 20% of the genome shows a circadian expression (about 3,000 genes in humans), while a recent study of non-human primates showed that >80% of *de novo* transcripts were rhythmic (possibly under circadian control but also possibly evoked by the light-dark cycle or the sleep-wake cycle) (Mure et al., 2018).

It is believed that circadian clocks appeared very early in evolution as an adaptive function linked to DNA replication. By limiting DNA replication to the night phase, UV-induced damage to DNA could be blocked (Pegoraro and Tauber, 2011). Over geological time selective pressure turned this simple passive process into an active one, allowing anticipation of predictable changes. Among the myriad daily and annual functions displaying clock-controlled rhythmicity are the rest/activity cycle, food intake, flowering, vertical and horizontal migration, growth, reproduction, and many more (Table 1). In addition to their ubiquitous character and the persistence of rhythmic activity under constant light (LL) or darkness (DD) (free-running), other characteristics of a circadian clock include (1) genetic determination (*i.e.*, each species has its proper period close to 24 h, but inter-individual variations are observable within the same species), (2) synchronization by other factors (*e.g.*, rainfalls, moon cycles, food intake, tides) in addition to the LD cycle; (3) temperature compensation, *i.e.*, the clock's period is not affected by temperature; (4) lengthening or shortening of the period with light intensity under constant light (LL); (5) induction of phase advances or phase delays by light sequences applied at different times under DD; (6) resynchronization by an environmental stimulus once constant conditions have ended. Virtually all cells possess internal clock machinery.

It is worth mentioning that in addition to the circadian clocks many organisms have developed circannual time measuring systems. As is the case for the circadian clocks, circannual clocks are ancestral, ubiquitous, autonomous, entrained by photoperiod and temperature compensated (Lincoln, 2019). The location and mechanisms of the circannual clocks, still poorly understood, are discussed elsewhere (Numata et al., 2015; West and Wood, 2018; Wood and Loudon, 2018; Murphy, 2019).

Localization of the Circadian System Plants

There is evidence that multiple and distinct circadian clocks are present in different tissues of plants. The first example was obtained from bean plants, in which stomatal opening,

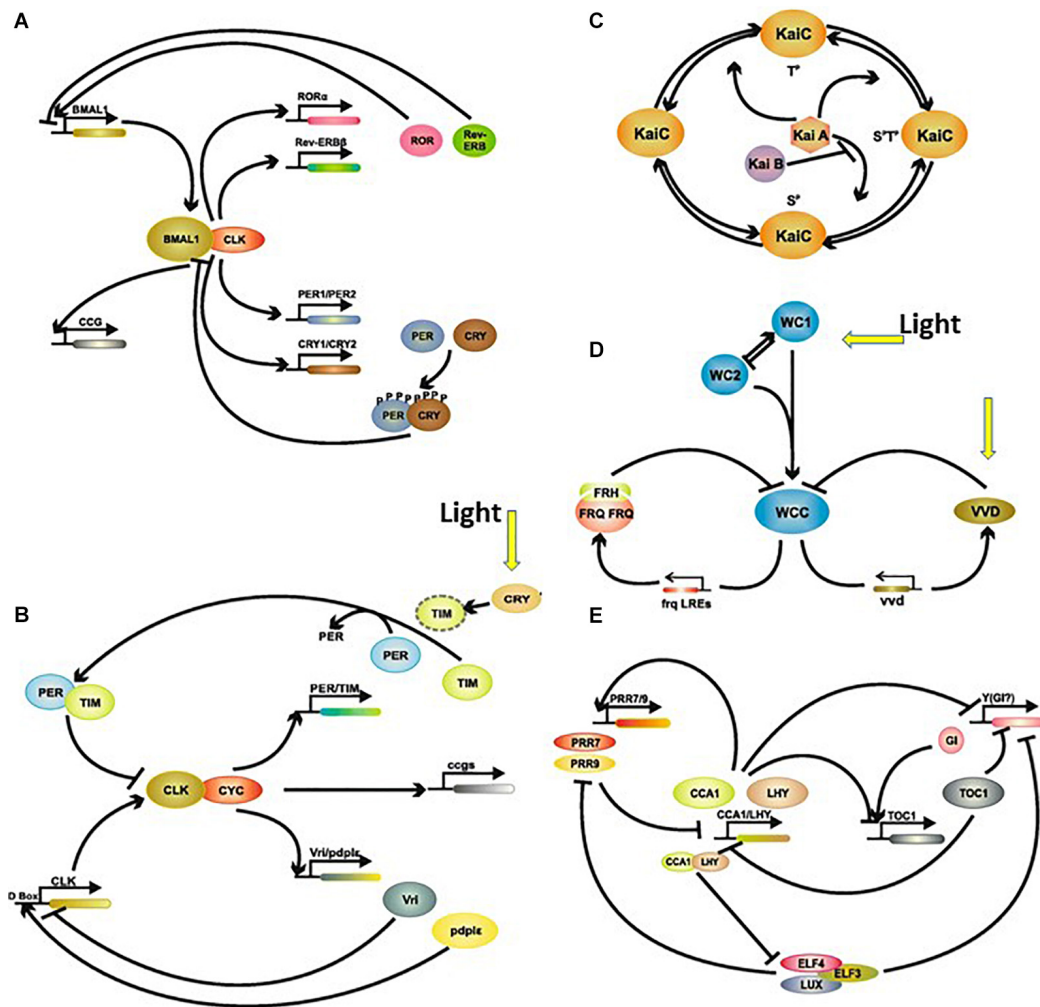


FIGURE 10 | Simplified schematic representation of the circadian clock in (A) mammals, (B) insects, (C) Cyanobacteria, (D) fungi, and (E) plants. For details see Saini R. et al. (2019). Abbreviations: CCA1, circadian clock associated 1; CCG, clock controlled genes; Clk, clock; CRY, cryptochrome; CYC, cycle; ELF, early flowering; FRH, FRQ-interacting RNA, helicase; FRQ, frequency; GI, gigantea; LHY, late elongated hypocotyl; LUX, lux arrhythmo; PER, period; Rev-Erb β (orphan nuclear receptor family 1); PRR, pseudo-response regulator; ROR α , retinoic acid receptor (RAR)-related orphan receptors; TIM, timeless; TOC1, timing of cab expression 1; VVD, vivid; WC, white collar; WCC, white collar complex. Modified from Saini R. et al. (2019) No special permission required.

photosynthesis, and leaflet movement rhythms displayed different periods under free-running conditions. In addition, it seems that in some cells the 24 h LD cycle is the dominant synchronizing factor, while in others it is the 24 h temperature cycle. The question has arisen as to whether there is a central pacemaker or a hierarchical coupling between different clocks in plants as is the case in animals, and how these different clock activities synchronize with each other. It has been hypothesized that the oscillations in sugar concentrations and/or microRNA (miRNA) might play this role (Endo, 2016).

More is known in invertebrates and vertebrates, where all cells possess molecular clock machinery, forming a network of more or less potent and hierarchically organized units (Falcón et al., 2007b; Dibner et al., 2010; Vatine et al., 2011; Ito and Tomioka, 2016). The hierarchical order varies according to the class and species considered.

Vertebrates

In fish and lizards, the circadian system is made of a network of independent and interconnected light-sensitive oscillatory units located in the retina, the pineal gland and probably also in the brain (Tosini et al., 2001; Falcón et al., 2007b). Studies in the zebrafish indicated that virtually all cells from any tissue are light sensitive circadian oscillators (Steindal and Whitmore, 2019), but the great variety of fish species precludes making any generalization. In any case, the pineal gland appears to act as a potent master oscillator, depending on the species (Underwood, 1989; Whitmore et al., 1998; **Figure 11**). The photoreceptor cells in the retina and pineal gland actually constitute full circadian systems by themselves, as they possess the light transduction machinery that provides input to the clock, as well as the machinery that produces the output signal of this clock, *i.e.*, melatonin (Pickard and Tang, 1994; Bolliet et al., 1997;

TABLE 1 | Some examples of demonstrated impacts of the clocks on organisms.

Fungi	Unicellular algae	Plants	Insects	Vertebrates
		Cell division		
		Metabolism		
		Enzymatic activities		
		Growth		
Reproduction			Reproduction	
			Mating	
			Neuroendocrine regulations	
		Seed germination & senescence	Hormonal fluctuations	
	Mobility	Movements (leaf, cotyledon, chloroplast, flowering, stomatal opening)	Locomotor activity, migration schooling behaviour (fish)	
			vocalisation (birds, insects)	
	Photosynthesis	Photosynthesis & respiration	Activity/sleep	Activity/sleep
			Feeding	
			Seasonal timing	
		Ion fluxes		Cardiovascular regulations
			Vocalisation	
	Susceptibility to drugs	Susceptibility to stress, immunity (vertebrates)		
				Pigmentation fur or feathers renewal
			Retinal and visual sensitivity	retino-motor movements (fish)

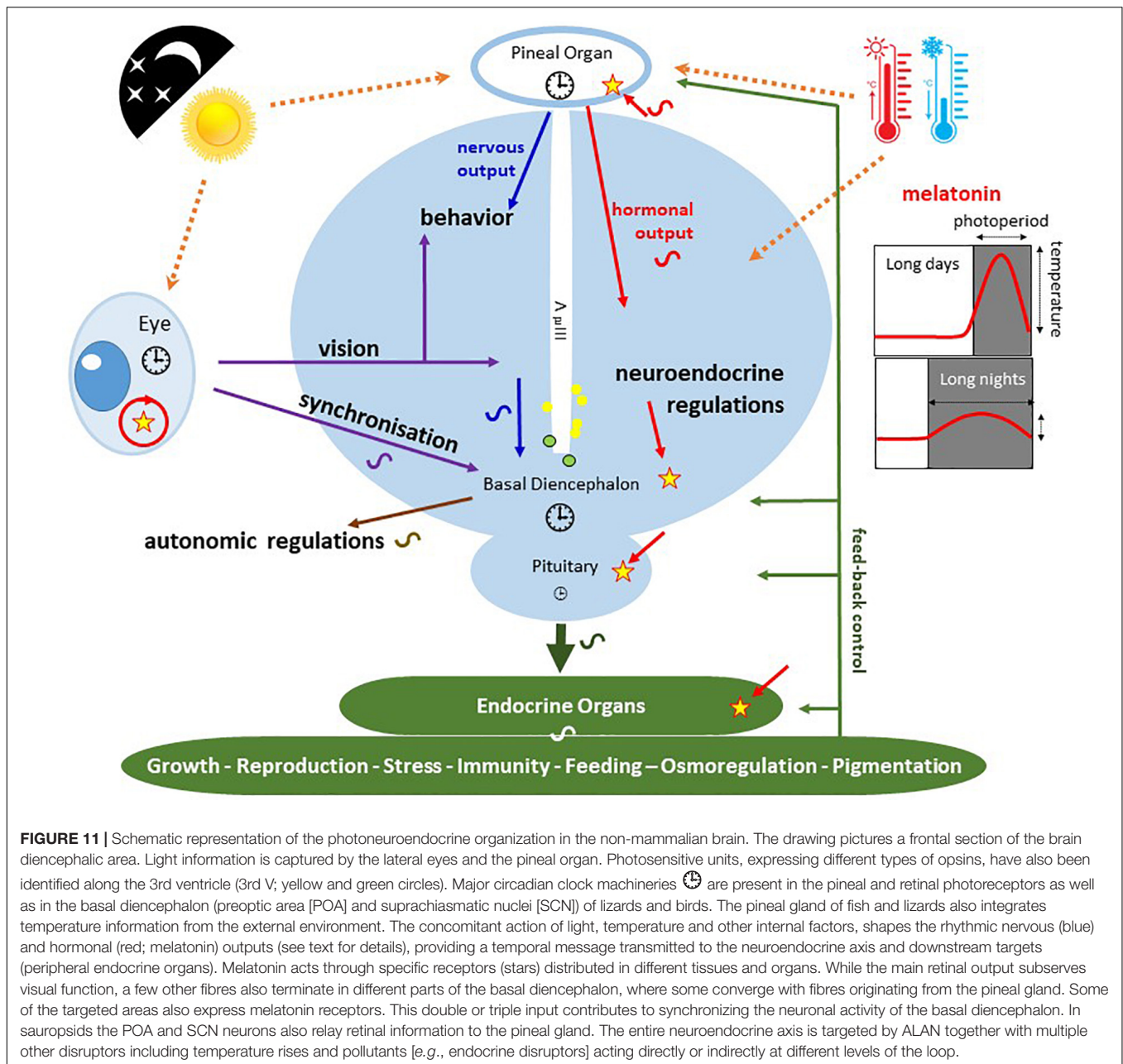
Gothilf et al., 1999). A major difference between the retina and pineal gland lies in the fact that retinal melatonin is generally used and metabolized locally (**Figure 11**). In the pineal gland, melatonin is typically produced in higher amounts at night than during the day, and is immediately released into the blood or cerebrospinal fluid. The duration of this nocturnal signal reflects the duration of the night, while its amplitude varies with temperature in a species-specific manner (Underwood, 1989; Falcón, 1999). Thus, daily and annual variations in the melatonin secretion profile provide a reliable indication of daily and calendar time, which is used as a time-keeping signal to synchronize physiological and behavioural processes with daily and annual variations in photoperiod and temperature (see section “Clock Outputs and Photoperiodism”).

The strength and reliability of the melatonin time-keeping signal is reflected in its conservation throughout vertebrate evolution. However the modality of melatonin production has been profoundly modified from fish to mammals as a result of dramatic structural and functional modifications of the whole circadian network. In mammals, the circadian components are located in distinct specialized areas. A “master clock” is located in the suprachiasmatic nuclei (SCN; ~5,000 to 30,000 cells) of the hypothalamus, which interacts with a network of peripheral oscillators (Harder and Oster, 2020). Photoperiodic input to the SCN comes from the retina *via* the retino-hypothalamic tract: while light information encoded by the retina is mostly directed to the visual cortex through ganglion cells (RGC), a small number of these - the melanopsin-containing or

intrinsically photosensitive (ip) RGC (see section “Type II or Animal Rhodopsins”) - send information to the SCN (as well as numerous other brain nuclei) (Do, 2019). One downstream effector of the SCN is the pineal gland, with its rhythmic melatonin production; but the gland has lost all intrinsic photoreceptive and circadian properties (Collin et al., 1988; Klein et al., 1997). Rhythmic information from the SCN is transmitted to the pineal gland *via* a poly-synaptic neural pathway (Klein et al., 1997; Falcón et al., 2007b). The few studies performed in Sauropsida (birds and reptiles) indicate that melatonin secretion by the pineal gland is controlled by both direct and indirect photosensitivity (Cassone, 2014).

Invertebrates

Insects include more than 1 million species, displaying a huge diversity in all aspects of organization and life style, and there is much variation in the anatomical organization of the circadian network in the insect brain (Bloch et al., 2013). Despite this diversity, there are striking similarities in the principal organization of circadian clocks. In the fruit fly *Drosophila melanogaster* the network consists of a few hundred neurons (Hermann-Luibl and Helfrich-Foerster, 2015). A master clock is located in scattered nuclei located in the optic lobes and brain, composing a neuronal network (Tomioka and Matsumoto, 2010; Hermann et al., 2013; Hermann-Luibl and Helfrich-Foerster, 2015). These neurons utilize mainly neuropeptides as signalling molecules, including pigment-dispersing factor (PDF), which appears to be well-conserved in putative master clock neurons of all insects studied so far (including apterygotes, orthopteroids, coleoptera, hymenoptera, lepidoptera and diptera



Tomioka and Matsumoto, 2010). In *D. melanogaster*, PDF is considered as the main output factor of clocks, acting as a neuromodulator and synchronizing signal between the different central clock neuron clusters (Helfrich-Forster et al., 2011; Hermann et al., 2013). In addition to these central clocks, there is evidence indicating that many other organs or tissues, either nervous (eye and eye stalk, antenna) or peripheral (gustatory system, Malpighian tubules, prothoracic gland, epidermis secreting endocuticle, testis and germinal vesicle), express circadian clock properties (Tomioka et al., 2012). Photoperiodic information captured by the ocular, and in some instances the ocelli photoreceptors, entrains the central

oscillators, which in turn deliver information to slave peripheral oscillators. In crickets and cockroaches this pathway is essential (Tomioka and Matsumoto, 2010; Tomioka et al., 2012). In other species (e.g., *Drosophila*) the central brain and some of the peripheral oscillators are fully integrated circadian systems as they are able to capture light and thus synchronize their clocks and output functions *in vitro* (Tomioka et al., 2012), in a manner similar to that described for the zebrafish (Whitmore et al., 1998). In the eye, the Rh1 and Rh6 rhodopsins are implicated in entrainment to red light (*D. melanogaster*), while in the brain and peripheral oscillators it is likely to be the UV A/blue pigment Cry1 (*Drosophila D. melanogaster* and Monarch butterfly

Danaus plexippus) (see section “Phytochromes”) (Tomioka and Matsumoto, 2010). It is noteworthy that the central brain circadian system is highly plastic as photoperiodic changes have been reported in fibre distribution or number of clock neurons (Shiga, 2013).

The Molecular Mechanisms of Circadian Clocks

The purpose here is to highlight the universality of the underlying principle as well as the wide range of situations encountered regarding the qualitative aspects of clock entrainment by light (Bhadra et al., 2017; Saini R. et al., 2019).

Irrespective of the organism studied, the molecular clock mechanism consists of one or more transcription/translation negative feedback loops of varying complexity (Figure 10). Because the functioning of the clock involves similar operating mechanisms with different molecular actors, it is thought that clocks have appeared independently several times during evolution (Pegoraro and Tauber, 2011). The number of these actors varies from a few (fungi, green algae) to many (plants, animals) (Saini R. et al., 2019). The molecular mechanisms of the circadian clocks, have been described in detail in Cyanobacteria, fungi (*Neurospora crassa*), plants (*Arabidopsis thaliana*), green algae (*Chlamydomonas reinhardtii*, *Ostreococcus tauri*), insects (*Drosophila melanogaster*) and several representatives of vertebrates including human (Tomioka and Matsumoto, 2010, 2015; Ukai and Ueda, 2010; Nakamichi, 2011; Peschel and Helfrich-Forster, 2011; Vatine et al., 2011; Hurley et al., 2015; Ito and Tomioka, 2016; Koritala and Lee, 2017; Gil and Park, 2019). Strong conservation of the operating modes is observed between insects and mammals, including at the level of the molecular actors (Tomioka and Matsumoto, 2015; Figure 10). It is worth mentioning that post-transcriptional regulation and protein modification, such as phosphorylation and oxidation, have been hypothesized as alternatives ways to building a ticking clock (Millius et al., 2019).

Light Input to the Clock

Light is the main input to the clocks. The effects on the circadian timing systems depend on the intensity, duration, spectrum and pattern of the light stimulus; for a review in humans see Prayag et al. (2019). In the animals investigated thus far, short and middle wavelengths are strongly involved in synchronization and entrainment. In vertebrates, the effective wavelengths are comprised between 420 and 500 nm, the highest efficiency being obtained between 450 and 480 nm (Ramos et al., 2014; Prayag et al., 2019). In mammals, this corresponds to the spectral response of melanopsin from the ipRGC of the retina (see “Type II or animal rhodopsins”). However, it is not excluded that the mechanisms of light-induced clock entrainment are more complex than believed. Indeed, it has been observed that colour opponent mechanisms can induce phase advances or phase delays in the circadian rhythm, depending on light intensity and spectral composition, in the pineal organ of fish, frogs and lizards (Spitschan et al., 2017). Opposing effects of wavelengths on circadian phase shifts have been shown in the cave-dwelling bat

Hipposideros speoris (blue vs. green) and wild rabbit *Oryctolagus cuniculus* (blue vs. yellow). It is noteworthy that a subset of ipRGC, sensitive to UV is also indirectly sensitive (via cone perception) to yellow wavelengths in the mouse *Mus musculus*.

In insects such as *D. melanogaster* and other flies, Cry1 is involved both in light capture (see section “Cryptochromes”) and molecular function of the clock (Figure 10; Saunders, 2012). Cry1 is sensitive to blue light (λ_{max} 470). In addition, Rh1 and Rh6 are implicated in entrainment to red light, and Rh1, Rh5, and Rh6 to green and yellow light (Tomioka and Matsumoto, 2010).

In plants, a variety of situations is observed regarding the wavelengths that entrain the clocks. In terrestrial higher plants, e.g., *A. thaliana*, phytochromes (see section “Phytochromes”) mediate the effects of red and infrared wavelengths (λ : 700–750 nm), while Cry1 and Cry2 mediate the effects of blue light (Figure 10; Chen et al., 2004; McClung, 2006). In microalgae such as *C. reinhardtii* the clock is reset by a wide range of wavelengths: violet, blue/green and red (Niwa et al., 2013; Ryo et al., 2016). Finally, in fungi the light entrainment of the clock is mediated by the WC1 blue photoreceptor species (Bhadra et al., 2017).

Clock Outputs and Photoperiodism

Clocks control a wide range of peripheral oscillators and related downstream processes, many of them vital, to keep in phase the myriad rhythmic events that take place over the course of a day or a year. We present below a short overview (summarized in Table 1), with the help of a few examples taken from unicellular organisms, fungi, plants and animals.

Unicellular Algae, Plants, and Fungi

Neurospora crassa was the first fungi in which endogenous circadian control of its sexual and asexual daily rhythms of reproduction was demonstrated (Zámborszky et al., 2014; Hurley et al., 2015). The asexual cycle consists in the production of conidia during the subjective night, and similar rhythms in conidiospore formation have now been reported in Myxomycetes, Zygomycetes and Ascomycetes (Correa and Bell-Pedersen, 2002). In *N. crassa* and other multinucleated fungi (*Physarum polycephalum* and *Aspergillus nidulans*), LD cycles also synchronize the timing of mitotic cycles (Edmunds, 1988; Hong et al., 2014). The involvement of the circadian clock has been demonstrated in *Neurospora*, in which 15–20% of the genes are clock-controlled (Zámborszky et al., 2014) (Table 1).

Virtually all functions of unicellular algae are rhythmic and synchronized by the LD cycle, including metabolism, enzymatic activities, photosynthesis, cell division cycle, mobility, morphology and chromosome topology, and even the susceptibility to drug treatments or infection by viruses (Table 1; Edmunds, 1984). The outputs are generated by 24 h LD rhythms in gene transcription/translation (Welkie et al., 2019).

Similarly, in more distantly related plants such as *A. thaliana*, the rhythms controlled by the circadian clock are plethoric, including gene expression, Ca^{2+} fluxes, chloroplast movements, stomata opening, flowering, cotyledon and leaf movements, metabolic and hormonal activities, or defence against pathogens (Barak et al., 2000; Table 1). In a large scale study comparing

nine representatives of Archaeplastida, including unicellular algae (*Cyanophora paradoxa*, *Porphyridium purpureum*, *Chlamidomonas Reinhardtii*), pluricellular algae (*Klebsormidium nitens*), mosses (*Physcomitrella patens*), early vascular plants (*Selaginella moellendorffii*), and late vascular plants (*Picea abies*, *Oryza sativa*, *A. thaliana*), it was found that they had similar diurnal transcriptional programs, despite large phylogenetic distances and dramatic differences in morphology and lifestyle (Ferrari et al., 2019; **Table 1**).

Animals

Vertebrates

The circadian clocks of vertebrates contribute to controlling a myriad of rhythmic metabolic, physiological and behavioural functions (Boissin and Canguilhem, 1998; **Table 1**). One main output signal from the circadian system of vertebrates is melatonin, the hormone secreted principally at night by the pineal gland (“Vertebrates” and **Figure 11**; Collin et al., 1988; Ekström and Meissl, 2003; Falcón et al., 2007a).

At the molecular level, the clocks govern rhythmic variations in plasma levels of ions, carbohydrates and lipids, and of brain and plasma steroids, and monoamines (serotonin, dopamine) (Delahunty et al., 1980; Olcese et al., 1981; Takahashi, 1996; Tong et al., 2013; Mendoza and Challet, 2014; Hernandez-Perez et al., 2015; Vancura et al., 2016; Song et al., 2017); furthermore, it also regulates the expression of genes or activities of enzymes involved in these changes (Falcón, 1999). At the physiological level, the neuroendocrine system, from the hypothalamus to the pituitary gland and peripheral organs, displays daily and annual fluctuations, which contributes to controlling a wide range of functions as critical as growth, reproduction, stress response, food intake, immunity or osmoregulation (Falcón et al., 2010; Tonsfeldt and Chappell, 2012; Wood and Loudon, 2014; Challet, 2015; Kim et al., 2015; Leliavski et al., 2015; **Figure 11**). The cardiovascular system (blood pressure and heart rate) and neuronal electrical activity (electroretinogram and electroencephalogram) do not escape the rule as they also fluctuate rhythmically (Boissin and Canguilhem, 1998; Peters and Cassone, 2005; Cameron and Lucas, 2009; Talathi et al., 2009; Wood and Loudon, 2014; Petsakou et al., 2015; Cavey et al., 2016; Paul et al., 2016; **Figure 11** and **Table 1**). Finally, in many tissues, clocks also control the cell division cycle (Boissin and Canguilhem, 1998; Steindal and Whitmore, 2019), as well as some adaptive cellular movements including retino-motor movements (the respective elongation and retraction of cones and rods observed in fish and amphibians retinas at the L-to-D and D-to-L transitions) (Kwan et al., 1996; Song et al., 2017). Accordingly, dozens of behavioural activities display daily and annual rhythms, including locomotor activity and sleep, schooling behaviour (fish), pigmentation or fur renewal, vertical (fish) and horizontal (all vertebrates) migration, behavioural thermoregulation (fish), vocalization (fish, birds), food intake, mating and reproduction, etc. (Zachmann et al., 1992; Lincoln et al., 2006; Cancho-Candela et al., 2007; Kantermann et al., 2007; Foster and Roenneberg, 2008; Kulczykowska et al., 2010; Cassone, 2014; Ruf and Geiser, 2015; **Table 1**).

Invertebrates

The data on invertebrates are not as abundant as for vertebrates, and relate mostly to insects, although more and more studies refer to marine invertebrates. All indicate that the clocks mediate the effects of photoperiod and temperature on a myriad of rhythmic daily and seasonal events (Helfrich-Forster et al., 2011; Arboleda et al., 2019). The most obvious relate to feeding (e.g., foraging in bees, and moths, bugs and mosquitoes bites), reproduction (e.g., courtship behaviour, mating and reproduction), and growth (larval and adult development, diapause, longevity) (Helfrich-Forster et al., 2011; Bloch et al., 2013; Rougvié and O'Connor, 2013; **Table 1**).

The neuromodulator PDF, important for transmitting clock information to downstream effectors, also acts as a circulating hormone (Bloch et al., 2013). There is anatomical and physiological evidence that the invertebrate circadian system influences circulating levels of endocrine signals, including juvenile hormone (JH), ecdysteroids, and “pheromone biosynthesis activating neuropeptide.” JH plays key roles in regulating the reproductive physiology and behaviour in insects as well as in controlling the age-related division of labour in social insects. The levels of transcripts of JH biosynthetic enzymes in the *corpora allata* display strong daily rhythms in the bee, mosquito and fruit fly. In the haemolymph, the circulating levels of JH, JH-binding protein and JH-degrading enzymes also display strong circadian dependent variations (Bloch et al., 2013). It is believed that the JH oscillations mediate the circadian rhythms in the levels of neurotransmitters (pheromone biosynthesis activating neuropeptide), and hormones (octopamine; serotonin; dopamine) thought to be important for locomotor activity or reproduction (including the production of pheromones, courtship, mating, and gamete production) (Koutroumpa and Jacquin-Joly, 2014). Similarly, it is suspected that PDF controls the rhythmic production of the prothoracicotropic hormone involved in the regulation of ecdysteroids, which control moulting (**Table 1**).

Finally, the electrical activity of invertebrates' eyes (electroretinogram) and of the entire visual system display circadian fluctuations (Hernandez and Fuentes-Pardo, 2001). In the Praying Mantis, *Hierodula patellifera*, rhythms are associated with cyclic changes in the colour of the eyes, neural control of eye movement, and gross locomotor activity (Schirmer et al., 2014).

IMPACT OF ALAN AND LEDs ON LIVING ORGANISMS

“Nature is perfect. I keep a diary. I write on which day of the month the flowers bloom and on which day of the month the insects begin to sing. Year after year, these dates hardly vary. They are very regular, this is one of the laws of nature. What goes with the laws is nature. Nature is in accordance with the laws. That's why I believe people should live by imitating nature... Nature does the truth in silence.”

Master Ekiyo Miyazaki (1902 – 2008).

The Generalization of LED Illumination

Initially motivated by the desire to provide more energy-efficient light sources for public lighting (Nair and Dhoble, 2015), the use of LED now concerns a wide range of technological, socio-economic and commercial applications. A variety of sources contributes directly or indirectly (glowing) to outdoors LED lighting: offices and homes, street lighting (**Figure 1**), vehicles, traffic signs, commercial advertising, tourism (architectural and landscaping enhancement), industry (factories, greenhouses), or recreational (outdoor and indoor sports) areas. Aquatic environments are also affected (shorelines and coastlines in urban and suburban areas, offshore platforms, commercial routes or fishing areas, especially night fishing). From such considerations it can be argued that investigations on the effects of outdoors LED are closely associated to those of ALAN, a situation clearly unfavourable to the preservation of the night sky.

Artificial lighting in general, and LEDs in particular, add to the list of numerous anthropogenic pressures that, decade after decade, are changing an equilibrium that has resulted from millions of years of evolution, affecting the tree of life, of which man is only one branch among thousands of others. In the vast majority of cases, studies investigating the impacts of a given factor consider mainly the effects on human health, while impacts on the animal and plant kingdoms are considered mainly within the context of improving productivity in order to satisfy growing human needs of livestock and derived products. This egocentric view is currently directing most of the research on LED; furthermore, the majority of studies are conducted in a controlled environment, while the impact on non-domesticated species and ecosystems are rarely taken into account.

We have given above an overview of the incredibly wide range of strategies that have been developed by unicellular and multicellular organisms (i) to capture and transduce light information into messages conveyed to appropriate targets, (ii) to orientate in space and time and ultimately (iii) to accomplish their essential biological needs. The development of internal clocks reflects adaptation to the highly predictable and reliable variations of the photic environment allowing anticipation and harmonization of the myriad of biological functions to the daily and annual changes of photoperiod. It is therefore not surprising that disturbances of this photic environment, whether in quality, quantity or duration, have more or less marked impacts on living organisms. Below we review, through a few representative examples, how human activities and ALAN, alone or in combination with other anthropogenic factors, alter individuals, species and communities.

Economical Purposes

Cultivation of Microorganisms and Plants

Many studies highlight the interest of LEDs for the greenhouse cultivation of plants (Yeh et al., 2014; Nair and Dhoble, 2015; Singh et al., 2015; Dueck et al., 2016; Urrestarazu et al., 2016; Rehman et al., 2017), fungi (Wu et al., 2013; Kim et al., 2014), and unicellular microalgae (Schulze et al., 2014) of agronomic, ornamental or medicinal interest. One major focus resides in the possibility to choose a particular wavelength (of narrow

spectral range) or a combination of wavelengths, targeting specific aspects of plant physiology in greenhouse environments (Rehman et al., 2017). In plants, day length, light intensity, and light quality affect morphology, growth and development. The effects of light (whether by LED or other sources) on fungi and plants depend on the range of frequencies they detect. **Table 2** summarizes the effects of different frequencies on the metabolism and physiology of plants. For example, far blue and UV lights are useful for eliminating bacterial and viral infections (Yeh et al., 2014; Kumar and Engle, 2016; Kim et al., 2017), while an adequate combination of blue and red/infrared wavelengths provides optimal effects in terms of metabolism (e.g., photosynthesis, lipid synthesis, energy production), germination, cell division, budding, growth, flowering, nutritional value and taste, or production of compounds with high added value (ergosterol, carotene). Little information is available on the impact of green lights.

However, several factors need careful attention:

- (1) The effects of a wavelength or cocktail of wavelengths depend on the species and, within the same species, on sex and stage of development; they also depend on intensity, positioning, periodicity or frequency of exposure (Dueck et al., 2016; Hernandez and Kubota, 2016). For example, cyanobacteria grow preferentially under green, yellow and red light, whereas microalgae preferentially grow under blue ($420 < \lambda < 470$ nm) or red ($\lambda = 660$ nm) light.
- (2) Potentially toxic compounds might be produced. For example, studies on Lamb's Lettuce (*Valerianella locusta*) indicate the plants can accumulate beneficial (polyphenols) as well as unwanted (nitrates) compounds depending on the proportions of red and blue light used (Dlugosz-Grochowska et al., 2016; Wojciechowska et al., 2016). In contrast, in *Brassica alboglabra* nitrate concentration in shoots increased significantly when grown in the shade compared to lit areas, while it was reduced after red- and blue-LED lighting (He et al., 2019).
- (3) The importance of plant and microbiome interactions, rarely taken into account, need more careful investigation, as light can affect both plant physiology and surrounding microbiome density and composition (including pathogenic species) differently (Alsanius et al., 2019).

TABLE 2 | Effects of wavelengths on plants (from Xu et al., 2016).

λ (nm)	Impact
280-315	minimal impact on morphology and physiology
315-400	Weaker chlorophyll absorption, impacts on cyclical activity & growth (tissues & stem)
400-520	Chlorophyll and carotenoid absorption proportion is the largest, the biggest influence on photosynthesis
520-610	Decreased absorption by pigments
610-720	Chlorophyll absorption rate is low, significant effects on photosynthesis and cyclical activity
720-1000	Minimal absorption, effects on photosynthesis, blooming and seed germination
> 1000	Convert to heat

Thus, while the use of LED in the food industry is promising, it is still at an experimental stage, and studies must be conducted on a case-by-case basis, as the physiological processes involved in the responses to light are incompletely understood (Delabbio, 2015) “For practice, more research is needed to optimize plant distances, light strategies and light intensities to make the technology more profitable and sustainable” (Nair and Dhoble, 2015; Moerkens et al., 2016).

Breeding

As mentioned above, the quality (λ), quantity (intensity), and duration (photoperiod) of the light phase play a major role in the regulation of metabolism, physiology and behaviour in the animal kingdom (Maise and Breton, 1996; Malpoux et al., 1996; Falcón et al., 2007b, 2010; Rocha et al., 2013; Espigares et al., 2017). During decades, manipulation of the surrounding light conditions has been part of the protocols used to control food intake, larval development, growth rate and reproduction in farm animals (Delabbio, 2015). For a given lighting condition, the response is species-specific; differences may also exist within the same species as a function of age, sex, or geographical location (Pan et al., 2015).

The use of LEDs to substitute for “conventional” lighting in aquaculture farms, poultry and mammal housing is the subject of an intensive promotional campaign, which emphasizes the advantages provided by LEDs (controlled choice of wavelength and lower running costs) (Delabbio, 2015). Field applications are still scarce (Pan et al., 2015; Yang et al., 2016). Studies aim to compare the effects of LEDs to conventional lighting on growth, food intake and conversion efficiency, weight gain, egg production or behaviour (aggressiveness, exploration) (Huber-Eicher et al., 2013; Pan et al., 2015). In spite of a noticeable increase in the number of publications, the data remain too scarce for definitive conclusions to be drawn. Some examples are reported below.

Insects

Light-emitting diodes have been used to select wavelengths that favour reproduction of the Black Soldier fly *Hermetia illucens*, a tropical fly species with great potential for the processing of several types of organic waste and by-products (Oonincx et al., 2016), or for trapping pests like the Cigarette Beetle, *Lasioderma serricorne* (Miyatake et al., 2016) and other harmful species (Cohnstaedt et al., 2008).

Corals

A positive impact of LEDs compared to other light sources has been reported on the growth of the ornamental corals *Stylophora pistillata* and *Galaxea fascicularis*, but not of *Acropora formosa* (Wijgerde et al., 2012; Rocha et al., 2013). In *A. formosa* and *S. pistillata*, wavelength affects macro- and micro-morphology (Rocha et al., 2014).

Molluscs

The predatory Dog Whelk *Nucella lapillus* exerts strong top-down control on biodiversity in intertidal coastal regions. Under nocturnal white LED illumination mimicking street lighting (~ 22 lx), individuals displayed higher activity, disregarded the

presence of other predators, and increased feeding on mussels (Underwood et al., 2017). The effects of LEDs of different wavelengths were also examined in the abalone *Haliotis discus* (Gao et al., 2016). It was found that under blue or green light, the survival and growth rates, food intake, and food conversion efficiency were lower than in groups exposed to red or orange light; the former displayed enhanced anaerobic metabolism and energy loss, while the latter showed higher amylase and cellulose activity.

Fish

Several studies reported the impact of different wavelengths on growth, hormonal control of reproduction, stress and pigmentation, biological rhythms (clock gene expression, melatonin secretion), thyroid activity (T3, T4) and expression of opsin genes (Rh, melanopsin) (Jung S. J. et al., 2016; Takahashi et al., 2016). They emphasized the interest and the potential use of white, mono or dichromatic LEDs in aquaculture and breeding, but underline the necessity of rigorous experimentation. Blue LEDs have the potential to kill unwanted pathogens in aquaculture plants. For example, LED light at 405 and 465 nm were efficient in Olive Flounder (*Paralichthys olivaceus*) and Carp (*Cyprinus carpio*) culture farms to eliminate *Miamiensis avidus* and *Edwardsiella piscicida* respectively (Roh et al., 2018). However, at 405 nm the dorsal part of the retina was damaged after 14 days in *P. olivaceus*, outlining the possibility that these treatments might have deleterious side effects on the fish itself. In the fisheries industry, there is evidence that LEDs are being used by fishermen to attract species of interest (Park J. A. et al., 2015; Kehayias et al., 2016).

Birds

The use of LEDs in avian farms has increased dramatically in recent years, with the aim to reduce production costs combined with improving reproduction and growth and reducing stress (Huber-Eicher et al., 2013; Parvin et al., 2014a,b; Yang et al., 2018; Arowolo et al., 2019). A huge variety of protocols have been used that take into account age and sex of animals, as well as light quality, intensity, periodicity and duration. For example, red LEDs advance sexual maturation while decreasing aggression compared to green or white LEDs in hens *Gallus domesticus* (Gongruttanun, 2011; Huber-Eicher et al., 2013); the effects were due to quality and not the amount of light provided. Green LEDs promote egg growth, and blue, green or yellow LEDs, used alone or in combination, promote immune defence and improve meat quality (Parvin et al., 2014a,b). The authors stated that more research on these aspects is needed in order to standardize intensities, durations, and exposure wavelength.

Impact on Species in Their Environment

Microorganisms and Plants

Artificial nocturnal illumination with white LED can influence biomass and community composition of terrestrial photoautotrophs¹. In diatoms and sedimentary *Cyanobacteria* white LED (6300 K) induce quantitative population remodelling, loss of annual variations in population composition, decreased

¹which use light as a source of energy and CO₂ as a source of carbon.

respiratory activity and redistribution of sedimentary microbial populations; these modifications are likely to change the CO₂ cycle and induce carbon accumulation in sediments (Hölker et al., 2010). Similarly, in freshwater ecosystems, three weeks of exposure to ALAN (white LED, 20 lx) decreased periphyton (the mixture of algae, microbes, cyanobacteria and detritus) biomass and the proportion of Cyanobacteria, while increasing the proportion of Diatoms (Grubisic et al., 2017, 2018a,b). In addition, it was shown that the replacement of high-pressure sodium (HPS) lamps by white LED at intensities commonly found in urban waters (~20 lx), induced similar but stronger effects (Grubisic et al., 2018b). Autotrophs within periphyton communities form the base of aquatic food webs and as such constitute a fundamental element in aquatic ecosystems. More studies are needed that should include the marine environment in which ALAN disturbs synchronized diel vertical migrations of zooplankton and where the vast majority of the zooplankton pelagic community exhibits a strong light-escape response in the presence of artificial light (Ludvigsen et al., 2018).

In plants, the intensity of lighting used in urban and suburban districts as well as on highways is sufficient to affect their physiology (Bennie et al., 2016; Massetti, 2018). The described effects of night lighting (including by LEDs) include tree leaf colouring, retention/abscission (on deciduous trees), budding, flowering, growth, or defence against pathogens. In the case of fungi involved in litter decomposition of streams, and which play a key role in the carbon and nutrient dynamics of stream ecosystems, ALAN can alter community structure and composition, resulting in inhibition of litter decomposition (Liu et al., 2020).

Animals

There is no longer any doubt that ALAN affects phototaxis and circadian rhythms, and consequently any ensuing functions and behaviours. It is beyond the scope of the present review to discuss the impacts of ALAN on human health and related studies (Attia et al., 2019). Rather, we focus on the available data that can aid understanding its impacts in the wild.

Invertebrates

One of the major problems with ALAN is the attraction of insect communities by nocturnal lights, and most of the studies on invertebrates focus on this (Honnen et al., 2019). In general, these studies indicate the observed effects depend on the species and quality of light (Longcore et al., 2015; Park J. H. et al., 2015; Silva et al., 2015; Wakefield et al., 2015; Acharya et al., 2016). In Ohio (United States) LED lamps attract a large number of insects, all species combined (Knop et al., 2017), but only half as much as incandescent lamps at an equivalent energy (Justice and Justice, 2016). In the Netherlands the number of Fog Moths (*Operophtera brumata*) caught outdoors was higher in the areas directly lit by LEDs than in the shadow, and the effect depended on the wavelength (in the following order of potency: green > white > red) (Geffen et al., 2015). Inhibition of food intake has also been observed regardless of light wavelength (Van Langevelde et al., 2017). In contrast, foraging activity was increased in spiders (*Eriophora biapicata*) (Willmott et al., 2018).

Reproductive success and growth of moths and spiders are also compromised by ALAN: sexual activity of females and attraction of males to females were disrupted by LED lighting of different wavelengths (red > white > green) in *Operophtera brumata* (Geffen et al., 2015). In *E. biapicata*, a 20 lx white LED at night accelerated maturation but reduced the number and size of juveniles (Willmott et al., 2018). In the mosquito *Culex pipiens f. molestus* (familiar in urban areas), ALAN (cool-white LED, 100–300 lx) applied during the first 3 h of the night phase resulted in females producing fewer and smaller eggs (Honnen et al., 2019); in addition, males and females were less active during the ALAN phase but females became more active thereafter. The sex-dependent differences were also seen in clock genes because the same ALAN conditions induced upregulation of *Cycle* in females and down regulation of *Clock* in males, with consequences on the median relative expression of clock genes and activity cycles (Honnen et al., 2019).

In fireflies ALAN has been rated as the second most serious threat after habitat loss, showing adverse effects on populations (Lewis et al., 2020). ALAN interferes with the production and perception of courtship messages, glowing (e.g., *Lampyrus noctiluca*) or flash dialogues (*Pteroptyx maipo*, *Photuris pyralis*). Ultimately, such effects impinge upon reproduction of the species (Bird and Parker, 2014; Owens et al., 2020).

In coastal areas of Chile the sandy beach isopod *Tylos spinulosus* is active at night. ALAN (120 lx; white LED) disrupted isopod locomotor activity and circadian rhythms, resulting in a dramatic avoidance of lit areas at night (Duarte et al., 2019).

Fish

Reproduction. Night lighting affects reproduction of fish in several ways, and in a complex manner (Figure 11). White LEDs of low intensity inhibited gonadotrophin expression (FSH, folliculo-stimulating hormone; LH, luteinizing hormone) in female Perch *Perca fluviatilis*, whereas monochromatic wavelengths (blue, green, or red) had no effect (Brüning et al., 2016). In the same study ALAN of different intensities (0.1 to 100 lx) inhibited secretion of the time-keeping hormone melatonin regardless of the LED wavelength used (Brüning et al., 2016). Under similar conditions melatonin levels were also affected in Roach *Rutilus*, whereas no effect was seen on gonadotrophin expression (Brüning et al., 2018a). However, in field experiments using HPS lamps, abundance of sex steroids (17 β -estradiol; 11-ketotestosterone) and FSH and LH mRNA was reduced in both *P. fluviatilis* and *R. rutilus*, while melatonin levels were not significantly affected (Brüning et al., 2018b). In dwarf fish, *Chrysiptera parasema* and *C. cyanea*, nocturnal exposure to monochromatic, but not white, LEDs promoted gonadal maturation (Shin et al., 2013; Yeh et al., 2014), the most effective wavelengths being green and blue in *C. parasema*, and red in *C. cyanea*. Oestradiol production was also stimulated in *C. parasema* (Shin et al., 2013), and gonadotrophins were stimulated in goldfish, *Carassius auratus*, when daytime illumination was replaced by monochromatic LEDs; green light, which also increased the expression of VAL-opsin, was the most potent (Song et al., 2015). White LED light at night (~23 lx illuminance) totally inhibited hatching in the Clownfish

Amphiprion ocellaris, although no impact was found on the frequency of spawning or fertilization success (Fobert et al., 2019). The authors speculated that fish with similar spawning strategies might respond similarly to ALAN.

Altogether, it is apparent that ALAN can interfere with components of the reproductive axis in fish (Figure 11). These conclusions are supported by long term laboratory experiments in zebrafish *D. rerio*. After 1 year under LL (fluorescent bulbs, 300 lx) the molecular clock was disrupted in the ovary, oestrogen levels were increased (~50%) while progesterone levels were decreased (~25%), and plasma, retina and brain melatonin rhythms were abolished (Khan et al., 2018). More importantly perhaps, there was molecular and histological evidence of tumorigenesis in the ovaries of the ALAN group. ALAN also affected the whole transcriptome, including genes involved in tumorigenesis and other physiological disorders (Khan et al., 2018).

Behaviour. Behaviour is also affected in coastal and fresh water fish (Figure 12A). In two lakes of Ontario (Canada), locomotor activity, and thus energy expenditure, of Black Bass *Micropterus dolomieu*, which nests and protects its offspring, was abnormally high in the presence of continuous or intermittent night lighting (White LEDs, 40 lx at the water surface) mimicking traffic lights (Foster et al., 2016). Intermittent lighting was the most aggressive. The effects were observed both during day and night phases and rendered offspring survival more random. Parental care occurs in 60% of freshwater fish families; ALAN could thus have negative consequences on many species that build nests in lake and river littoral zones. An escape behaviour has also been reported in the Largemouth Bass, *Micropterus salmoides*, in response to LED lights (green, yellow, orange, and red) pulses applied during the day time (Sullivan et al., 2016). This may be related to the observation that street lighting acted as a light barrier in Atlantic salmon, *Salmo salar*, fry (Riley et al., 2013) (and section “The Migrating Atlantic Salmon - A Case Study”). Light disrupted the daily rhythm in fry dispersion and delayed downstream migration. These changes in migratory behaviour may impact on fish fitness and increase predation risk.

Altogether, the available studies, although scarce, suggest that ALAN is “an unpredictable threat for light sensitive species, communities, and consequently biodiversity” (Brüning et al., 2018a,b), a danger potentiated by the observations that responses depend on the species and their life strategies (Fobert et al., 2019).

Frogs

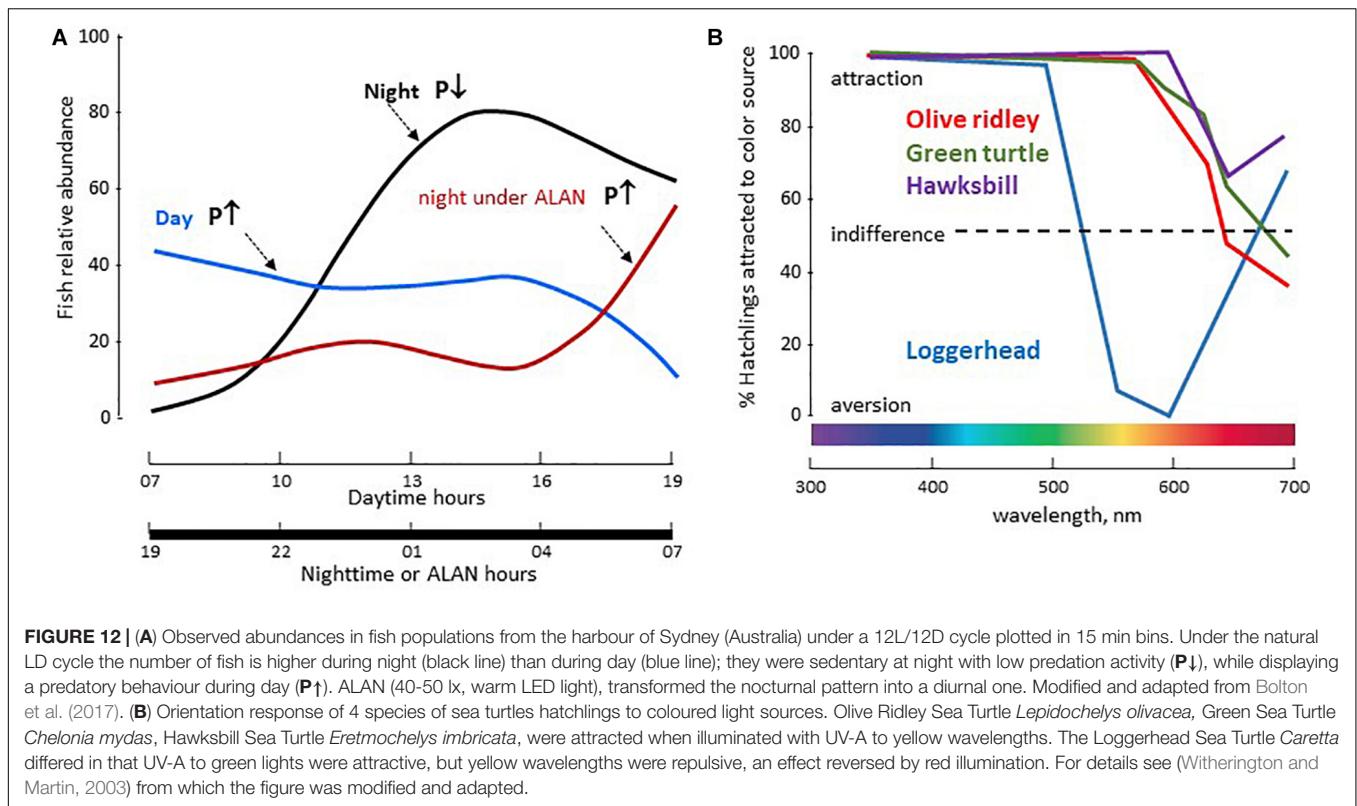
Only a few studies explored the physiological consequences of ALAN on amphibians, all indicating it is likely to have negative effects on populations. Thus, white LED lighting (equivalent to that produced by street lighting) affects the nocturnal distribution as well as choice of preferred substrate of the unisexual Blue-Spotted Salamander (*Ambystoma laterale jeffersonianum*), but had no such effect on the frog *Rana sylvaticus* (Feuka et al., 2017). The authors concluded that these choices are likely to affect the survival of both species as salamanders must choose a substrate of lower nutritional quality while frogs become more exposed to nocturnal predators. In field experiments, nocturnal LED light (Blue/green spectrum

and intensities consistent with those found under street light) reduced larvae metamorphosis duration and juvenile growth in the American toad *Anaxyrus americanus* (Dananay and Benard, 2018). In addition ALAN also affected periphyton biomass, as mentioned before (section “Breeding”). In the Pennsylvanian wood frog *Lithobates sylvaticus* tadpoles, ALAN (indoors white LED) did not change metamorphosis duration but reduced hatching success (May et al., 2019). Furthermore, while *A. americanus* larvae kept a high rate of activity under illuminated night (comparing to daytime), *L. sylvaticus* tadpoles moved less, and after metamorphosis individuals exposed to ALAN were more susceptible to NaCl challenge and trematodes. Reduced activity and altered metabolism were also reported in male common toads, *Bufo* exposed for 20 days to ALAN (white LED; 0.1, 5, or 20 lx illuminance) (Touzot et al., 2019). As the effects were observed at the onset of the breeding period the authors suggested that ALAN could be a serious threat for many nocturnal amphibian species.

Reptiles

Although scarce, studies on reptiles indicate ALAN is a major threat. Many studies focussed on sea turtles of coastal areas all around the world; the impact of ALAN on nesting and hatchlings has been documented since the early 80's (Witherington and Martin, 2003). Sea turtle nesting and hatching occur at night, generally eggs from one nest hatch together, though sometimes a main group of hatchlings may be preceded or followed by smaller groups (Witherington and Martin, 2003; Robertson et al., 2016). Coastal light at night causes spawning at sea and abandonment of nests or alteration of the choice of nesting site in several species of the Caribbean islands (Green Turtle, *Chelonia mydas*; Hawksbill Turtle, *Eretmochelys imbricate*; Leatherback Turtle, *Dermochelys coriacea*). Modelling studies predict light pollution will substantially accelerate the extinction of these species (Brei et al., 2016). Similar data were obtained along Australian shores: *C. mydas* hatchlings were disoriented in the presence of shore lights, and those that reached and entered the sea returned to shore if reaching an area lit by shore-based artificial lights (Truscott et al., 2017). Low-pressure sodium-vapor (LPS) yellow lights were believed to provide a more “turtle-friendly” environment in Loggerheads and Green Turtles, as UV-blue and green wavelengths were the most attractive to hatchlings, while the red ones were not (Witherington and Martin, 2003; Figure 12B). However, more recent investigations indicated LEDs emitting in the red (narrow band, 600-670 nm, λ_{max} 640 nm) and yellow (wide band, 600-750 nm, λ_{max} 620 nm) induced total disorientation of Loggerhead hatchlings in their race towards the sea at equal intensities (Robertson et al., 2016). The maximum effect depended on the number of lighting spots with amber coloured emissions being the most potent in the absence of moonlight. According to the authors, coastal lighting is a dramatic threat to the species.

Little information is available concerning terrestrial reptiles, although a long list of species, likely to be affected by ALAN in urban and suburban locations, has been documented (Perry et al., 2008). Recent observations on the nocturnal behaviour and activity patterns of two species of diurnal anole



from Antigua (West Indies; Leach's Anole *Anolis leachii* and Watts's Anole, *A. wattsi*), describe an increased activity under ALAN, albeit restricted to males and primarily related to the increase in the number of arthropods attracted by light (Maurer et al., 2019).

Birds

There is abundance of data on the impact of ALAN on birds with dozens of publications over the last five years (Dominoni et al., 2013a, 2016; Zhao et al., 2014; Ronconi et al., 2015; de Jong et al., 2016b; Krüger et al., 2017; Raap, 2018; Jiang et al., 2020). Overall, ALAN disrupts the circadian system in both sedentary and migratory birds, affecting phototaxis and altering endogenous daily and annual rhythms. These effects are observed both inland and above the sea where lights emitted by drilling and extraction platforms, as well as vessels, have significant effects. Birds are attracted by light and become disoriented. Collisions with solid structures (or contact with flames from chimneys) have dramatic effects, causing the death of hundreds or even thousands of individuals (Ronconi et al., 2015; Krüger et al., 2017; Rodriguez et al., 2017). These effects may vary depending on the quality and intensity of the light source, LPS and LED being less harmful than metal halide lamps (Ronconi et al., 2015). In addition, when collision is avoided, the migratory birds may end up turning in circles around the platforms, negatively impacting the trajectory and migration time, energy expenditure and ultimately survival. In addition to collision, ALAN affects the stopover habitat use by inland migrating birds, which avoid bright areas (McLaren et al., 2018).

Artificial-light-at-night also induces indirect effects through the disorganization of the birds' circadian system. In a study comparing rural and urban tree sparrows *Passer montanus* of Mizoram (India) differences were found in the phase and/or amplitude of clock gene mRNA abundance in the retina, pineal gland and hypothalamus (Renthlei and Trivedi, 2019). Downstream *cgc* genes (including melatonin receptors) also differed in their rhythmic expression and abundance between rural and urban birds. In addition, the rhythm in melatonin production itself was also different. The mismatches between the rhythms of different components of *P. montanus* circadian system and effectors seen in urban birds are likely to have consequences on circadian controlled processes. Indeed, indoors experiments with *P. montanus* of the Beijing area (China) have shown that ALAN alters the whole neuroendocrine reproductive axis (Zhang X. J. et al., 2019); mRNA abundance corresponding to FSH, THS (thyroid stimulating hormone) and Dio2 (deiodinase II) were upregulated with low illuminance levels (85 lx; cold white) and down regulated with high illuminance levels (150 and 300 lx) of ALAN. The rise and amount of plasma LH and oestradiol were earlier and higher in the 85 lx group, and later and lower in the other groups, indicating reproduction timing and efficiency were altered.

Light-emitting diodes covering a wide spectrum ($450 < \lambda < 700$ nm) affect daily rhythms of locomotor activity, body temperature, singing and sleep (duration and quality), night-time production of melatonin, proliferation of brain stem cells, immunity and oxidative stress markers, as reported in several species, including the Great Tit *Parus*

major (Ouyang et al., 2015; Raap et al., 2015, 2016a,c; de Jong et al., 2016a, 2017; Raap, 2018), Blackbird *Turdus merula* (Dominoni et al., 2013b), Indian Weaver Bird *Ploceus philippinus* (Kumar et al., 2018), Japanese Quail *Coturnix japonica*, chicken *G. domesticus* and King Quail *Excalfactoria chinesis* (Saini C. et al., 2019), Zebra Finches *Taeniopygia guttata* (Moaraf et al., 2020), and Weaver *Ploceus philippinus* (Singh et al., 2012). In laboratory experiments the effects were dose-dependent (0.05 to 5 lx) and varied with the spectral composition (de Jong et al., 2016a, 2017). In urban areas with conventional street lighting, whenever possible tits avoided night-time illumination (de Jong et al., 2016b). ALAN did not affect markers of oxidative stress (Casasole et al., 2017), but corticosterone levels were higher in chicks under white, red, blue or green LEDs (8 lx) (Ouyang et al., 2015). The effects depended on wavelength and distance between the nests and light source. The number of chicks was also decreased in nests under ALAN. Finally, a negative correlation was found between the number of chicks and corticosterone levels (Ouyang et al., 2015), as well as the distance to the light source (de Jong et al., 2015). Under similar conditions no effect was observed on the Black Flycatcher (*Ficedula hypoleuca*).

Artificial-light-at-night also has impacts on reproduction, and affects the annual breeding rate (Le Tallec, 2014; Longcore et al., 2015). In the Blackbird *T. merula*, a 0.3 lx white light induced a one-month phase advance in the annual rhythm of reproduction (monitoring size and functionality of testes and steroid levels) and moulting (Dominoni et al., 2013b). Interestingly, these parameters differed depending on whether the blackbirds were captured in the city or forest, suggesting that habitat induced adaptive changes in the species. Similar data were obtained from the California Jay, *Aphelocoma californica*, in which testosterone, oestradiol, melatonin and LH plasma levels showed sex-specific alterations under low night-time (3.2 lx) illumination (*i.e.*, corresponding to that measured in suburban areas at Davis, CA, United States) (Schoech et al., 2013). In Mockingbirds *Mimus polyglottos* and American Blackbirds *T. migratorius*, ALAN induced dose-dependent changes in the dawn onset of singing and courtship behaviour as well as the start of the breeding season (Longcore, 2010).

Finally, the impact of continuous or partial nocturnal illumination on avian circadian clocks is believed to be responsible for ametropia (abnormal refractive condition) (Nickla and Totonelly, 2016) and developmental delays observed in the visual system and eye of young birds, as is the case in primates (Attia et al., 2019).

Altogether, it appears that the avian responses to ALAN are complex, depending very much on the species, sex and age, geographical area as well as on the experimental conditions. In general, the data obtained under laboratory conditions agree with those obtained on site, using measures of urban lighting (Raap et al., 2016b).

Mammals

The potential influence of ALAN and LEDs on mammals has not been investigated in depth and concerns only a limited number of species, despite the fact that 69% of mammalian species are nocturnal. ALAN affects nocturnal activity in terrestrial

vertebrates: an inverse correlation has been found between surfaces lit by ALAN and mammalian species richness (Duffy et al., 2015; Ciach and Frohlich, 2019). Mice (Rotics et al., 2011a,b) and small tropical forest mammals (Bengsen et al., 2010) are less active under ALAN to minimize the risk of predation. The opposite holds true with diurnal and crepuscular species, more active under ALAN, particularly those feeding on insects (Lacoeuilhe et al., 2014; Minnaar et al., 2015; Russ et al., 2015). A study compared the impact of LPS and white LED lighting during the day (equal intensity, but with a stronger blue component for LEDs) in rats (*Rattus norvegicus*): LED-lit individuals had higher nocturnal melatonin levels (seven-fold increase), increased food intake, drinking, growth and lipid levels (in several tissues), while protein levels were lower (Dauchy et al., 2016). In the blood, arterial O₂ and CO₂ rhythms were not altered, but titres were higher under LEDs. Conversely, glucose, leptin, lactate and corticosterone levels were decreased in the LED-lit rats, with either a phase delay (leptin) or a phase advance (glucose and lactate) under LEDs compared to LPS lights.

In the normal life cycle of the Siberian hamster (*Phodopus sungorus*), gonads, body mass, and number of spermatogonia are reduced in winter (short photoperiod), fur becomes thicker and white (Table 1), all changes being adaptations to rigorous winter conditions. Under ALAN (5 lx, white light) these changes were no longer observed; hamsters maintained summer characteristics (long photoperiod) (Ikeno et al., 2014). In addition, a number of genes displayed altered expression, including *Per1* (clock function), *Mell1a* (melatonin receptor), *eya3* (involved in development), or TSH, Gonadotrophin Inhibiting Hormone or Gonadotrophin Releasing Hormone (GnRH) (reproduction). Finally, locomotor activity and immune responses were altered, also observed in mice *Mus musculus* exposed to similar conditions (Fonken and Nelson, 2014). Mice also displayed altered body temperature. Changes in body temperature and locomotor activity were also observed in the Gray Mouse Lemur *Microcebus murinus* exposed during 2 weeks to either artificial moonlight (of the same irradiance as natural full moonlight) or to ALAN (HPS street lamps, Le Tallec et al., 2016). The daily rhythm profiles of locomotor activity were altered between the two paradigms in both phase and amplitude, in both males and females, irrespective of the season. Other changes in ALAN-exposed animals included the frequency and duration of torpor phases (decreased), urinary oestradiol (higher in post oestrus and pre-oestrus females), testosterone levels, and testes size (progressively increased in males). Finally, it is worth mentioning that in rats, non-human primates and sheep, disruption induced by ALAN results in major changes in foetal development (shorter pregnancy, low weight), with long-term impacts on offspring at different metabolic and physiological levels (Torres-Farfan et al., 2020).

The most abundant documentation in mammals relates to the family of bats, which account for 30% of existing mammals; 17% of the 1232 bat species are in danger of extinction. Their nocturnal activity is by far the greatest of all known nocturnal mammals. They make short-distance (for foraging and feeding of offspring) and long-distance (search for hibernation sites or at transition sexual/rest phases) trips. Bats show a great wealth

and diversity of habitats (caves, cellars, trees, etc.) and eating habits, some being carnivorous (insectivores for the majority) others vegetarian (fruits, flowers, or nectar). They occupy all stages of the food chain, and play a particularly important role in regulating insect populations (including pests), pollination or seed dispersal (Boyles et al., 2011; Kunz et al., 2011). The duration, beginning and end of the nocturnal activity is specific to each species. Thus, lactating females start early at dusk compared to other individuals, while pregnant females or slow-flying species start later at night. Insectivores (*Pipistrellus* spp. and *Nyctalus* spp.) have activity peaks at evening twilight, and it is the presence of prey rather than levels of light that regulates these behaviours (although *Pipistrellus* avoid flying under bright light, Mathews et al., 2015). In contrast, slow fliers (gleaners) or nocturnal butterfly eaters (e.g., *Barbastella barbastellus*, *Myotis nattereri*, *M. bechsteinii*) are more sensitive to lighting and prefer complete darkness.

Bats have been classified in two groups depending on their tolerance or intolerance to ALAN (Lacoeuilhe et al., 2014). Field studies indicate that ALAN has a greater impact than land loss (due to urban extension and agriculture) on the distribution of different species of bats (*Pipistrellus pipistrellus*, *Eptesicus serotinus*, *P. kuhlii*, *P. nathusius*, *Nyctalus leisleri*) (Azam, 2016). In natural and urban environments ALAN (LPS or white LED) affects bat behaviour (Polak et al., 2011; Stone et al., 2012; Lewanzik and Voigt, 2014, 2017; Leliavski et al., 2015; Mathews et al., 2015; Minnaar et al., 2015; Azam, 2016; Rowse et al., 2016). Among the most notable effects are a delay to leave the nest, decreased sexual activity, changes in flight speed and paths (trajectory, height) as well as significant increases in collisions (~25%) in the presence of lit obstacles (indicating that echolocation is not the only navigation tool for some species). The effects are species dependent. Gleaners or bats relying 100% on echolocation (*Rhinolophus* spp., *Plecotus* spp., *Myotis* spp.) emerge more rarely and modify their routes in a midnight light environment, while large fast-flying insectivorous species (*Lasiurus* spp., *Eptesicus* spp., *Nyctalus* spp., *Pipistrellus* spp.) are attracted by ALAN (Lewanzik and Voigt, 2014; Mathews et al., 2015; Azam, 2016). Others like *Eptesicus bottae* accelerate flight speed and stop hunting insects (Polak et al., 2011).

In Southern England and Wales, population richness and activity of *P. pipistrellus*, *Nyctalus* spp., *P. pygmaeus* and *Myotis* spp. did not change after replacement of LPS by white LED in the street lamps (Rowse et al., 2016). Another investigation found no change in activity of the fast-flying *P. pipistrellus*, *P. pygmaeus* and *Nyctalus/Eptesicus* spp. (even at the highest illuminance of 49.8 lx), but observed a significant reduction in activity of slow-flying bats, *Rhinolophus hipposideros* and *Myotis* spp. (even at low light levels of 3.6 lx) (Stone et al., 2012). In another field study close to Nurnberg (Germany) it was found that replacing conventional mercury vapour street lamps with white LEDs changed the impact of ALAN on urban bats: some species showed a clear reduction in their activity (by 45% in *P. pipistrellus*) while others did the opposite (*Myotis* spp.) (Lewanzik and Voigt, 2017). This indicates that replacement of conventional street lighting by LEDs produces complex and species-specific responses in bats.

LEDs AND ECOSYSTEMS

While experiments studying the impacts of ALAN on living organisms are on the increase, two aspects that need greater consideration have been only poorly investigated. One aspect is the impact on whole ecosystems, both aquatic and terrestrial. Indeed, species are linked by trophic or symbiotic interactions, and any type of impact of any anthropogenic pressure on one component of an ecosystem has consequences on the whole community, which may lead to remodelling or collapse of the entire system (Bennie et al., 2015a,b, 2016; Sanders et al., 2015; Zapata et al., 2019). Ascending and descending effects may be observed, depending on the trophic position of the species affected. Non-trophic interactions refer to the ALAN-induced impact on pollinating or seed dispersal species (more than 75% of global crops depend to varying degrees on animal pollination), or resource competition between species with diurnal, nocturnal or twilight activity and whose activity rhythms are altered by ALAN-induced photoperiod changes. The other aspect is the impact of concomitant or successive actions of a long list of anthropogenic factors, including physical (ALAN, noise, plastics...) and chemical (pesticides, herbicides, heavy metals, nanoparticles...) pollution, climate change (rise in temperatures, oceanic acidification, changing currents...), modification and reduction of natural spaces (urbanization, deforestation, and physical barriers), etc. Together they are likely to have more than additive effects, with severe implications on species and assemblages. These issues are discussed below.

Aquatic Ecosystems: Grazing Fish and Sessile Invertebrates

Assessment of ALAN in coastal ecosystems, including estuaries, is limited (Zapata et al., 2019), although 60% of the world's largest cities are located within 100 km of the coast, and more than 20% of coastal areas are exposed to ALAN (Bolton et al., 2017). A study conducted in Sydney Harbour (Australia) investigated the effects of ALAN using warm light LED spotlights that provided similar or lower levels of ALAN as recorded in other urban coastal cities. Under a natural LD cycle, fish abundance, all species combined, varied over the 24-h cycle (Figure 12A): overall, fish were more abundant, but more sedentary at night than during daytime, and predation on sessile invertebrates was higher during daytime (Bolton et al., 2017). ALAN modified this pattern with night predation increasing to levels observed during the day. Although the abundance of fish (including predators) was markedly reduced, predation on sessile invertebrates was increased. As a consequence, the structure of the sessile assemblage was disrupted at night, which may have dramatic consequences: these assemblages perform essential activities (spawning, settlement, and feeding) at night when predation pressure is low. The authors concluded that ALAN had implications for the structure of the trophic web system that might lead to altered functioning (Bolton et al., 2017). These data agree with investigations showing cool white LED lighting (19 lx or 30 lx at water surface) affected colonization by sessile and mobile benthic species (13 quantified), inducing reduction or suppression in some species while leading

to increases in others (Davies, 2014). Imbalance of interspecific interactions were also shown from a study on Dog Whelks *Nucella lapillus*. *N. lapillus* are widely distributed across the North Atlantic (including illuminated coastal areas) and feed on barnacles and mussels; they were more likely to, respond to, and handle prey under, a white LED light (~21 lx) compared to controls, irrespective of the presence of a snail predator (the common shore crab *Carcinus maenas*) (Underwood et al., 2017). Alterations of trophic interactions were also reported to occur under ALAN in studies performed along the Italian coast, where the population of grazing snails *Melarhaphe neritoides* has positive effects on the diversity of epilithic heterotrophic bacteria under a natural LD cycle (Maggi et al., 2020). ALAN (white LED, 27 lx) modified this by reducing the density of grazers (thus erasing the positive effects on heterotrophic bacteria) and increasing autotrophic Cyanobacteria. The authors concluded ALAN was likely to alter natural systems by annihilating positive interactions across trophic levels.

Aquatic Ecosystems: Crossing Boundaries With Riparian Ecosystems

Artificial light at night, irrespective of the light source, induces redistribution of insect populations (Meyer and Sullivan, 2013; Davies et al., 2017), some species increase in number while others decrease. Globally, observations indicate significant alterations in the number of represented species and in the size and weight of individuals. For example, mimicking street lighting levels using wide spectrum LEDs at a few sites of the Ohio river (United States), resulted in a 44% decrease in the number of *tetragnathidae* spiders, a 16% decrease in biodiversity and a 76% decrease in the average body size of the species; conversely, the size of neighbouring terrestrial arthropods was increased by 309% (Meyer and Sullivan, 2013). The authors concluded ALAN altered the structure of communities in this system *via* changes in reciprocal aquatic–terrestrial fluxes of invertebrates. Another field study was conducted in the same area, studying the impact of ALAN (0 to 20 lx) provided by HPS and cool white LED lamps (Sullivan et al., 2019). At moderate to high levels of ALAN, the density of predatory orb-web spiders (*Tetragnathidae* and *Araneidae*) was particularly affected in riparian areas. At the community level, both density and family richness were affected, altering arthropod community structure; increasing ALAN induced larger proportions of predators wolf spiders, [*Lycosidae*]; rove beetles (*Staphylinidae*) and detritivores (*Oniscidae*), and smaller numbers of omnivores (ants [*Formicidae*]). In wetland systems, aquatic insect density increased and the composition of emergent insect families was different under LED or HPS or natural night lighting. ALAN also decreased the invertebrate food chain length and altered the flows of energy between aquatic and terrestrial systems (Sullivan et al., 2019).

Terrestrial Ecosystems: Redistribution of Insect Populations

Attraction by light and redistribution of populations characterize the effects of ALAN on insects. Attraction of flying insects is a

well-known phenomenon. At Hawkes Bay (New Zealand) the number of flying insects captured under street lighting sources was 48% higher when using white LED (2700 to 6500 K) than with HPS lamps (Pawson and Bader, 2014). The authors suggested that the replacement of sodium lamps by LEDs is likely to increase the deleterious effects of ALAN with unpredictable consequences, as harmful species (e.g., the patchy Bombyx *Lymantria dispar* whose caterpillars attack forests) might develop at the expense of endemic species. Also, most moths attracted by street lamps abandon fields and open ground, leading to population decreases of 50%, while biodiversity is also reduced by ~25% (Macgregor et al., 2015, 2017). Redistribution of surface terrestrial insect communities has been observed near light sources, regardless of the time of day or night (Davies et al., 2012, 2017; Bennie et al., 2015a). In a 3-year experiment, it was shown that nocturnal lighting by LEDs of different quality and intensity altered the distribution of arachnid and coleopteran species on the ground (Davies et al., 2017; **Figure 13A**). The effects were diminished, but not suppressed, upon reduction of intensity or duration of the light signal. Species of predators and scavengers were most represented near lighted areas, suggesting an alteration of the local ecosystem.

Street lighting also increased the activity of flying insects in the surroundings. They are thus likely to carry less pollen, with possible consequences on plant pollination. Such a phenomenon has been observed in a field study at sites that had never previously experienced ALAN and carried an identical variety of plants (*Cirsium oleraceum*, *Eupatorium cannabinum*, *Valeriana officinalis*, *Epilobium angustifolium*, and *Silene vulgaris*) (Knop et al., 2017). Half of the sites were illuminated at night using white LEDs (4000 K), the other half remained in the dark. Under these conditions ALAN reduced visits of pollinating nocturnal insects by 62%, with negative consequences on the reproduction of plants. In addition, the diurnal population of pollinating species was also negatively impacted. The result was a general reduction of plants as well as the insects that feed on them (**Figure 13B**; Knop et al., 2017). Direct and indirect effects have also been observed in a field study in the Denver area (CO, United States), investigating the impact of ALAN (HPS lamps) on the relationship between the Smooth Brome *Bromus inermis* and larvae of the moth *Apamea sordens* that feeds on seed heads and leaves (Grenis and Murphy, 2019). Plants growing under normal periodic darkness were harder than those under street lamps, and the effects of street lighting on larvae were both direct (larvae were smaller when reared under streetlights) and indirect (plant traits led to reduced larval growth).

Terrestrial Ecosystems: Plants, Insects and Their Parasites

Sanders and colleagues investigated the impact of white LED street lighting (30 lx) in a plant-aphid-parasitoid community. The first investigation included three aphid species, *Aphis fabae*, *Acyrtosiphon pisum* and *Megoura viciae*; their parasites, respectively *Lysiphlebus fabarum*, *Aphidius ervi*, and *A. megourae*; and the aphids' food source, the broad bean *Vicia faba* (Sanders et al., 2015, 2018). In the absence of anthropogenic pressure

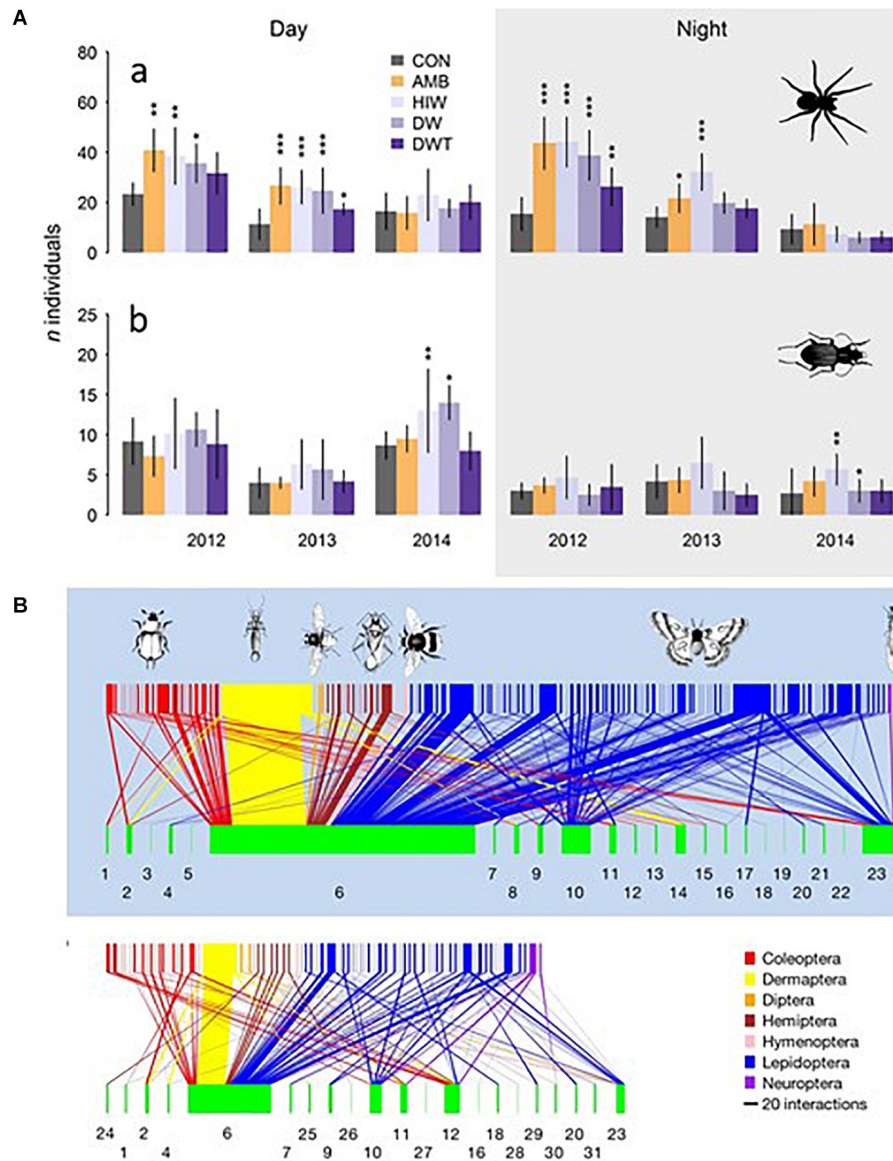


FIGURE 13 | (A) The impact of alternative LED lighting strategies on the total numbers of individual grassland spiders (*Araneae*) (a) and beetles (*Coleoptera*) (b) caught in each year, respectively. LED lighting was equivalent to that experienced at ground level under LED street lighting for HIW (high-intensity white 29.6 ± 1.2 lx), under dimmed street lighting for DW (dimmed white, 14.6 ± 0.3 lx), or under timed dimmed street lighting for DWT (14.4 ± 0.8 lx, switched off between 00:00 and 04:00 GMT). AMB was amber lighting (18.2 ± 1.3 lx, $\lambda_{max} = 588$ nm). Controls (CON) experienced total darkness. Bar heights and error bars denote means 95% confidence intervals. Stars denote differences with the controls that were significant with 95% (*), 99% (**), and 99.9% or greater (***) confidence. From Davies et al. (2017). No special permission required. **(B)** Effects of artificial lighting on parameters of overall quantified nocturnal plant-flower visitor networks of seven dark sites (above) and seven experimentally illuminated sites (below). The rectangles represent insect species (top) and plant species (bottom), and the connecting lines represent interactions among species. Species codes for the plants and a list of insect species are given in Knop et al. (2017). The study was run in 14 sites of the Swiss Alps; illumination was using neutral white LED street lamps (4,000K) that provided 52.0 ± 4.2 lx on the ground. Adapted from Knop et al. (2017). More details in the original publication. With permission.

this community is very stable. ALAN reduced bean plant biomass and, most likely as a result of bottom-up effects, the abundance of two aphid species by 20% over five generations. For *M. viciae* the effect was reversed under autumnal conditions (ALAN promoting continuous reproduction of the species). All three parasitic species were negatively affected by ALAN, as a result of host number reduction (Sanders et al., 2015).

The second investigation (greenhouse and field experiments) tested the effects of different illuminance levels (0.1 to 100 lx) on the same mesocosm that also included barley *Hordeum vulgare*, as a resource for the aphid *Sitobion avenae*, and *Praon dorsale*, which attacks the three aphids *S. avenae*, *A. pisum* and *M. viciae*. The lowest levels of ALAN (0.1 to 5 lx; equivalent to severe sky glow) induced the strongest effects, reducing

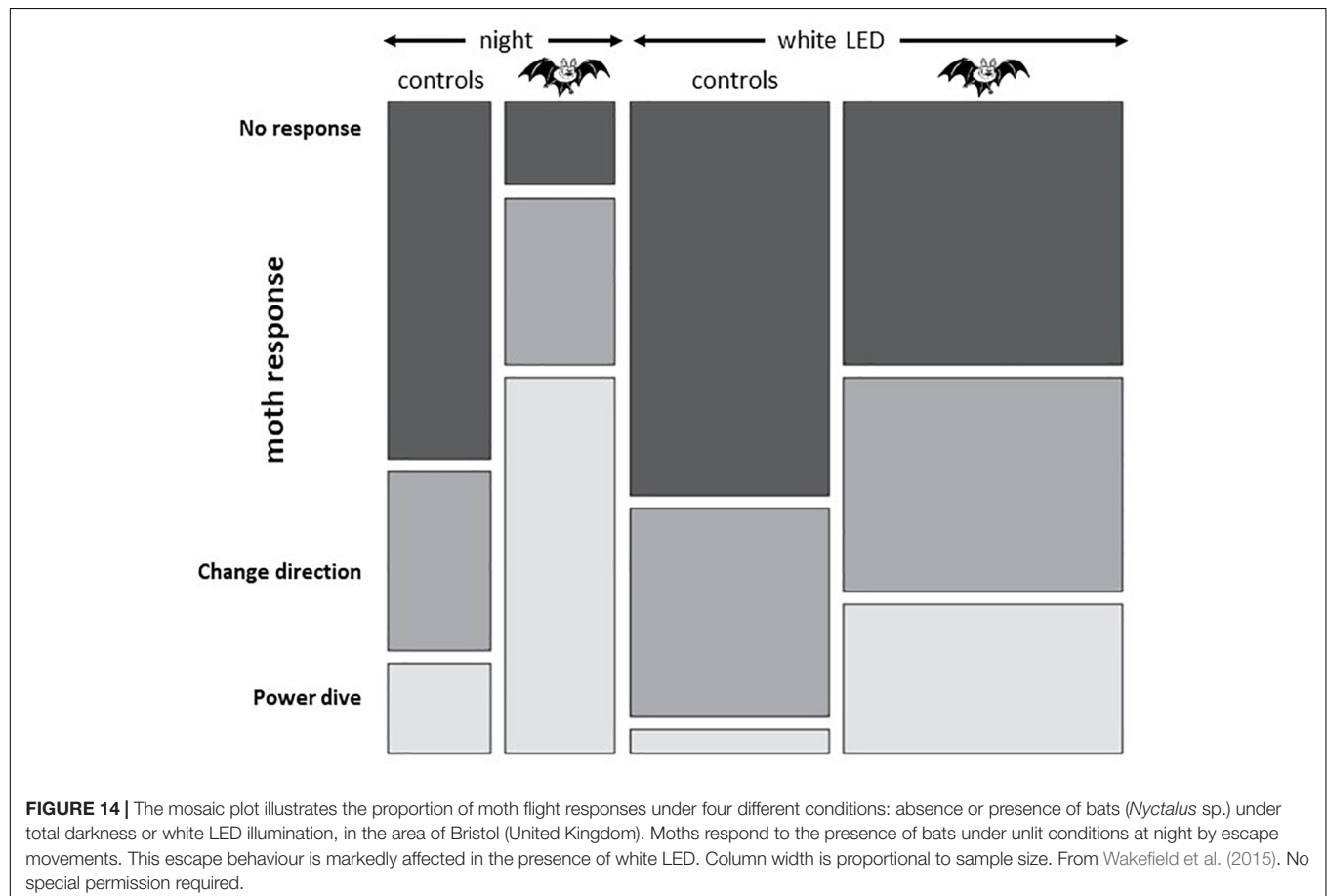
aphid densities by 45% as a result of parasite being twice more efficient in attacking aphids. The effects were reversed at higher light intensities because the parasites spent less time on their hosts (Sanders et al., 2018). *M. viciae* was the main aphid species affected, while *A. fabae* responded with a negative effect at 10 lx and a positive effect at lower or higher intensities; *S. avenae* was not affected. There was a positive relationship between plant biomass and light intensity in the greenhouse experiment, while in the field only *V. faba* responded (and only at 20 lx illuminance level). According to the authors, while not discarding a possible bottom-up effect through increased plant biomass (providing more resources for aphids under higher light intensities), the interaction between aphids and parasites was the critical driver for the responses observed in the field experiment (Sanders et al., 2018).

Terrestrial Ecosystems: Bats, Moths, and Pollination

The impacts on bats (as reported in “Animals”) have major consequences on insect populations, especially moths (Minnaar et al., 2015; Wakefield et al., 2015). The attraction that ALAN exerts on insects in general, and moths in particular, is one reason why their world population is steadily decreasing (Macgregor et al., 2015, 2017). Attraction of moths by ALAN induces alterations in behaviour (flight, foraging or searching

for sexual partners) and reproductive function. In addition, ALAN also disturbs the ultrasound detection system that some moths (*Geometridae*, *Noctuidae*, or *Notodontidae*) use to detect bat predators (Figure 14; Wakefield et al., 2015). A major consequence is the widespread reduction in moth populations and a redistribution of insect populations in the local environment. Remodelling of this kind is likely to have consequences for the entire ecosystem, affecting both plants (because moths are among the largest pollinators across the globe; see section “Aquatic Ecosystems: Crossing Boundaries With Riparian Ecosystems” above) (Macgregor et al., 2015, 2017, 2019), and other predators (spiders and small vertebrates) that feed on these moths. Consequently, ALAN constitutes a short-term advantage for flying predators, while disadvantages appear in the medium- and long-term, with the risk of increased bat mortality (due to collision) and the scarcity of prey leading to negative population dynamics (Altringham and Kerth, 2015; Azam, 2016).

The survival of some plants is also likely to be affected by decreases of fruit-eating and nectar-eating bats (Lewanzik and Voigt, 2014). *Carollia sowelli* is an American tropical bat species important in seed dispersal of *Piperaceae* (pepper) and *Solanaceae* (potato, tomato, eggplant, chili pepper). Bats are repelled by light: in the presence of 4.5 lx HPS lighting their activity was reduced by 50%, fruit consumption by 20% and the hour of consumption



delayed by more than 100%. Accordingly, this may have harmful consequences on plant reproduction (Macgregor et al., 2015, 2017). The authors concluded that more studies are needed to further elucidate the impact of ALAN on bats and the plants that rely on them for seed dispersal and pollination (including plants of agricultural importance such as tea).

LEDs AND OTHER ANTHROPOGENIC FACTORS: SOME EXAMPLES

The continuous increase of human activities leads to permanent reorganization of spaces. The extension of urban and peri-urban areas, industrial and agricultural surfaces, communication routes (roads, railways, sea lanes), all lead to decreases in, and fragmentation of, natural habitats. With this come additional threats: obstacles (dams, pumps, and turbines), physical pollutants (light, noise, plastics and other trash), chemical pollutants (including endocrine disruptors [polychlorobiphenyls (PCBs), synthetic steroids, organochlorine pesticides, detergents, etc.], nanoparticles, heavy metals, radioactive waste...) and climate change (rising temperatures, ocean acidification ...). Thus, artificial light either during daytime or night-time, is not the only anthropogenic pressure on wildlife, and the question arises as to what is the impact of simultaneous and/or successive actions of these factors, since many of these targeting the same organs or associated and interconnected organs as is the case for the neuroendocrine system of vertebrates (**Figure 11**). In more than half the cases, simultaneous action of several of these factors resulted in synergistic or cooperative effects, while in other cases the effects were additive or even antagonistic (Mora et al., 2007; Darling and Côté, 2008; Côté et al., 2016). For example, overexploitation, temperature rise or habitat fragmentation, taken independently, all induce a decline in rotifer population; but taken together the rate of decline is increased by 50-fold (Mora et al., 2007). The number of studies reporting on the combined effects of ALAN and other anthropogenic factors remains scarce.

Frogs and Midges

The singing behaviour of the male frog *Engystomops pustulosus* is intended to attract females at night. A parasite of *E. pustulosus*, the fly *Corethrella* spp., is also only attracted by the song of the male at night, as during the day they are eaten by the host. In urban areas, both noise and light affected the singing behaviour of the male; and both, noise (by acoustic interference) and light (by reducing locomotor activity) diminished the ability of the parasitic midge to locate and feed on its host (McMahon et al., 2017). The combination of the two anthropogenic factors was dramatic as it led to total disappearance of the midges. The authors highlight the need to consider the multiplicity of urban anthropogenic factors in community impact studies.

Birds and Noise

The great tit *Parus major* is a diurnal species very sensitive to ALAN (see section “Birds”). Under a natural LD cycle tits display

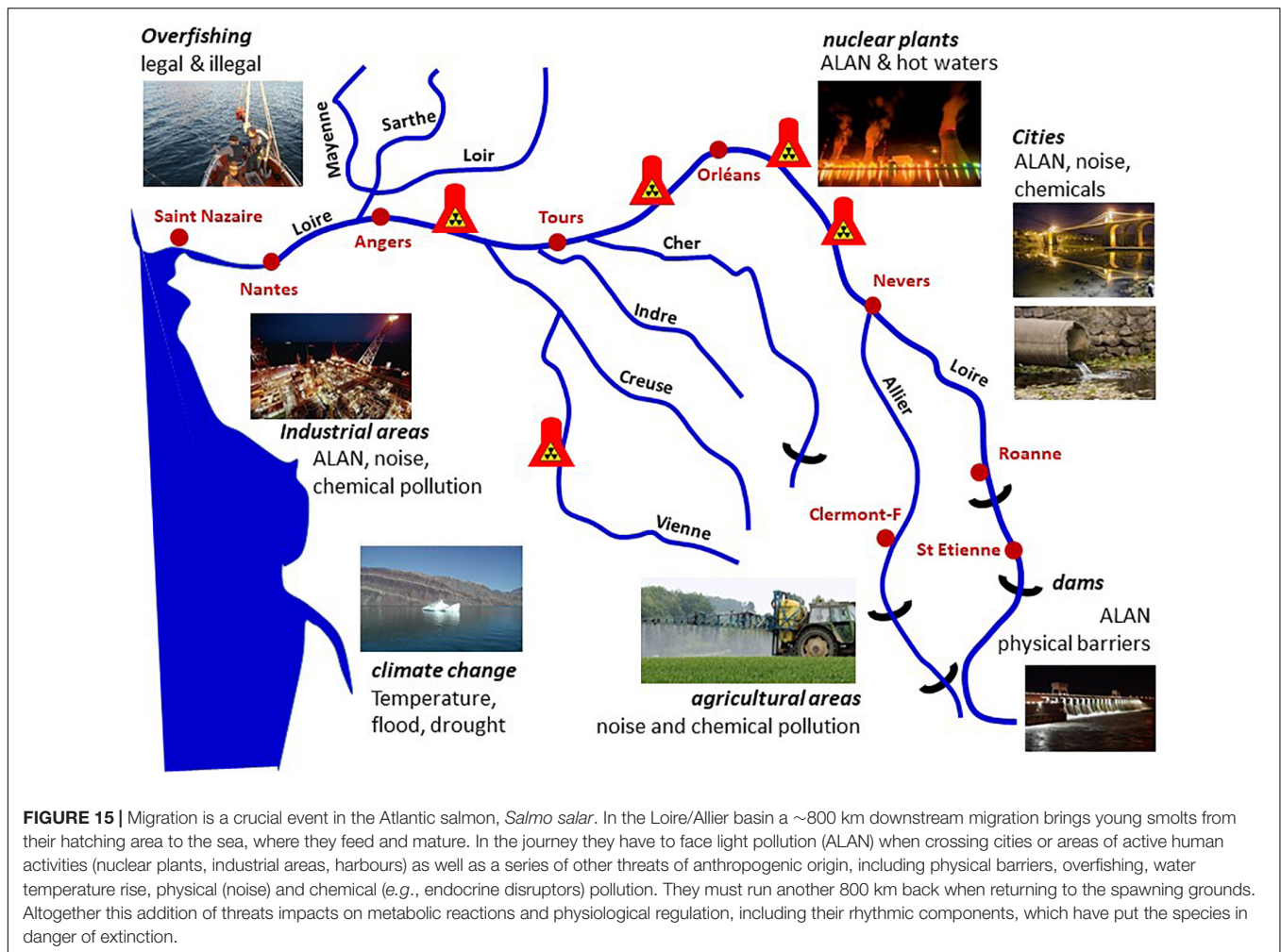
rhythmic diurnal activity patterns, which differ slightly between urban and forest birds (Dominoni et al., 2020). Both ALAN and noise affect this pattern in opposite ways: ALAN increased the overall activity while noise had the opposite effect. Both factors together had synergistic effects on night-time activities, but the effects were antagonistic for daytime activity. Moreover a significant difference was found between urban and forest birds as the interactive effects of light and noise on daytime, night-time, dusk-time and offset of activity were seen in urban but not forest birds (Dominoni et al., 2020).

Bats and Roads

Roads destroy, fragment and reduce surface habitat, degrading habitat by introducing physical barriers, noise, light and chemical pollution, and inducing lethal injuries through collision with traffic. The effects on avian and mammalian populations (in decline) can be seen up to several km away from the roads. Bats are particularly affected by all the above-mentioned factors in a species-dependent manner (Altringham and Kerth, 2015). For example, populations of small and low-flying bats are more affected than those of large high-flying bats. Most importantly, the above-mentioned factors exert cumulative effects with dramatic consequences that may only appear after several generations (Altringham and Kerth, 2015).

The Migrating Atlantic Salmon - A Case Study

Catches of Atlantic salmon, *Salmo salar*, from the Loire/Allier (France) basin have dropped from 30,000 at the end of the 19th century to less than 1500 nowadays (Marchand et al., 2017), without mentioning a dramatic reduction in the size of the captured animals. This population decay is due to a chain of cascading reactions (**Figure 15**): (i) natural predation; (ii) overfishing (recreational, industrial, and poaching), (iii) sporadic and continuous chemical pollution due to urban and agricultural activities (including endocrine and metabolic disruptors), (iv) physical pollution due to ALAN, which affects vision (because of the strongly illuminated bridges and buildings; see section “Fish”), rhythmic metabolism, and behaviour (locomotor activity, daily vertical migration as well as down-stream and upstream migration), noise and temperature (due to global warming as well as release of warm waters from nuclear run-off basins), (v) physical barriers (pumps, turbines [particularly from nuclear plants], dams and control of water flows) (**Figures 11, 15**). These are multiple sources of nuisance affecting metabolism, physiology and behaviour (Scholz and Mayer, 2008; Casals-Casas and Desvergne, 2011; Lambert et al., 2015; Bedrosian et al., 2016). Salmon navigating long distance rivers are likely to be more affected than others, as they will face a concomitance and/or succession of these factors along a course of at least 700 km. Laboratory investigations have provided evidence that the effects of combining LED lights with endocrine disruptors or temperature changes depend on the wavelength (**Figure 11**). In the perciform *Oplegnathus fasciatus*, bisphenol A activated hepatic and plasma markers of oxidative and lipid stress, increased DNA degradation and cell apoptosis and decreased melatonin and circulating immunoglobulins; these effects were



mitigated by green (530 nm) but not red (620 nm) LED light of 0.3 and 0.5 W/m² (Choi et al., 2016). Similar results were obtained in *C. auratus* (Jung M. M. et al., 2016). In addition, in the latter a rise in temperature of 22 to 30°C induced (1) an increase in glucose, cortisol, T3 and T4 thyroid hormones in the blood and (2) T3 and T4 receptors in the brain, but (3) a decrease in hepatic and plasma immunoglobulins. Green LED lighting or the administration of melatonin, reversed these effects (Jung S. J. et al., 2016). **Figure 11** provides a schematic presentation of how many of these factors are likely to affect the fish neuroendocrine system.

CONCLUSION

Recent years have seen a growing global awareness of the potential negative consequences of exposure to ALAN. Over the last 20 years both the number of light-emitting sources, and the intensity of radiated light, have increased dramatically across the surface of the globe, not only within vast tracts of urbanized land but also along coastal areas and even in relatively isolated regions like deserts, mountain ranges and open ocean. A fierce debate has arisen in many countries as documented scientific

evidence has begun to suggest that prolonged exposure to ALAN can have adverse effects on human health, with a substantial number of studies indicating links between ALAN and sleep loss and fatigue on the short term, and cancer, metabolic syndrome, mental health and cognitive disturbances on the long term (Lunn et al., 2017). Much of the scientific rationale underpinning these effects concerns the disruptive effects of ALAN upon the proper synchronization of the circadian clock, a fundamental regulatory system, which exists in virtually all living organisms and originated at the beginning of evolution. The over-riding principle of circadian networks is that they align inner physiology with the natural day-night cycle, in order to optimize energy expenditure. It is hence obvious that exposure to ALAN creates a temporal disturbance leading to misalignment of physiology and metabolism with the fluctuating day-night cycle. The paramount importance of this system is now recognized in subjects as diverse as agriculture and medicine, and was recently highlighted by the attribution the 2018 Nobel Prize in Medicine and Physiology to the three pioneers in the field of chronobiology.

In vertebrates including humans, a key clock-mediated process involves altered secretion of melatonin, a neurohormone involved in the regulation of many rhythmic processes but also

as promoting antioxidant protection in the brain and elsewhere. Melatonin has strong impact on the neuroendocrine system. Normally secreted only during the dark, nocturnal light exposure diminishes or even suppresses melatonin secretion, which if occurring over a long period leads to overall deprivation in melatonin, with consequent problems (e.g., sleep) and potentially longer-term effects (e.g., on cognition, metabolism (diabetes), fertility and heart disease). It has been argued that ALAN can be considered as a source of endocrine disruption in human, since so many hormones, pheromones and metabolites are under circadian control (Russart and Nelson, 2018). This is strengthened by the observation that ALAN together with other external cues and disruptors often target the same neuroendocrine areas in vertebrates (Figure 11).

While the scientific literature is beginning to report many studies showing possible detrimental side-effects of ALAN upon human health and well-being, the effects of ALAN on the natural world, both flora and fauna, has been less talked about and is less prominent in the public consciousness. The constant increase in ALAN through anthropogenic activity means that nowadays large areas of the earth's surface (even including oceans) are permanently bathed in light, obscuring the natural order of alternating periods of light and darkness. The day-night cycle, and also that of seasonal changes, is a critical aspect of the adaptive responses of living organisms to their shifting environment, and a correct « reading » of these cycles is essential to the correct timing of such processes as flowering, reproduction and foraging, among many others. Living organisms have developed a huge variety of strategies to integrate the visual information and to decode time. It is not surprising therefore that ALAN impacts natural systems at all levels of organization, from unicellular to eukaryotes, from systems physiology to community structures, from population behaviour to trophic interactions.

The mechanisms of light capture and of adaptation to the daily and annual changes in photoperiod started at the origin of life, and have become increasingly complex over billions of years of evolution. ALAN is now challenging this in a time scale of decades only. The ongoing extension of urban areas contributes to the cumulative effects of ALAN together with a range of anthropogenic pressures on wildlife and ecosystems (demography, over-exploitation of resources, physical obstacles, reduction of natural spaces, pollution, climate change, etc.). The result is a dramatic acceleration in extinction of species, followed by disorganization and collapse of ecosystems. The great majority of species is unable to overcome such additive stress factors and to develop new strategies in such a short period of time. Reversing or even slowing down this process will need a profound

reconsideration of our environmental policies, which implies re-examination of our modern life style. With regard to ALAN the international political decision to replace pre-existing lighting systems with LED may further complicate the current scenario, due primarily to a wider emission spectrum and an enriched emission of short wavelength light to which circadian clocks are particularly sensitive. We propose that efforts should be made to limit night-time illumination to more essential purposes (e.g., road safety), within more narrowly defined areas and at more restricted hours. The use of directed lighting to minimize wasted un-useful radiation and with carefully selected spectral emissions should permit human activity to continue unhindered while significantly reducing the impact on species.

“What we conserve defines what we are or pretend to be. We must establish and promote comprehensive dialogs among social scientists, ecologists, and evolutionary biologists to explore the biological and cultural roots of our interactions with nonhumans and to understand the origins of our inertia in the face of the urgency of biodiversity erosion. Addressing this major challenge for humanity may also enhance our ability to respect each other in our societies” (Sarrazin and Lecomte, 2016).

AUTHOR CONTRIBUTIONS

JF coordinated the work and wrote the manuscript. AT, CG, CM, DA, FB-C, FV, and DH contributed to discussions and reading of the manuscript. DH contributed to English editing. All authors contributed to the article and approved the submitted version.

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OPINION

WILEY Global Change Biology

Why artificial light at night should be a focus for global change research in the 21st century

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Abstract

The environmental impacts of artificial light at night have been a rapidly growing field of global change science in recent years. Yet, light pollution has not achieved parity with other global change phenomena in the level of concern and interest it receives from the scientific community, government and nongovernmental organizations. This is despite the globally widespread, expanding and changing nature of night-time lighting and the immediacy, severity and phylogenetic breadth of its impacts. In this opinion piece, we evidence 10 reasons why artificial light at night should be a focus for global change research in the 21st century. Our reasons extend beyond those concerned principally with the environment, to also include impacts on human health, culture and biodiversity conservation more generally. We conclude that the growing use of night-time lighting will continue to raise numerous ecological, human health and cultural issues, but that opportunities exist to mitigate its impacts by combining novel technologies with sound scientific evidence. The potential gains from appropriate management extend far beyond those for the environment, indeed it may play a key role in transitioning towards a more sustainable society.

KEYWORDS

artificial light at night, ecology, global change, human health, human–environment interrelationships

INTRODUCTION

While artificial light at night (ALAN) has been a long established man-made disturbance (Longcore & Rich, 2004), the number of studies documenting its ecological and human health impacts has grown dramatically in the last decade (Figure 1). Collectively, this body of research now highlights the pervasiveness of ALAN's impacts across a broad array of biomes, ecosystems, species and behaviours. The measured biological responses occur at intensities and spectra of artificial light that are currently encountered in the environment, and the global distribution of night-time lighting means that it is likely already having widespread impacts in marine, freshwater and terrestrial habitats around the world.

While ALAN research has gained notable momentum in recent years, it is yet to achieve notoriety among environmental scientists as a driver of global change. Here, we argue that ALAN should be a focus for global change research in the 21st century. Our argument

is broken down into 10 points that highlight the global extent of ALAN, the geographic scale of its influence, the potential to reverse its environmental impacts, the rise of new human–environment conflicts with emerging lighting technologies, its evolutionary novelty, the diverse array of species now known to be affected, the extreme sensitivity of organisms to light, impacts on human health, cultural impacts on human–environment interrelationships, and the feasibility of solutions. While we do not assert that ALAN is more important than other global change phenomena, we draw comparisons where they help highlight the need for greater parity of concern.

1 | GLOBALLY WIDESPREAD

As with greenhouse gas emissions, ALAN is a globally widespread environmental pollutant. It is estimated that 23% of the land

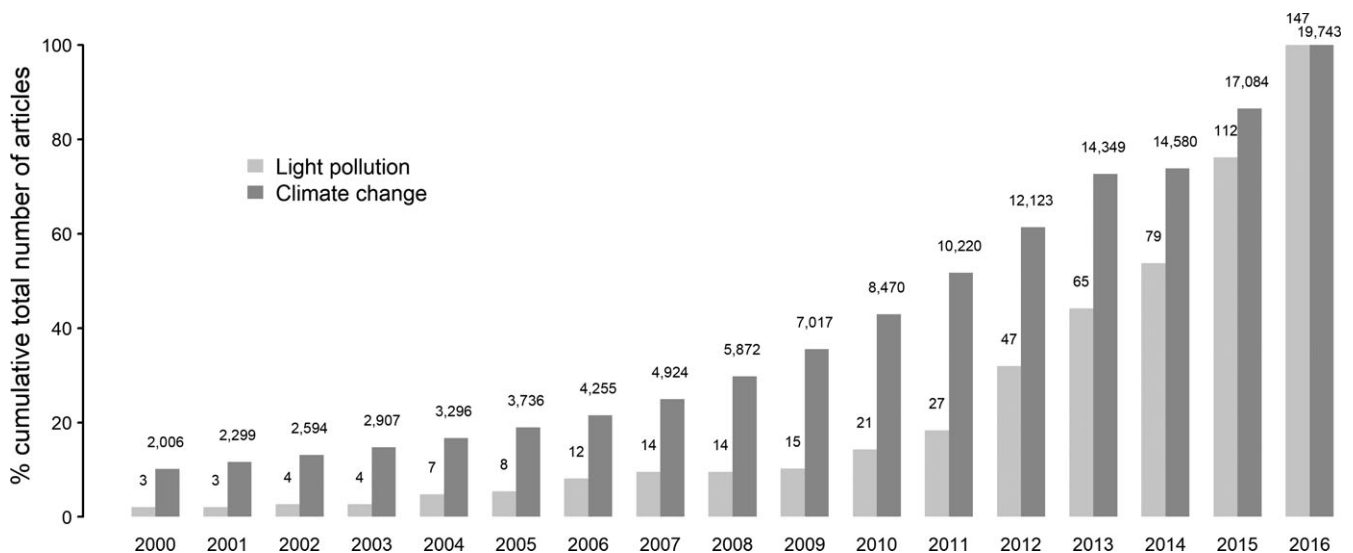


FIGURE 1 The trend in research outputs associated with light pollution and climate change since the year 2000. Bar heights represent the cumulative number of articles expressed as a percentage of the total number of articles published by the end of 2016; numbers are the cumulative number of articles published by the end of each year. Note that the total number of articles does not reflect the total number published in the research area, only the number returned from the search. The data were collected from a Web of Science search for phrases in article titles. The search phrases used for light pollution research outputs were "Light pollution" OR "Artificial Light at Night" OR "Nighttime lighting" OR "Night-time lighting" OR "Night time lighting" OR "Street Lighting" OR "LED lighting" OR "Light-emitting diode lighting." The search phrase for climate change was "Climate change" and results were not refined by research area. The search for articles on light pollution was refined by research areas: (Plant Sciences or Ornithology or Psychology Multidisciplinary or Environmental Sciences or Evolutionary Biology or Physics Applied or Entomology or Engineering Environmental or Ecology or Urban Studies or Fisheries or Biodiversity Conservation or Biology or Physics Multidisciplinary or Zoology or Oceanography or Geography Physical or Geography or Remote Sensing or Physiology or Marine Freshwater Biology or Public Environmental Occupational Health)

surface between 75°N and 60°S (Falchi et al., 2016) is exposed to artificial skyglow (artificial light that is scattered in the atmosphere and reflected back to the ground). This is comparable to the area of global ice-free land converted to either pasture or cropland, estimated to be 35% in the year 2000 (Klein Goldewijk, Beusen, van Dreht, & De Vos, 2011). The degree of exposure increased in all global terrestrial ecosystems between 2008 and 2012, with those important for biodiversity conservation often most affected (Bennie, Duffy, Davies, Correa-Cano, & Gaston, 2015). Exposure to ALAN is not limited to terrestrial environments, with current best estimates indicating that 22% of the world's coastal regions (Davies, Duffy, Bennie, & Gaston, 2014) are experiencing some degree of artificial illumination and 20% of marine-protected areas are exposed across their entire range (Davies, Duffy, Bennie, & Gaston, 2016). The amount of artificial light is also increasing in 13,061 terrestrial protected areas across Europe, Asia and South and Central America (Gaston, Duffy, & Bennie, 2015) and 1,687 (14.7%) of the world's marine-protected areas (Davies et al., 2016). Given that more than 95% of global population increases are projected to occur in the cities of economically developing countries over the next 50 years (Grimm et al., 2008), and levels of light pollution are closely associated with population density and economic activity (Gallaway, Olsen, & Mitchell, 2010); ALAN will continue to expand both in spatial extent and intensity throughout the 21st century without intervention.

2 | SPHERE OF INFLUENCE

Artificial light arises from point sources (municipal, industrial, commercial and residential), giving the impression that its impacts on the environment are highly localized. Indeed, the majority of studies into the ecological impacts of ALAN quantify responses to direct lighting (Gaston, Visser, & Hölker, 2015). Artificial skyglow increases the sphere of ALAN's potential influence far beyond a patch of habitat in the vicinity of a street light (Falchi et al., 2016; Kyba & Hölker, 2013). Numerous taxa are adapted to make use of spatial and temporal patterns of natural sky brightness at intensities equivalent to or less than those created by artificial skyglow (Dacke, Baird, Byrne, Scholtz, & Warrant, 2013; Last, Hobbs, Berge, Brierley, & Cottier, 2016; Moore, Pierce, Walsh, Kvalvik, & Lim, 2000; Naylor, 1999; Warrant & Dacke, 2016), suggesting that lights in urban centres will have impacts on environments tens to hundreds of kilometres away. A dung beetle navigating its landscape using the Milky Way could, for example, become disorientated by artificial skyglow from a city tens or perhaps even hundreds of kilometres away (Kyba & Hölker, 2013), an effect comparable to a moth becoming disorientated by a street light hundreds of metres away (van Grunsven, Lham, van Gefen, & Veenendaal, 2014).

While ALAN can be misconstrued as being a highly localized anthropogenic stressor, climate warming is likewise misrepresented as globally widespread in its occurrence. Like ALAN, ecologically

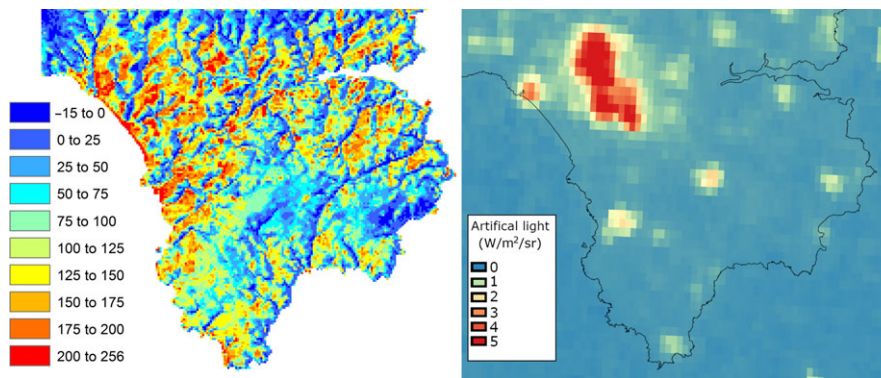


FIGURE 2 A comparison of fine-scale spatial variability in environmental warming and artificial light at night on the Lizard peninsula, Cornwall, UK. (a) The increase in the number of growing degree days (a measure of change in growing season length expressed in °C Days) between 1977 and 2014 (100 m resolution). Adapted with permission from Maclean et al. (2016). (b) The distribution of artificial light across the same area (750 m resolution) recorded from the VIIRS sensor on board the Suomi NPP satellite

relevant warming occurs at more localized spatial scales (Hannah et al., 2014) (Figure 2) and is influenced by variable topographical features such as slope and aspect that create refuges where rates of warming are reduced (Bennie, Huntley, Wiltshire, Hill, & Baxter, 2008; Maclean, Suggitt, Wilson, Duffy, & Bennie, 2016). The ecological impacts of climate change — like light pollution — are therefore likely to be spatially heterogeneous for organisms with low mobility, but more widespread for taxa that depend on large-scale movements for their survival and reproduction. In the case of both stressors, population impacts on the former species are manifest foremost through the loss and fragmentation of suitable habitat (Hannah et al., 2014), while impacts on the latter species are manifest via direct effects on population demography (Gaston & Bennie, 2014).

3 | LAG EFFECTS

Abating future rises in global temperatures constitutes one of the most significant challenges facing humanity in the 21st century. Yet even if all fossil fuel combustion ceased with immediate effect, the recovery of atmospheric CO₂ concentrations, global temperatures, ocean pH and oxygen concentrations to preindustrial levels would take hundreds to thousands of years (Frölicher & Paynter, 2015; Frölicher, Winton, & Sarmiento, 2014; Mathesius, Hofmann, Caldeira, & Schellnhuber, 2015), and there is the very real possibility that temperatures would continue to rise in the medium term (Frölicher et al., 2014). In contrast, globally widespread artificial light can be “switched off” instantaneously. There would be no lag effect on the physical environment following such an event, allowing the biological environment to immediately begin the recovery process. While such a scenario would likely prove controversial, recent technological advances present tangible ways of mitigating the ecological impacts of artificial light at night (see reason 10). Failure to abate the environmental consequences of a man-made disturbance using available viable solutions would not inspire confidence in our ability to solve the apparently insurmountable challenges posed by global climate change phenomena.

4 | THE RISE OF LEDs

Light-Emitting Diodes (LEDs) have grown from a 9% share of the lighting market in 2011 to 45% in 2014 and are forecast to reach 69% by 2020 (Zissis & Bertoldi, 2014). Their rising popularity stems from the variety of colours that LEDs can be tailored to produce, their improved energy efficiency over alternative electric light sources, and ability to produce “white” light that is aesthetically pleasing and provides enhanced visual performance (Pimputkar, Speck, Denbaars, & Nakamura, 2009; Schubert & Kim, 2005). While LEDs are often advocated for their potential to reduce global CO₂ emissions and the ability to tailor their spectra to avoid unwanted environmental impacts (see “Feasibility of solutions”), environmental scientists and human health experts have raised concerns about the broad-spectrum light (Davies, Bennie, Inger, De Ibarra, & Gaston, 2013; MacGregor, Pocock, Fox, & Evans, 2014) and prominent short wavelength peak (Haim & Portnov, 2013; Haim & Zubidat, 2015) that the commonly used white models emit (Figure 3).

Firstly, the broad range of wavelengths emitted by white LEDs likely enables organisms to perform colour-guided behaviours at night that were previously only possible during the day (Davies et al., 2013). A range of intra- and interspecific interactions could be affected including foraging (e.g. seeking nectar-rich flowers), predation (ability to locate and successfully capture prey), sexual communication (ability to locate, identify and assess the fitness of conspecifics through visual displays) and camouflage (ability to avoid detection by predators). Nocturnal species may find themselves competing for resources with diurnal species where such interactions had previously not existed (MacGregor et al., 2014), and differences in the sensitivity of animal visual systems to white LED light spectra could change the balance of species interactions (Davies et al., 2013). Some alternative lighting technologies also emit light across a broad range of wavelengths (e.g. Metal Halide and Mercury Vapour lighting, Figure 3); however, the energy efficiency of LEDs makes them the lighting of choice in the 21st century, and as such research should focus on how any unforeseen deleterious impacts can best be mitigated.

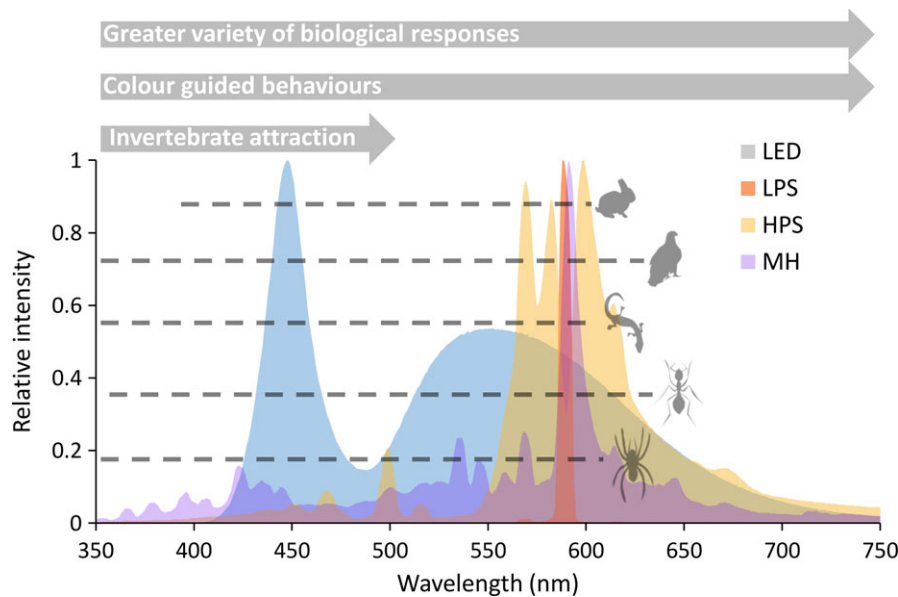


FIGURE 3 The potential ecological impacts of white Light-Emitting Diode lighting compared to other light sources. Spectral power distributions are given for white Light-Emitting Diode (LED), Low-Pressure Sodium (LPS), High-Pressure Sodium (HPS) and Metal Halide (MH) lights recorded using a MAYA 200 pro spectrometer from street lighting in Cornwall. The amount of light at each wavelength is standardized to relative intensity (radiant energy divided by the maximum radiant energy recorded at any wavelength for each light source) so that the relative distribution of radiant energy across the light spectrum can be compared for each light source. Grey arrows represent the wavelength range over which different types of biological response are expected/recorded. Dashed lines represent the range of wavelengths over which mammal, bird, reptile, insect and arachnid visual systems can detect light [adapted from Davies et al. (2013)] [Colour figure can be viewed at wileyonlinelibrary.com]

Secondly, the short wavelength peak emitted by white LEDs coincides with the wavelengths to which many biological responses are known to be sensitive. Many invertebrate behaviours (Cohen & Forward, 2009; Gorbunov & Falkowski, 2002; Haddock, Moline, & Case, 2010; van Langevelde, Ettema, Donners, Wallisdevries, & Groenendijk, 2011) and the melatonin response (West et al., 2011) are sensitive to short wavelengths of light (between 350 and 500 nm), and some studies have demonstrated that white LED lighting has a greater impact on short wavelength sensitive responses compared to alternative lighting technologies (Pawson & Bader, 2014).

Thirdly, because LEDs illuminate a broad range of wavelengths, they have the potential to affect a greater variety of biological responses that are sensitive to specific wavelengths of light. To give one example, while many invertebrate behaviours and the melatonin response are most sensitive to short wavelength light, the phytochrome system in plants—which is associated with the timing of flowering—is sensitive to red/far red light (660 and 720 nm) (Bennie, Davies, Cruse, & Gaston, 2016). Using broad wavelength light sources, such as white LEDs, therefore risks affecting more biological responses across a greater variety of taxa than using narrow wavelength light sources, such as low-pressure sodium lighting (Gaston, Davies, Bennie, & Hopkins, 2012).

Fourthly, the improved energy efficiency offered by LEDs may encourage growth in the amount of artificial light produced around the world. This “rebound effect” can be observed in historical lighting trends (see Kyba, Hänel, & Hölker, 2014) and partly explains why

aesthetic and decorative lighting installations are now increasingly seen in municipal centres, on monuments, bridges and waterfront developments.

Finally, improvements in the energy efficiency of LED lighting coupled with the production efficiency of solar cells have resulted in a rapid growth in off-grid lighting installations, typically in remote regions containing previously artificial light naive ecosystems (Adkins, Eapen, Kaluwile, Nair, & Modi, 2010; Dalberg Global Development Advisors 2013; Mills & Jacobson, 2007). The greatest ecological impacts of ALAN over the next 50 years will likely occur in these previously artificial light-naive regions, with an ecology not previously shaped by night-time lighting.

5 | EVOLUTIONARY NOVELTY

Organisms have evolved with large-scale fluctuations in atmospheric CO₂, climate temperatures and ocean pH throughout history while sudden changes to natural light regimes are unprecedented over evolutionary time scales. The harmonic movements of the earth, moon and sun provide reliable cues to which many biological events are now highly attuned (Kronfeld-Schor et al., 2013).

The ability of organisms to rapidly adapt to the introduction of ALAN through behavioural, genetic or epigenetic changes is likely to be far more limited than for climate warming due to the unprecedented nature of this change (Swaddle et al., 2015). Furthermore, the scattered growth of artificial lighting around the world is a significant

barrier to predicting where organisms will be able to seek out suitably dark habitats in the future and identifying where to allocate dark corridors that enable such migrations to happen. Although challenging, identifying where species need to go to survive climate warming, and how they get there, is made simpler by the predictability of regional climatic shifts (e.g. poleward migrations by land and sea and upward migrations in high-altitude regions) (Hannah et al., 2007).

6 | DIVERSITY OF BIOLOGICAL RESPONSES

Artificial light at night is now known to cause a plethora of environmental impacts from altering organism physiology to changing the structure of ecological communities. The diversity of taxa affected continues to grow and now includes birds (Dominoni, 2015; Kempenaers, Borgström, Loës, Schlicht, & Valcu, 2010), bats (Rydell, 1992; Stone, Jones, & Harris, 2009), sea turtles (Kamrowski, Limpus, Moloney, & Hamann, 2012; Witherington, 1992), marsupials (Robert, Lesku, Partecke, & Chambers, 2015), rodents (Bird, Branch, & Miller, 2004), anurans (Hall, 2016), freshwater and marine fish (Becker, Whitfield, Cowley, Järnegen, & Næsje, 2012; Brüning, Hölker, Franke, Preuer, & Kloas, 2015; Riley, Davison, Maxwell, & Bendall, 2013), moths (Frank, 1988; Wakefield, Stone, Jones, & Harris, 2015), beetles, spiders, harvestmen, woodlice and ants (Davies, Bennie, & Gaston, 2012; Davies et al., 2017), branchiopod (Moore et al., 2000), amphipod (Davies, Coleman, Griffith, & Jenkins, 2015; Davies et al., 2012; Navarro-Barranco & Hughes, 2015) and copepod (Davies et al., 2015) crustaceans, polychaete worms, colonial ascidians and hydrozoans (Davies et al., 2015), corals (Kaniewska, Alon, Karako-Lampert, Hoegh-Guldberg, & Levy, 2015), and terrestrial plants (Bennie, Davies, Cruse, Inger, & Gaston, 2015; Bennie et al., 2016; Ffrench-Constant et al., 2016). The documented impacts include those on animal communication (van Gefen et al., 2015; Kempenaers et al., 2010), reproductive development (Dominoni, Quetting, & Partecke, 2013; Hansen, Stefansson, & Taranget, 1992), the timing of reproduction (Kaniewska et al., 2015; Robert et al., 2015), orientation (Frank, 1988; Witherington, 1992), habitat selection (Davies et al., 2012, 2015), predator avoidance (Wakefield et al., 2015), predation pressure (Becker et al., 2012; Bolton et al., 2017; Rydell, 1992), circadian disruption (Brüning et al., 2015; Raap, Pinxten, & Eens, 2015, 2016), plant phenology (Bennie et al., 2016; Bennie, Davies, et al., 2015; Ffrench-Constant et al., 2016) and ecosystem services (Knop et al., 2017; Lewanzik & Voigt, 2014).

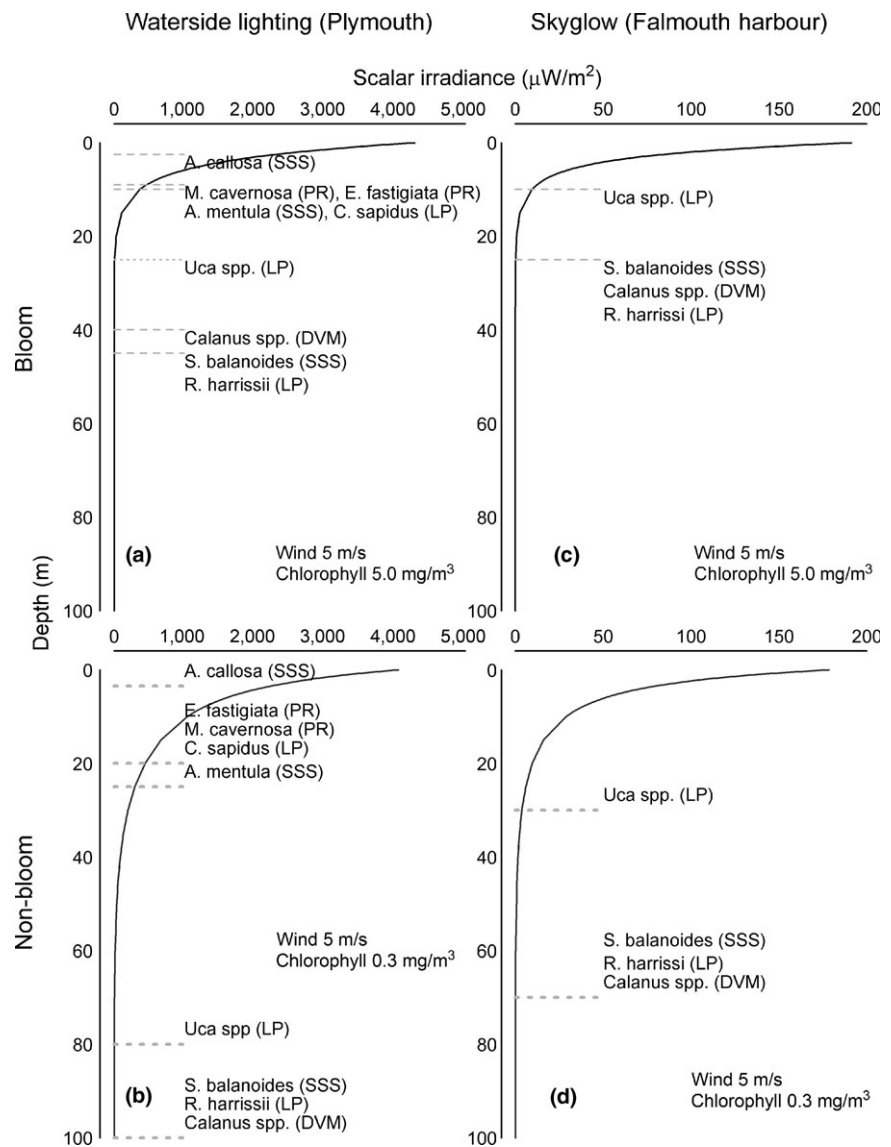
While those impacts on survival and reproductive success highlight that ALAN is likely causing widespread population losses for a variety of taxa, no population-level effects have so far been reliably demonstrated. This is in part because satellite images of night-time lights are not available in sufficiently high spatial resolution for inferences to be drawn regarding impacts on species populations that can be variable on the scale of tens to hundreds of metres (Elvidge et al., 2007). Disentangling the effects of street and residential lighting from those of urbanization and land use change is challenging since all of these explanatory variables likely contribute to

population declines but all covary. Analyses using higher resolution images from the international space station (capable of identifying individual roads) may yield further insights, but tend to be focused on cities, preventing comparisons from being drawn across sufficiently large spatial scales. Recent developments in hemispherical photography allow “biologically relevant” artificial skyglow to be mapped from ground level across thousands of square kilometres (Luginbuhl et al., 2009; Zoltan, 2010), better enabling ecologists to quantify its impacts on populations of organisms that utilize celestial patterns of sky brightness, but perhaps not the population effects of direct lighting. Techniques to model the distribution of artificial light across towns and cities have also been developed (Bennie, Davies, Inger, & Gaston, 2014); however, such models can be computationally expensive and have not yet been applied to the question of whether direct lighting has an impact on organism populations. Before After Control Impact (BACI) experiments have the potential to provide insights into the long-term responses of sessile species populations and those mobile taxa with <1 km home ranges; however, the finances and time required to implement them at appropriate spatial and temporal scales make this approach less feasible in a limited funding environment. For now, quantifying the population-level impacts of ALAN remains one of the most important and challenging problems facing ecologists working in this area.

7 | SENSITIVITY OF BIOLOGICAL RESPONSES

Many organisms are extremely sensitive to natural light, utilizing light cues as dim as the moon and the Milky Way to orientate themselves, navigate landscapes and identify conspecifics and resources at night (Dacke et al., 2013; Last et al., 2016; Ugolini, Boddi, Mercatelli, & Castellini, 2005; Warrant & Dacke, 2016). Perhaps, most striking is the growing number of documented responses to white LEDs in marine systems (Bolton et al., 2017; Davies et al., 2015; Gorbunov & Falkowski, 2002; Navarro-Barranco & Hughes, 2015), where species are both adapted to utilize short wavelengths that penetrate deeper in seawater and are incredibly sensitive to natural light. Examples of this extreme sensitivity include copepods (*Calanus* sp.) that undergo diel vertical migration to depths of 50 m guided only by variations in moonlight intensity during the arctic winter (Båtnes, Miljeteig, Berge, Greenacre, & Johnsen, 2013; Last et al., 2016); sessile invertebrate larvae that move and identify suitable settlement locations guided by light levels equivalent to moonless overcast nights (Crisp & Ritz, 1973; Thorson, 1964) and polychaete worms, corals and echinoderms that synchronize broadcast spawning events using monthly and annual variations in lunar light intensity (Naylor, 1999). Many of these responses are clearly sensitive enough to be affected both by direct lighting and artificial skyglow (Figure 4), and indeed such impacts have been demonstrated for zooplankton diel vertical migration in freshwater ecosystems (Moore et al., 2000). Given the spatial extent of artificial skyglow in coastal regions (Davies et al., 2014; Falchi et al., 2016), the disproportionate

FIGURE 4 The sensitivity of marine invertebrates to direct artificial light and artificial skyglow. Solid lines represent the attenuation of scalar irradiance (between 400 and 700 nm) with depth estimated using radiative transfer models under winter (a & c; Chlorophyll = 0.3 mg m³ uniform profile, wind = 5 m/s) and spring (b & d; Chlorophyll = 5 mg m³ uniform profile, wind = 5 m/s) water column properties. Models of scalar irradiance with depth are derived from spectral power distribution recorded from the spring high tide mark under a white LED street light on the Barbican in Plymouth (a & b), and artificial skyglow from predominantly white Metal Halide spectra recorded above Falmouth Harbour (c & d). Grey dashed lines indicate the maximum depth at which sufficient artificial light is available to perform species behaviours. SSS = Settlement Site Selection; PR = Polyp Retraction; LP = Larval Phototaxis; DVM = Diel Vertical Migration. Sensitivities to white light were calculated from experimentally derived values in existing literature (Båtnes et al., 2013; Crisp & Ritz, 1973; Forward, Cronin, & Stearns, 1984; Gorbunov & Falkowski, 2002; Svane & Dolmer, 1995; Tankersley, Mckelvey, & Forward, 1995; Young & Chia, 1982)



importance of these regions for global biogeochemical cycles [coastal zones account for 30% of global ocean primary production but only 10% of global ocean surface area (Wollast, 1998)], and the role of diel vertical migration in maintaining these cycles (Hays, 2003), it is not unreasonable to surmise that ALAN could have detectable effects on ocean carbon and nutrient budgets in the near future.

8 | IMPACTS ON HUMAN HEALTH

In 2007, the World Health Organisation classified shift work that disrupted human circadian rhythms as a probable human carcinogen (International Agency for Research on Cancer, 2007). While this classification is primarily associated with shift work, exposure to ALAN has been linked to a variety of health disorders in people through the same circadian disruption mechanism. These include sleep disorders, depression, obesity and the progression of some cancers (Cajochen et al., 2011; Chang, Aeschbach, Duffy, & Czeisler, 2014; Haim & Portnov,

2013; Keshet-Sitton, Or-Chen, Yitzhak, Tzabary, & Haim, 2015). The prominent peak of blue wavelength light emitted by LEDs is of increasing concern since it occurs at the most effective frequency for suppressing the production of melatonin (Haim & Zubidat, 2015; West et al., 2011), a hormone released by the pineal gland that regulates sleep wake cycles and acts as an antioxidant. Over the last decade, LEDs have become a ubiquitous feature of human life and can be found in street, residential, commercial and aesthetic lighting installations, laptops, televisions, e-readers, smart phones and tablets. Late evening exposure to LED light from handheld devices has been linked to circadian disruption of sleep wake cycles and alertness and cognitive performance during the day (Cajochen et al., 2011; Chang et al., 2014).

The extent to which outdoor lighting impacts human health is yet to be reliably determined. While epidemiological studies have found correlations between the amount of outdoor lighting and some health effects (Kloog, Haim, Stevens, Barchana, & Portnov, 2008; Koo et al., 2016), as with ecological patterns, they are limited

by the inferences that can be drawn from satellite images (Defence Meteorological Satellite Programme Operational Line Scan) with insufficient spatial resolution (5 km) to differentiate exposure to ALAN from other factors that covary across city districts at fine spatial scales (Elvidge et al., 2007; Kyba, 2016). The need for higher resolution images or novel approaches that can disentangle the effects on both ecology and human health of multiple urban pollutants that covary is clear, although individual-level sensors can also reveal important impacts of daily light exposure on circadian disruption and stress (Figueiro et al., 2017). A more recent analysis using higher resolution (0.75 km) images from the Visible Infrared Imaging Radiometer Suite (VIIRS) on board the Suomi National Polar-orbiting Partnership satellite has revealed a significant association between ALAN and breast cancer incidence in the Greater Haifa Metropolitan Area in Israel (Rybnikova & Portnov, 2016). This analysis accounted for several potential covarying explanatory factors, but not noise pollution, and atmospheric pollution explicitly.

9 | HUMAN-ENVIRONMENT INTERRELATIONSHIPS

In a recent analysis that combined high-resolution night-time satellite images with atmospheric dispersion models of artificial skyglow, Falchi et al. (2016) estimated that more than 80% of the world's population currently live under light-polluted skies, such that the Milky Way is hidden from one-third of people alive today. This extraordinary change in our night-time environment escalated in the developed world during the mid to late 20th century and is now rapidly transforming the cultures of billions in the developing world. The trend is concurrent with urbanization [66% of the world's population will reside in urban areas by 2050 (United Nations, 2014)], and it contributes to the growing disconnect between people and nature that has become known as “the extinction of experience” (Miller, 2005). This growing disconnect undermines public support for conservation issues by preventing individuals from connecting with, understanding and forming attachments to the natural world (Miller, 2005).

The extinction of experience is another of the great challenges facing humanity in the 21st century. Miller (2005) argues that it can be addressed by designing urban landscapes to facilitate “meaningful interactions with the natural world.” There is perhaps no more profound way in which people can reconnect with nature than giving them access to the Milky Way and allowing them to experience the natural rhythms of moonlight and sunlight that they are evolutionarily preadapted to synchronize their physiology and behaviour with (Cajochen et al., 2013; Wright et al., 2013). Like biodiversity conservation, however, pristine skies have become tourist attractions restricted to regions awarded special status for their value to dark sky conservation (Collison & Poe, 2013; Pritchard, 2017; Rodrigues, Rodrigues, & Peroff, 2014) where many in the developed world can no longer afford to reside or visit. Pritchard (2017) argues that dark sky protection programmes also risk suppressing the economic and cultural development of poorer nations in a way analogous to

biodiversity conservation in the 20th century. In her appraisal of NASA's “City Lights,” composite satellite image of the world's lights at night (<http://earthobservatory.nasa.gov/Features/IntotheBlack/>) Pritchard (2017) warns against “neo-colonial approaches to the conservation of natural night-sky brightness.” While it is clear that the continued growth in artificial lighting risks perpetuating the disconnect between people and the environment—and this will inevitably contribute to the concomitant shifting baseline in conservation objectives (Papworth, Rist, Coad, & Milner-Gulland, 2009; Pauly, 1995)—any intervention should seek to support the modernization of societies while retaining their connections with the natural world. Pritchard (2017) describes achieving this balance as a “new frontier in 21st century conservation.”

10 | FEASIBILITY OF SOLUTIONS

While the recent growth in LED lighting has raised concerns among environmental scientists and human health experts, this technology offers lighting managers greater flexibility when it comes to tailoring the timing, intensity and spectral power distribution of municipal lighting systems (Davies et al., 2017; Gaston, 2013). Of the local authorities in England, 23% are engaged in permanent part-night lighting schemes where street lights are turned off between midnight and 04:00 to 05:00 a.m., while 39% are engaged in permanent dimming schemes where lights are dimmed for at least some period of the night (Campaign to Protect Rural England, 2014). Increasing constraints on local authority budgets have incentivized the adoption of these lighting strategies in the wake of the 2008 global financial crash; however, more often the reasons given for their implementation are improved energy savings and reduced CO₂ emissions. Both dimming and part-night lighting are better enabled by switching to LED and introducing central management systems that use wireless communication technology to programme individual street lights remotely.

The ecological benefits of dimming and part-night lighting are not yet well explored (although see Azam et al., 2015; Day, Baker, Schofield, Mathews, & Gaston, 2015; Davies et al., 2017). A recent emphasis in the ecological literature has instead been on tailoring spectral power distributions to reduce known ecological impacts (Brüning, Hölker, Franke, Kleiner, & Kloas, 2016; Davies et al., 2017; van Geffen et al., 2015; Longcore et al., 2015; Pawson & Bader, 2014; Rivas, Tomillo, Uribeondo, & Marco, 2015; Spoelstra et al., 2015), despite this approach being less popular among lighting managers and engineers who often focus on the improved visual performance offered by broad-spectrum lighting as a key selling point. These studies collectively present an inconsistent picture of whether spectral manipulation can be used to effectively mitigate the ecological impacts of ALAN. This is partly because some studies compare narrow spectrum (e.g. red, green and blue) light with broad-spectrum light sources, while others either decrease the amount of light occurring at wavelengths known to manifest certain ecological responses (usually shorter wavelengths in the visible spectrum), or increase the

amount of light occurring at wavelengths that do not give rise to these responses (longer wavelengths in the visible spectrum). Even if a unified approach was adopted in spectral manipulation experiments, it seems unlikely that a publically acceptable light spectrum that does not give rise to any ecological impacts can be developed, because different species responses are evolutionarily adapted to utilize different wavelengths of light.

Examples of this are abundant in the emerging literature on the ecological impacts of artificial light. The number of beetle taxa aggregating under white LED lighting can be reduced by switching to amber, but this has no discernible effect on the number of spider taxa that aggregate (Davies et al., 2017). Many animal responses are sensitive to short-wavelength light (van Langevelde et al., 2011; Rivas et al., 2015; Spoelstra et al., 2017), while phenological responses in plants are most sensitive to the longer wavelengths recommended to avoid such effects (Bennie et al., 2016; Bennie, Davies, et al., 2015). Male caterpillars of the moth *Mamestra brassicae* reared under green artificial light reached a lower maximum mass, pupated earlier and obtained a lower pupal mass than those reared under red light (van Geffen, van Grunsven, van Ruijven, Berendse, & Veenendaal, 2014), while red light inhibited the attractiveness of a female pheromone lure to more adult males of the winter moth *Operophtera brumata* than did green light (van Geffen et al., 2015).

Studies investigating the ecological benefits of part-night lighting have also highlighted that different taxa respond in different ways (Azam et al., 2015; Davies et al., 2017; Day et al., 2015), and the adoption of part-night lighting schemes is often inhibited by a perception among political actors that they lack popular support. There are both perceived and realized benefits of artificial light for society, including in the areas of road safety, crime and the economy (Gaston, Gaston, Bennie, & Hopkins, 2015). The night-time economy in the United Kingdom, for example, was worth £67bn in 2016 (MAKE Associates, personal communication) and accounted for up to 27% of town and city centre turnover and 10% of most locations overall employment figure in 2009 (VisitEngland, 2012).

While modern lighting technologies offer the potential to reduce the ecological impacts of ALAN, identifying how this is best achieved is clearly complex. Studies are needed across a wide variety of taxonomic groups and lighting approaches, to develop options that are both socially and ecologically acceptable.

CONCLUSION

Research into the ecological, human health and societal consequences of ALAN is now growing rapidly. Here, we have highlighted 10 reasons why ALAN should and likely will be a focus for global change research in the 21st century. Most important to consider is the notion that while ALAN is having widespread and profound impacts on people and the environment, strategies for abating them are already being explored. Solving the challenges posed by ALAN would not only improve environmental and human health outcomes but also enhance the human experience of nature and change perceptions of the natural world in a way that facilitates the necessary

transition towards a more environmentally orientated and hence sustainable society. It would also inspire greater confidence in our ability to tackle the problems posed by other global change phenomena. The challenge now is identifying how best to address the complex array of ecological, human health and cultural problems presented by society's propensity for illuminating the night.

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A meta-analysis of biological impacts of artificial light at night

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Natural light cycles are being eroded over large areas of the globe by the direct emissions and sky brightening that result from sources of artificial night-time light. This is predicted to affect wild organisms, particularly because of the central role that light regimes play in determining the timing of biological activity. Although many empirical studies have reported such effects, these have focused on particular species or local communities and have thus been unable to provide a general evaluation of the overall frequency and strength of these impacts. Using a new database of published studies, we show that exposure to artificial light at night induces strong responses for physiological measures, daily activity patterns and life history traits. We found particularly strong responses with regards to hormone levels, the onset of daily activity in diurnal species and life history traits, such as the number of offspring, predation, cognition and seafinding (in turtles). So far, few studies have focused on the impact of artificial light at night on ecosystem functions. The breadth and often strength of biological impacts we reveal highlight the need for outdoor artificial night-time lighting to be limited to the places and forms—such as timing, intensity and spectrum—where it is genuinely required by the people using it to minimize ecological impacts.

The development of electric lighting technology has transformed human societies, lengthening the time available for both work and pleasure¹. Associated with human settlement, transport networks and industry, it has also profoundly altered the natural night-time environment. Large areas of the Earth now experience light that differs from natural regimes in timing, intensity and spectrum^{2,3}. Nearly a quarter of the global land area already lies under artificially light-polluted night-time skies⁴. The area experiencing direct emissions from artificial light sources is estimated currently to be expanding at approximately 2% per annum, with localities that were previously lit brightening further at a similar rate⁵.

Artificial light at night (ALAN) is predicted to constitute a significant anthropogenic pressure on natural biological systems because (1) such systems are organized foremost by light, and particularly by daily and seasonal cycles of light and dark^{6–8}, and (2) there have been no natural analogues, at any timescale, to the form, extent, distribution, timing or rate of spread of artificial lighting³. More obvious impacts like delayed retention of leaves on trees close to streetlights and attraction of insects and birds to outdoor lights, have long been documented^{9–11}. However, particularly the last decade has seen rapid growth in the number of empirical studies testing for the impacts of ALAN on a broad array of biological phenomena across a wide diversity of organisms (for example, refs. ^{12–16}). Although there have been qualitative reviews of this literature^{2,17,18}, quantitative analyses and understanding of the frequency and strength of the biological impacts of ALAN are lacking.

In this study, we report the results of a meta-analysis that takes into account the hierarchical structure of data due to the non-independence of several outcomes coming from the same study^{19,20}, to build a quantitative understanding of the biological impacts of ALAN on a variety of responses from organisms and ecological communities. After a systematic search, we iden-

tified 126 publications from the peer-reviewed literature testing for the impacts of ALAN on organisms. Each individual measure was assigned to one of five major response categories: organismal physiology; seasonal phenology; life history traits; daily activity patterns; and population/community. The entire dataset covered a wide range of different measurements for each of the five categories and of different study organisms and habitats and included field and laboratory studies.

Results and discussion

Overall, the dataset was dominated by physiological, life history trait and population/community-based measures, ranging from strong negative to strong positive responses to ALAN exposure (Fig. 1). Thirty-five studies documented 338 observations reporting the impact on organismal physiology, 7 studies yielded 35 observations reporting the impact on organismal phenology, 58 studies reported 411 life history measures, 27 studies described 139 daily activity measures and 42 studies provided 381 observations of the impact on populations and ecological communities. We organized these measures into subcategories within each of the five main response categories (Methods and Fig. 2). This led to the exclusion of 196 measures from the analysis of subcategories because these were only included if they had measures from at least 5 different studies.

Regarding the physiological measures, the effect sizes for the hormone levels (mostly melatonin) indicated that these were consistently and markedly reduced across all studies included (Fig. 2b). By contrast, gene expression varied markedly in effect sizes, including a number of very strong positive responses (Fig. 2b). The impact on these two measures is important because this can have knock-on effects on other physiological parameters, such as health and alertness. The other three physiological measures (immune and stress responses and glands/structures) did not show an overall response to ALAN; however, the frequency distributions of effect sizes

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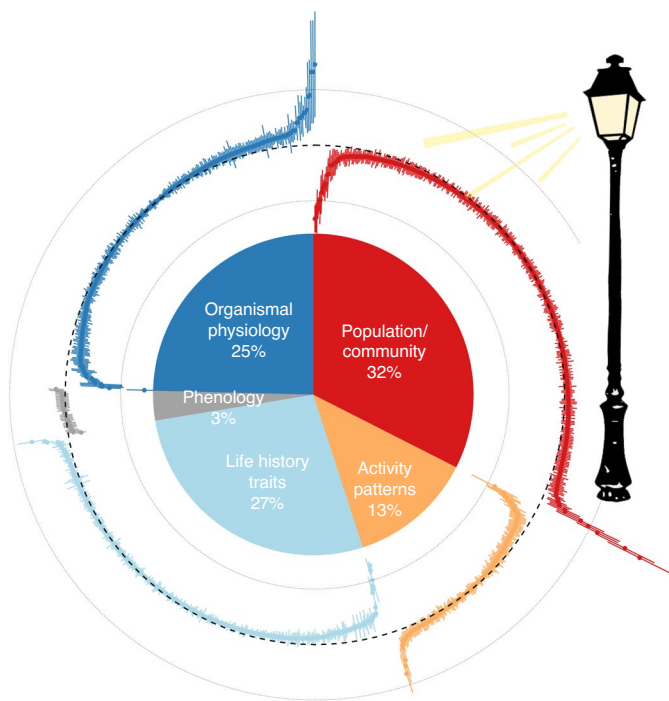


Fig. 1 | Physiological, phenological, life history trait, activity pattern and population/community-based responses to ALAN exposure. Single effect size measures (Hedges' d with 95% confidence interval) with responses from organismal physiology (blue), phenology (grey), life history traits (light blue), activity patterns (orange) and population/community (red) arranged in sequence according to increasing effect size (negative to positive). The circle dashed line indicates the zero effect size and the solid lines at effect sizes of 10 and -10 . The pie chart indicates the proportion of measures belonging to each of the five categories.

for immune and stress responses (Fig. 2d–f) show that this does not mean that ALAN has no impact. Rather, depending on the conditions of the study, the response may be either positive or negative. For stress responses, the frequency distribution of effect sizes is bimodal, with peaks at low negative and higher positive values (Fig. 2e).

While single studies found evidence of phenological shifts in plants under ALAN exposure²¹, our dataset suggests that across plants and birds both positive and negative effect sizes for phenology have been documented (Fig. 2g), with no evidence for an overall consistent directional shift.

Among measures of life history traits (the term being used broadly), overall measures of cognition (mostly the performance of rodents in experimental tests) and offspring number were negatively impacted by ALAN; measures of predation were positively impacted (Fig. 2). Most conspicuously, and including some high effect sizes, measures of seafinding by young turtles (that is, the ability to find the right direction towards the sea) were regularly strongly impacted by ALAN (Fig. 2h), reflecting movement towards the (landward) light source. This has significant consequences for turtle survival, although the impact can be mitigated to some degree by careful design, positioning and shielding of lights²².

ALAN impacts were particularly marked for daily activity patterns with, overall, the onset of activity being pushed earlier and its cessation being delayed (Fig. 2). This did not manifest as an overall strong effect of ALAN on the duration of diurnal or nocturnal activity; however, in both cases the impacts were very varied and included strong positive and negative effect sizes (Fig. 2q,r). This highlights the diversity of influences of ALAN on different species,

increasing the duration of activity for some while reducing it for others^{23,24} and acting as an attractor for some while as a repellent for others²⁵. We looked in more detail at this directional variation for two animal groups, rodents and birds, which have been disproportionately well studied. For rodents, the duration of activity of both diurnal and nocturnal species tended to be reduced by exposure to ALAN (Fig. 3a). In contrast, for birds—with all of those included strictly diurnal—ALAN was more likely to lead to an extension of the duration of their activity, with onset and cessation of singing and foraging showing especially marked responses. This goes further in some groups, such that diurnal species can use the so-called 'night-time niche' to extend their activity into the night-time¹⁵.

We found little evidence for a strong overall or net impact of ALAN on the abundance of species or the diversity of communities (Fig. 2). This outcome could potentially be explained as a consequence of the variation in, and possible trade-offs and synergies between, individual-level physiological, phenology, life history and activity responses. Indeed, abundance responses showed some of the greatest variation in effect sizes, from strongly negative to strongly positive, of any measured biological impacts of ALAN (Fig. 2s). For bats, for which the impacts of ALAN have attracted disproportionate scientific and policy attention²⁶, activity (used as a measure of the presence or abundance of species rather than of the timing of individual movements) did not show an overall strong negative response (Fig. 2). However, while some effect sizes were positive, there was also a long tail of marked negative responses, highlighting that some bat species are strongly repelled by artificial light (Fig. 2t). Such complex patterns of responses may be typical of many taxonomic groups, with the overall response being driven by those species that are most dominant.

Species interactions are an important building block of ecological community structure. Predation, the most frequently studied interaction, was typically increased by ALAN exposure (Fig. 2m), indicating that interactions between species can be highly sensitive to ALAN and are key for understanding how whole communities are impacted (as shown in food webs¹⁵ and pollination networks¹³). In turn, this likely leads to impacts of ALAN on ecosystem functions, but so far these have been little studied^{13,15}; therefore, they could not be separately addressed in this meta-analysis.

ALAN might be predicted to impact nocturnal species more strongly than diurnal ones because the loss of light conditions (dark or light) under which organisms are active is probably more limiting than is their extension. There is evidence in our dataset that this is indeed the case. For life history and activity measures, the mean effect sizes were more negative for nocturnal species than for diurnal ones (Fig. 3b); however, there was a more negative response for physiological measures in diurnal species.

Overall, for most variables we did not find evidence for publication bias in effect sizes, in particular there was no evidence of P -hacking in any of the variables and no evidence of funnel plot asymmetry for most of them (Supplementary Table 1 and Supplementary Fig. 1). There was some statistical evidence for funnel plot asymmetry for hormone levels, seafinding by turtles and activity on and offset as well as for gene expression, gland structure and bat activity but these showed no strong overall directional effect size (Supplementary Table 1 and Supplementary Fig. 1). However, in all of these cases, this asymmetry may be driven by the biological nature of these responses rather than being the result of publication bias. For example, effect sizes for hormone levels predominantly concern the suppression of melatonin levels by artificial light, with overproduction being an unlikely outcome. Likewise, for seafinding in turtles, any diversion of movement from the direction of the sea is negative for the individuals concerned and results in a negative effect size; any normal movement would be regarded as an absence of effect (rather than a positive one).

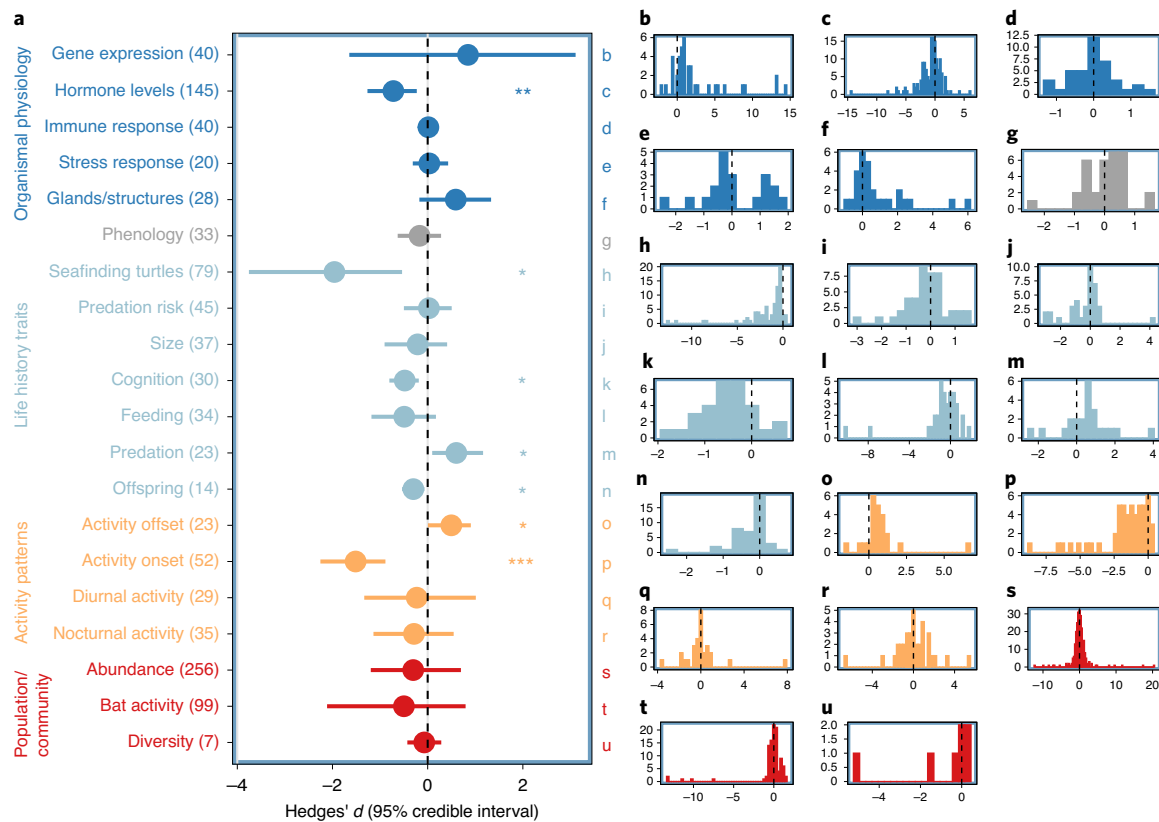


Fig. 2 | Effect sizes for the measures from the main categories. **a**, Effect sizes (Hedges' d) with post-mean and 95% credible intervals based on results from MCMCglmm for each variable from the five main categories (organismal physiology, phenology, life history traits, activity patterns and population/community). The numbers in brackets indicate the sample size and the asterisks the significance level for the pMCMC statistic, with * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. **b–u**, Histograms showing the distribution of the effect sizes for each of the categories shown in **a**, with the black dashed line indicating the zero x-axis intercept, the range of the effect size values on the x axis and frequency on the y axis.

Across the different studies, the levels of ALAN used in the experiments and observations were skewed towards low lighting of around 1–2 lx (such levels can occur approximately 10–20 m from an isolated streetlight) but covered the whole range up to 100 lx (similar to levels beneath stadium-type floodlighting), which we set as the upper limit for realistic ALAN exposure in nature. Lux is a measure of luminous flux per unit area based on human photopic vision but is typically used in studies of the biological effects of ALAN because it enables a direct link to illuminance as commonly measured in the environment and employed in the design and mitigation of artificial lighting systems. A meta-regression analysis found no relationship between the intensity of artificial light and effect size magnitude for the responses across all categories (Fig. 3c). Thus, while positive dose–response relationships have been documented for some individual physiological and behavioural responses to ALAN²⁷, there is little evidence for an overall effect across a diversity of such responses. This is probably because of the wide variation in the form of dose–response relationships for individual biological responses to ALAN because in some cases no simple such relations exist and because of variation in spectral sensitivities. Consequently, the biological impact of even low intensities of ALAN may be marked^{15,28}.

Notwithstanding the widespread nature of the biological effects of ALAN demonstrated by the results reported in this article, marked biases continue to exist in the taxonomic groups and regions for which empirical studies of these effects have been conducted. Of the 1,304 effect sizes included in the meta-analysis, 24 were for microbial communities, 143 for plants, 388 for invertebrates and 746 for vertebrates. The dataset includes almost double the number of field studies (82) compared to laboratory experiments (42), with

the majority of field studies in the meta-analysis from Europe (46), North America (17) and Australia (7). Tropical regions were markedly under-represented, despite the prediction that effects of ALAN could be particularly strong at low latitudes because of the limited natural seasonal variation in the lengths of daylight and night-time⁶. Further, more research is needed on the response of whole ecological communities and their functions to ALAN exposure²⁹; the strong response of trophic behaviour to ALAN suggests that species interactions change and with them whole community structures and their functions will shift. Interactions with other human pressures, especially climate change, are of particular interest since for species that exploit the night-time niche their behaviour at night is often temperature-dependent.

Conclusions

The results reported in this article have significant implications for the much-discussed mitigation of the effects of ALAN on the natural environment^{30,31}. First, they underline how widespread these effects are, including on diurnal species, and that where possible mitigation should be routine rather than limited to places and times when taxa perceived to be of particular concern (for example, bats) are active. Second, they highlight the challenge of making recommendations to regulate the maximum intensities of particular kinds of lighting, given that marked biological impacts of ALAN occur across a wide range of intensities including very low lighting levels (below 1 lx). Third, we show that ALAN especially changes the physiology and behaviour of organisms by affecting hormone levels, the onset of daily activity, feeding and phototaxis but typically with a less strong impact on particular community responses, such as abundance and

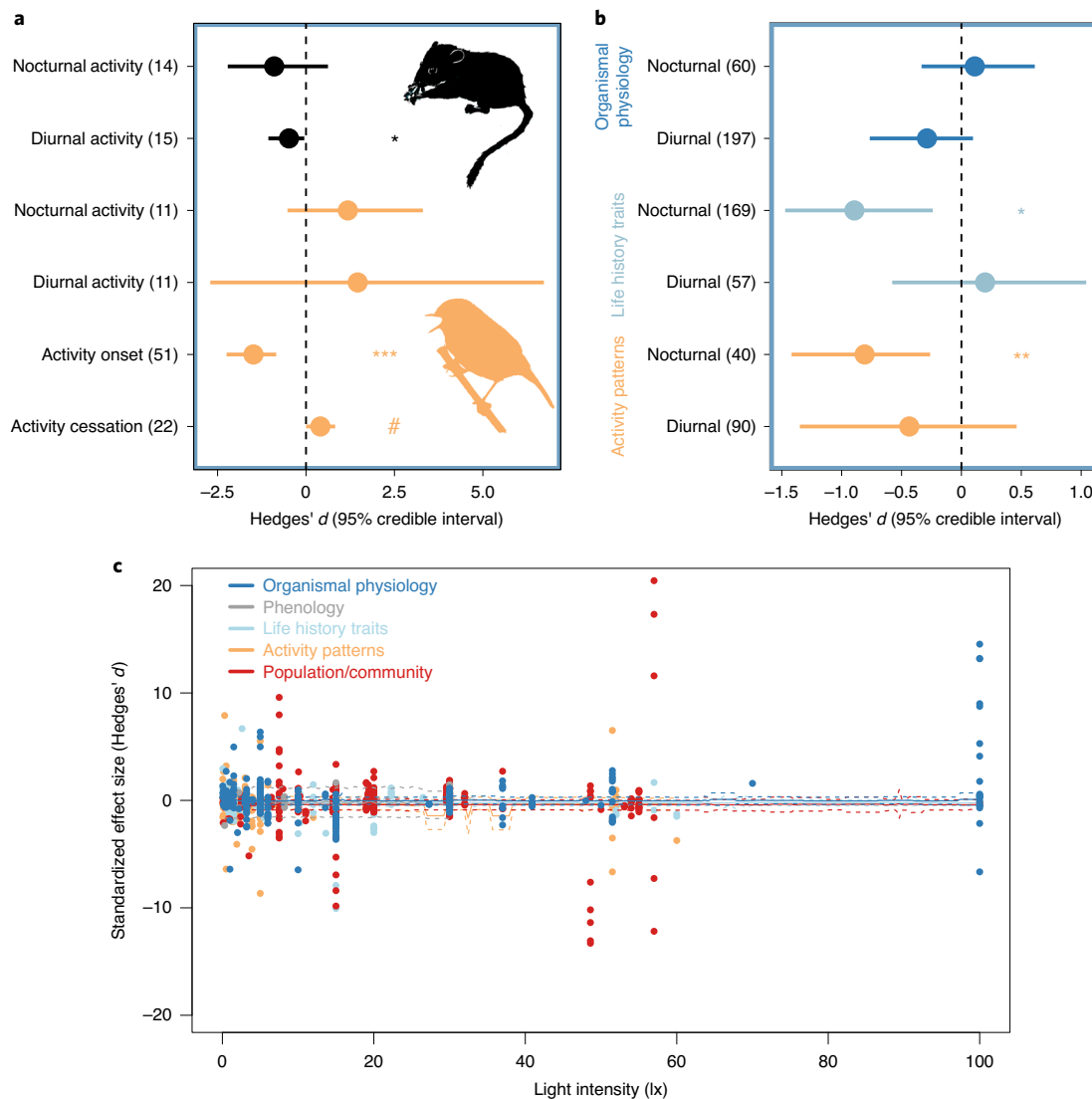


Fig. 3 | Activity patterns and light intensity. a, Impact of ALAN on rodent and bird activity. Effect sizes (Hedges' *d*) with post-mean and 95% credible intervals based on the results from the MCMCglmm package for each variable. **b**, Impact of ALAN on diurnal and nocturnal species for the categories of organismal physiology, life history traits and activity patterns. **c**, Meta-regression of effect sizes and artificial light intensity levels for organismal physiology (blue), phenology (grey), life history traits (light blue), activity patterns (orange) and population/communities (red). The numbers in brackets indicate the sample size and the asterisks the significance level for pMCMC, with * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, # $P < 0.06$.

species richness; this suggests that the impact on community structure and diversity might be less clear and depends on the impacts on key players (species or groups²⁹). Although species richness was not systematically affected in our study, it is possible that ALAN is often altering community composition (that is, beta diversity) so that sensitive species are being replaced.

Concern has repeatedly been expressed about the impacts of the loss of natural night-time light cycles on humans that span from their physiology to their psychological sense of place⁹. In this study, we show that a broad array of marked impacts also occur on other organisms.

Methods

Literature search. We identified relevant literature using keyword searches in Web of Science (we used the 'All databases' option including Web of Science Core Collection, BIOSIS Citation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index and SciELO Citation Index) and Scopus, finding any available papers published until 22 October 2019. (We constrained our searches to these databases to focus on peer-reviewed studies and tested

for publication bias.) We used the terms: "TS=((('Artificial light* at night' OR 'Light* pollution' OR 'Light* at night' OR 'night time light*') AND ('species' OR 'ecosystem*' OR 'ecological commun') AND ('abundance' OR 'behaviour' OR 'richness' OR 'reproduction' OR 'mating' OR 'diversity' OR 'composition' OR 'predation' OR 'herbivory' OR 'activity' OR 'timing' OR 'physiology' OR 'flight to light*' OR 'melatonin' OR 'development' OR 'trophic' OR 'biomass' OR 'pollination'))". After removing 352 duplicates, combining the searches resulted in 614 publications that were screened for the inclusion criteria. To be included in the meta-analysis, studies needed to (1) test for ALAN effects on organisms either in the field or the laboratory; (2) have a control group that was exposed to natural light levels at night (or a dark control) and treatment groups with exposure to ALAN up to 100 lx—studies with higher levels were excluded since these are unlikely to occur in the field; (3) have at least 2 replicates per treatment; and (4) contain data on means, estimation of variation and sample size. If only box plots were presented, we extracted the median and interquartile range³². This resulted in 126 papers, with a total of 1,304 effect size measures (refs. ^{12,13,15,16,25,27,28,33–151}).

Categorization of effect size. We categorized the effect size measures into five different main groups: response to exposure to ALAN of (1) organismal physiology, (2) phenology, (3) life history traits, (4) activity patterns (for example, daily diurnal, nocturnal activity) or (5) population/community. For the analyses,

we were interested in which factors drive the response within each category. We selected subcategories within each of the five major categories that we thought described the dataset best. For each subcategory to be included in the analysis, it needed to have data that were extracted from at least five different studies. Below, we briefly explain the subcategories.

Organismal physiology. Several studies measured the impact of ALAN on the level of gene expression and hormones produced. We also included immune response and stress response. Gland structure includes the size of glands but also the size of structures adjacent to them and neuronal structures.

Phenology. This describes seasonal timings of events such as flowering dates in plants and egg-laying in birds (measured in Julian days).

Life history traits. Life history traits are traits that affect the life table of an organism and therefore its fitness. Based on the biology of the different species studied, the different effect sizes were classified as either having a positive or negative relationship with fitness. To express the fitness consequences of all effect sizes, effect sizes were multiplied by -1 when the relationship between the trait and fitness was negative. Thus, effect sizes larger than zero express a benefit for the organism, whereas the opposite is true for values lower than zero. A total of seven categories were considered: seafinding in turtles; predation risk; body size; cognition; feeding; predation; and reproductive output.

A large number of effect sizes concern sea turtles and their ability to find the sea after emerging from eggs or after egg-laying by females. Turtles are expected to reach the sea as fast as possible to avoid predation and other risks, so increased time or distance in doing so and large differences in the direction of a straight line between egg emergence or laying and the sea are considered as negatively related with fitness. Predation risk is a trait negatively related to survival, which has been measured in many ways. In this category, most effect sizes come from studies of pairwise predator–prey interactions. Predation risk has been measured as (the sign after each trait expresses whether the trait is positively or negatively associated with fitness): attacks suffered by prey ($-$); attack attempts by predators ($-$); activity of predators ($-$); anti-predatory behaviours shown by prey ($+$); and abundance of prey in response to experimental exposure to predators ($+$). Size has been considered as having a positive effect on fitness since larger individuals are usually more fecund and live longer. Although considered as an independent category, cognition strongly relates to feeding efficiency and survival because individuals with poor cognition are less likely to forage efficiently, escape predation and ultimately survive. Cognition has been measured with the following traits (the sign after each trait expresses whether the trait is positively or negatively related to fitness). In rodents, cognition has been measured as the time spent to escape from a maze ($-$) and in birds as the time to solve a cognition test ($-$). Indirect measures of cognition include measuring sleep debt by either estimating sleep debt directly on animals ($-$) or by estimating the concentration of oxalic acid in blood (that is, a molecule that signals sleep debt) ($-$). For primary consumers, the traits included are preference over the habitual food source, food consumption, time spent eating and food absorption efficiency. Reproduction includes reproductive output, but also pre- and post-reproductive behaviours.

Activity patterns. The data for daily activity patterns contain measures of when animals started or ceased their activity (mostly measured against sunrise and sunset) and the duration of their activity. This resulted in four subcategories: activity onset; activity cessation; diurnal activity duration; nocturnal activity duration. One study measured the time spent while inactive; this was included in activity duration by changing the sign of the effect size.

Population/community. This category mostly contained data on the abundance of single species and communities (groups of species, such as functional groups) in the presence and absence of ALAN. Bat density is usually estimated indirectly as the number of passes, a variable that does not really describe activity but an indication of abundance. A few studies looked at the species richness of communities (diversity).

Data analysis. The meta-analysis was conducted in R v.3.6.0 (ref. ¹⁵³) using the package metafor version 2.4-0¹⁵³ to estimate the standardized mean difference (Hedges' d) and corresponding sampling variance for each data point using the 'escalc(measure = 'SMDH')' command. These values were then used to fit a meta-analytic model in MCMCglmm version 2.29¹⁹. To achieve this, the random term idh(SE):units was fixed to one in the prior so that all measurement errors could be considered as independent of each other. In addition, to account for study-level non-independence due to multiple measurements per study, 'Study' was included as a random effect. The Markov chain Monte Carlo chain ran for 150,000 iterations and it was sampled every 50 iterations with the first 50,000 removed as burn-in to prevent autocorrelation among subsequent iterations. Autocorrelation between consecutive samples was always lower than 0.1 and convergence of the chains was inspected visually to ensure that there were no trends in the chain and that posterior distributions were not skewed. Significance is reported as the pMCMC statistic^{19,154}. Since we did not have any a priori knowledge on the distribution of our data, we

used a flat prior: the inverse-gamma prior ($V = 1$, $\nu = 0.002$). Hedges' d was used to compare measures of the variables between treatment and control. We present the mean effect size and 95% credible intervals; the mean effect size was considered significantly different from 0 if its 95% confidence interval did not include 0.

Further, additional analyses used light intensity in lux as a moderator (equivalent to main effects in standard linear models).

Testing for publication bias. For all variables in the meta-analysis, we assessed evidence of publication bias. Publication bias implies that studies with low effect sizes were less likely to be published than studies with larger effect sizes¹⁵⁵. However, these assumptions are not always valid and some authors have suggested that publication bias is mostly caused by significance levels and P -hacking¹⁵⁶. The first form of bias was tested using asymmetry in funnel plots of meta-analytic residuals against the inverse of their precision (defined as $1/\text{sampling variance}$)³⁰. For multilevel meta-analysis models, funnel plots based on meta-analytic residuals (the sum of effect size-level effects and sampling variance effects) are better suited than those based on effect sizes¹⁵⁷. We interpreted asymmetry in funnel plots carefully given the small sample sizes for some of the variables, and the lack of bidirectional outcomes for light impact on some traits, which will inevitably lead to a biased plot. For example, for turtles, if there is an impact of exposure to ALAN on seafinding this will always be negative. Further, we ran Egger's regressions using the meta-analytic residuals as the response variable and precision as the moderator¹⁵⁷. If the intercept of the Egger's regression does not overlap zero, estimates from the opposite direction to the meta-analytic mean might be missing, which can be evidence of publication bias¹⁵⁷. P -hacking was tested with the P -curve technique, which can provide evidence of P -hacking if values close to a significance level of 0.05 are over-represented in the data^{156,158}. The P -curve was performed with the function `pcurve` from the `dmeter` package version 0.0.9000¹⁵⁹.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data generated or analysed during this study are available from the Dryad Digital Repository¹⁶⁰.

Code availability

The computer code for the meta-analysis is available from the Dryad Digital Repository¹⁶⁰.

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Author contributions

K.J.G. conceived the study. K.J.G. and D.S. designed the study. D.S., R.K. and C.P. extracted the data. E.F. and D.S. analysed the data. D.S., E.F., R.K. and K.J.G. prepared the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Study description	To understand the impact of artificial light at night on physiology and behavior of organisms and ecological communities, we conduct a meta-analysis, following a systematic search.
Research sample	We identified 126 publications from the peer reviewed literature testing for the impact of ALAN on organisms.
Sampling strategy	We identified relevant literature using keyword searches in Web of Science (we used "All databases" including Web of Science Core Collection, BIOSIS Citation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index and SciELO Citation Index) and Scopus, finding any available papers published until 22 October 2019 (we constrained our searches to these databases to focus on peer-reviewed studies, and tested for publication bias – see below). We used the terms: "TS= (("Artificial light* at night" OR "Light* pollution" OR "Light* at night" OR "night time light*") AND ("species" OR "ecosystem*" OR "ecological commun") AND ("abundance" OR "behaviour" OR "richness" OR "reproduction" OR "mating" OR "*diversity" OR "composition" OR "predation" OR "herbivory" OR "activity" OR "timing" OR "physiology" OR "flight to light*" OR "melatonin" OR "development" OR "trophic" OR "biomass" OR "pollination"))". After removing 352 duplicates, combining the searches resulted in 614 publications that were screened for inclusion criteria. To be included in the meta-analysis, studies needed to (1) test for ALAN effects on organisms either in the field or the lab; (2) have a control group that was exposed to natural light levels at night (or a dark control) and treatment groups with exposure to ALAN up to 100 lux - studies with higher levels were excluded as these are unlikely to occur in the field; (3) have at least 2 replicates per treatment; and (4) contain data on means, an estimation of variation and sample size. If only box plots were presented, we extracted the median and interquartile range. This resulted in 126 papers, with a total of 1304 effect size measures.
Data collection	Data were extracted from publication using reported effect sizes, from figures and supplementary data files.
Timing and spatial scale	<i>Indicate the start and stop dates of data collection, noting the frequency and periodicity of sampling and providing a rationale for these choices. If there is a gap between collection periods, state the dates for each sample cohort. Specify the spatial scale from which the data are taken</i>
Data exclusions	No data were excluded from the overall presentation (Figure 1). We organised the extracted measures into subcategories within each of the five main response categories (Fig. 2). This led to the exclusion of 196 measures from the analysis of subcategories because these were only included if they had measures from at least five different studies.
Reproducibility	All search and inclusion criteria are described in the manuscript, see above.
Randomization	n/a
Blinding	Three researchers were involved in the literature search and selection process, and compared their independent outcomes and discussed less obvious cases.
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