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INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

A spotlight on the phytobiome: Plant-mediated interactions in an illuminated world

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Abstract

Artificial light at night (ALAN) is a growing phenomenon threatening the world's natural ecosystems. ALAN has received a lot of attention in relation to many different taxa. However, comparatively little is known about how ALAN affects plant growth, fitness and physiology, and how this alters interactions in the phytobiome food web. There is a lot of evidence for involvement of light cycles and light quality in plant growth and physiological processes, including seasonal timing and defense regulation. Surprisingly, however, only very few studies have investigated how ALAN, typically light of low density and occurring at night, affects plant-mediated interactions. A handful of studies describe bottom-up and top-down effects in plant-aphid-parasitoid systems, pollinator responses and effects on ground-dwelling nocturnal organisms. How herbivores of other feeding guilds are impacted is not clear. Importantly, very little is known about how ALAN may impact mutualistic and antagonistic associations with the plant microbiome, above- and belowground. In this Invited View, I synthesize what is known about effects of ALAN on plants and plant-mediated interactions. I identify several key knowledge gaps that exist in the literature and discuss areas that need future attention.

Keywords: Artificial Light at Night (ALAN); light pollution; LED; phytobiome; plant-insect interactions; food web

Introduction

Our planet changed substantially over the course of the past centuries, and particularly so over the past few decades

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(Vitousek 1994). The earth's surface temperatures are on the rise, oceans are acidifying, soil quality is decreasing, and natural habitats are being destroyed, disrupted and fragmented. These are only some of the factors that drive global change. Most of these factors are a direct consequence of anthropogenic activities and the increasing pressure to sustain a growing human population using the earth's available resources (Crutzen 2006; Lewis & Maslin 2015). As most of these changes involve physical pollution and destructive events, their presence in, and consequences for ecosystems are in many cases quite obvious. However, there are also elements of global change that are far less obvious because they are not clearly associated with direct physical pollution or destruction of habitats, and therefore often go overlooked. One such factor is **artificial light at night (ALAN)**, which includes light emitted from man-made structures, such as streetlights, vehicle lights and advertisement lights, as well as the diffuse reflection of man-made light via the atmosphere, better known as skyglow (Longcore & Rich 2004; Rich & Longcore 2006).

Light pollution is a unique aspect of anthropogenic global change, as light levels are both constantly increasing and truly unprecedented (Gaston, Hölker & Visser 2015). ALAN by now is very common in most urban areas in the world, but also increasingly illuminates the more rural parts of the world, including many natural ecosystems (Longcore & Rich 2004; Rich and Longcore, 2006; Schroer and Hölker, 2016). Increases in light pollution levels have been steepest in industrialized countries, but in the last decades developing countries are also experiencing a surge, correlating closely with their more recent technological and economic advancements (Hölker et al. 2010). Furthermore, light technology is also rapidly becoming cheaper and more easily available, and as a result, light pollution levels keep increasing annually and are predicted to do so in the coming decades (Hölker et al. 2010; Kyba et al. 2017). Following these predictions, one can assume that light pollution will also very much be a problem of the future.

The effects of light pollution on several taxa (i.e., birds and bats) are well-covered in the scientific literature. However, comparatively little is known about effects of ALAN on the **phytobiome**, i.e., plants and their environment, including micro- and macroscopic interacting organisms (Leach et al., 2017). Very recently, a meta-analysis (Sanders et al., 2021) revealed two important aspects of the impacts of ALAN on natural ecosystems. First, ALAN has a strong impact on many living organisms, predominantly via alterations in organismal physiology, life history traits, and changes in activity patterns. Second, the used database revealed clearly that most studies in the past two decades have focused on the effects of ALAN on animal species, initially with a strong bias towards vertebrates (Sanders et al., 2021). Plants and microbes made up a relatively small proportion of the dataset. Although plants have received some attention in the context of ALAN (Bennie et al., 2016; Briggs, 2006; Singhal et al., 2019), there are only few recent studies that experimentally tested the effects of ALAN on plants. More importantly, a mechanistic understanding of how ALAN affects plants at the molecular level (e.g., through signaling pathways) and how this mediates plant interactions with their living environment, is severely lacking.

In this Invited View, I review the literature on what is known about the effects of ALAN on plants and discuss how ALAN may affect interactions occurring in the phytobiome. Importantly, I try to take a holistic view that includes above- and belowground interactions, and goes beyond plant-herbivore interactions, by including plant interactions with microbial taxa. I identify critical knowledge gaps that are present in this field of research that urgently require more ALAN research.

Perception of ALAN by plants

How is light perceived by plants?

Processes in plants are tightly tuned to the environmental conditions in which they grow. Plant vegetative and reproductive processes often follow specific patterns that match stable annual (i.e., seasonal) patterns (Legris et al. 2017). At shorter temporal scales, plants also regulate specific processes, such as defenses, starch turnover, and germination, tuned to diurnal cycles (Franklin, 2009; Stitt & Zeeman 2012). Two obvious factors differ strongly in both annual and diurnal cycles: temperature and light. Indeed, many processes in plants are fine-tuned by temperature, light, and often by both (Franklin 2009).

Plants evolved a series of receptors that enable them to perceive light conditions. Although a full review of their functions is beyond the scope of this manuscript, this section is meant to broadly summarize them and illustrate how they alter plant signaling. Plants use the energy of light as a resource (by means of photosynthesis) and for this they have evolved carotenoids and chlorophyll pigments in which they harness light to convert carbon dioxide into glucose. These pigments have specific absorption spectra between 400-700nm (known as the photosynthetically active radiation; PAR) and therefore plants can only photosynthesize within this spectrum. The best-characterized non-photosynthetic receptors are cryptochromes (390-480nm; Ahmad et al. 2002), phytochromes ('PhyA' 540-690nm; 'PhyB' 695-780nm; Shinomura et al. 1996) and phototropins (320-500 nm; Briggs & Christie 2002; Christie 2007). Stimulation of photoreceptors can trigger various complex signaling pathways that mediate a broad range of functions in the plant. For instance, cryptochromes are involved in regulation of seed germination, plant development, and DNA repair (Somers et al. 1998; Poppe et al. 1998; Kami et al. 2010). Phytochromes - often together with the cryptochromes - are involved in the regulation of circadian clock responses (Somers et al. 1998), shade avoidance (Ballaré

2009), and appear to be involved in the timing of phenological events such as germination, flowering and budburst (Chory et al. 1996; Howe et al. 1996; Donahue et al. 2007). Phototropins play an important role in phototropism, the movement of plants relative to a light source (Briggs et al. 2001; Kimura & Kagawa 2006).

What makes ALAN different from daylight?

There are various aspects of ALAN that set it apart from daylight and influence how it is perceived by plants. A first aspect is the realized level of illuminance emitted by sources of ALAN. Whereas unfiltered direct sunlight can reach levels over 100.000 lux, or lumens per square meter (Cailean et al. 2018), a modern LED streetlight may only deliver an illuminance of roughly 5-30 lux at night (Bennie et al. 2016). Illuminance strongly depends on the type of light source, the individual brand, and the placement of the light source (Cathey & Campbell 1975a; 1975b). Notably, some sources of ALAN, such as vehicle lights, advertisement lights or sport stadium lights reach levels that are substantially higher than those of streetlights (Bennie et al. 2016), but these levels are still not anywhere close to the illuminance delivered by the sun. The high illuminance of daylight results in high levels of relative intensity across a broad range of the light spectrum, i.e., light levels that are usable for photosynthetic activity. The low illuminance delivered by most ALAN sources result in a much lower relative intensity across the light spectrum, and therefore ALAN sources may have only a limited effect on photosynthesis, but photosynthesis is only one of a wide range of functions in plants that is mediated by photoreceptors and therefore influenced by light (Briggs 2006).

Illuminance is strongly determined by the output of the light source and the distance between the receiving environment and the source. At the landscape scale, spatial differences in natural illuminance between locations in the receiving environment, even when they are located hundreds of meters distance apart, are negligible due to the much larger distance between earth and the sun. This means that a given area in the landscape will receive the same level of illuminance at any given time point. In the case of ALAN on the other hand, the source is often just a couple of meters away, and illuminance rapidly decreases with increasing distance from the light source. This effect is also very pronounced in the case of vehicle lights, which generally move, and therefore create pulses of light.

Diurnal light patterns are the result of the rotation of earth around its own axis. Annual patterns are determined by the rotation of earth around the sun. Due to seasonal and diurnal patterns, the quality and illuminance of daylight present in a given area depends on the time of the day and time of the year, following stable and predictable patterns. In response to these predictable patterns, many organisms have evolved lifestyles to match, being either active during day (diurnal), or night (nocturnal). In contrast to natural light, ALAN sources generally follow an on-off pattern that matches the dark periods of the natural light cycle. Less permanent sources such as vehicle lights follow much less consistent patterns of illuminance, depending on traffic and are therefore harder to predict (Bennie et al. 2016). Sport stadium lights and advertisement lighting may be only switched-on during parts of the night. In other words, daylight and ALAN strongly differ in quality and quantity of light output. What makes ALAN so unique and hard to predict is that it is a growing phenomenon. It is not only increasing, but also evolving rapidly with ongoing technological advancement. Many questions remain about how natural systems will respond to ALAN, but at first glance, it does not look good.

ALAN and plant responses

Unlike most animals, plants are mostly sessile and hence behavioral responses, such as attractance or repellence are not applicable to them. In fact, once a source of ALAN is placed near a plant, there is very little that a plant can do to escape it. Given the many processes in plants that are regulated by light, as I discussed above, it seems almost obvious that plants will be affected by ALAN.

Very few studies have empirically tested the direct effects of ALAN on plants, especially so under ‘natural’ conditions (Bennie et al. 2016; Briggs 2006). Early literature reports that plants under different ALAN sources can respond with growth alterations and changes in phenology, such as the onset and duration of flowering, leaf senescence, or leaf abscission (Cathey & Campbell 1975a; 1975b; Matzke 1936; Runkle et al. 1998; Schroeder 1945; Whitman et al. 1998), all of which may have potential ecological consequences (for an elegant review of these see Bennie et al. 2016). It is also clear that some plant species, such as those sensitive to day length, are highly sensitive to ALAN, whereas others are not (Cathey & Campbell 1975a, 1975b). Only very few recent studies have looked at the effects of ALAN on wild plants in natural systems. For instance, a recent study on grasses revealed species-specific effects on grass biomass depending on light type and study year, with *Agrostis tenuis* being smaller under ALAN, whereas *Anthoxanthum odoratum* and *Holcus lanatus* grew bigger under most ALAN types (Bennie et al. 2018). Notably, the impacts were strongest in the year that was marked by an extremely cold winter, which suggests that ALAN may also interact with other global change factors, such as temperature (Bennie et al. 2018). A study by the same group reports a decrease in the number of inflorescences in *Lotus pedunculatus* when grown under two different types of ALAN (Bennie et al. 2015). Another recent study on milkweed, *Asclepias syriaca*, shows that ALAN has positive effects on growth parameters, and importantly, that ALAN shows strong interactive effects with soil moisture, suggesting that ALAN may have stronger effects in drier areas

(Hey et al. 2020). The literature describing the effects of ALAN on plants generally is limited to classical ecological plant parameters pertaining to phenology or growth. However, thanks to advancements in molecular biotechnology and biochemistry in recent decades, it has become quite clear that plant ecological interactions can be impacted by many more factors than size alone, and that many plant responses to the environment may take the form of strong changes in plant tissue quality that are not necessarily reflected by their growth responses - or the lack thereof (Huberty et al., 2020; Zhu et al., 2018). An important, but thus far unanswered question is how ALAN affects plants at deeper levels of their organization, such as via transcriptomic or metabolomic processes in their roots, shoots and reproductive tissues, and how these link to interactions in the phytobiome.

Plants express a great diversity in structural and chemical traits in their roots and shoots that mediate ecological plant interactions in the community of organisms associated with the plant - the phytobiome (Westoby & Wright 2006). Defense traits are important mediators of plant interactions (Schoonhoven et al. 2005). For instance, structural traits can help in deterring unwanted guests, but on the other hand may also serve as cues or entry points for various symbiotic relationships. Furthermore, chemical traits may also have repellant effects but can also be used as cues that attract

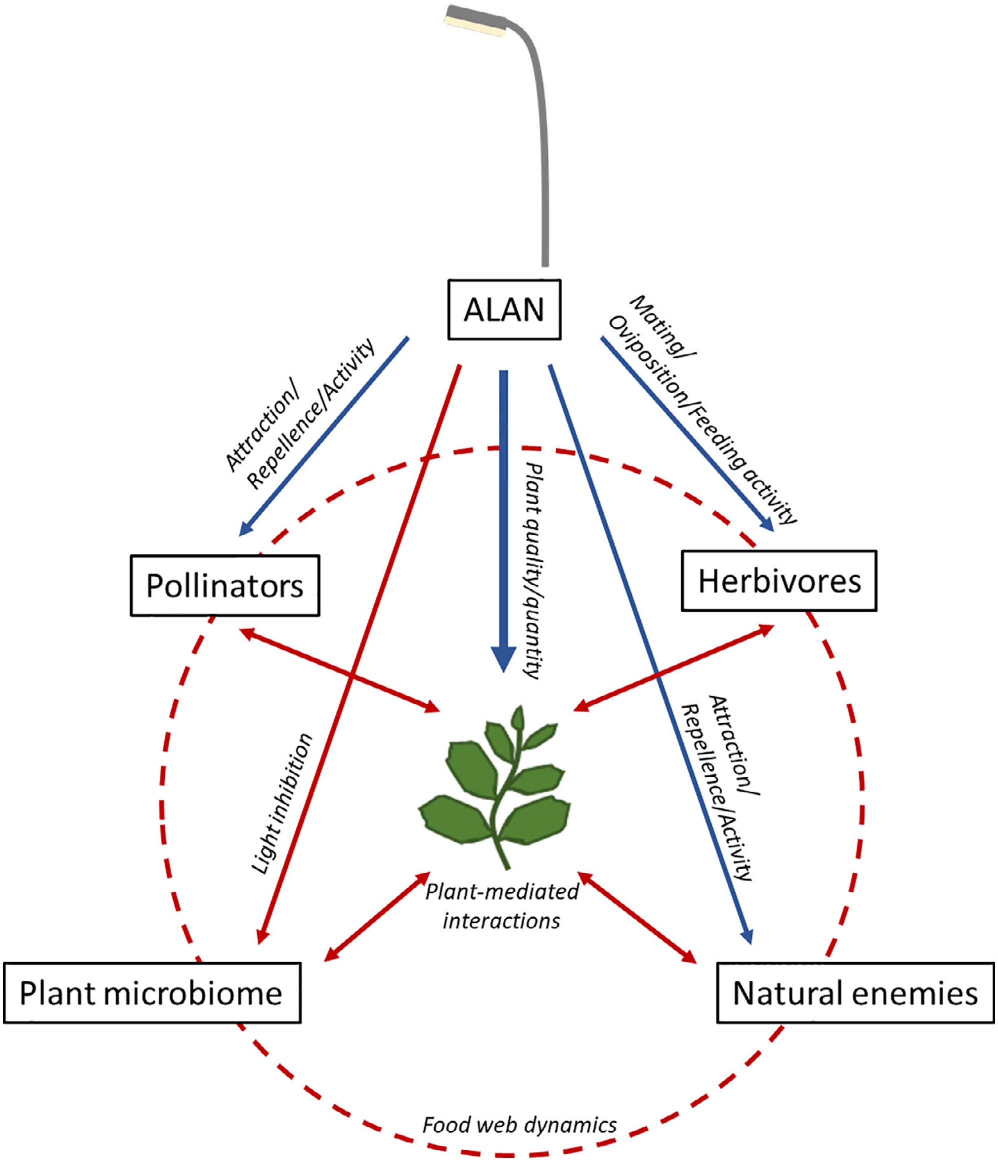

Fig. 1. A simplified conceptual diagram of direct and indirect interactions under ALAN conditions. Solid arrows represent direct interactions between two organisms. Direct effects of ALAN on organisms may lead to alterations between affected organisms and host plants and co-occurring organisms that are present in the phytobiome. Arrows (solid) represent the direct interactions. Indirect interactions or shifts in the phytobiome food web are indicated by the dashed circle. Blue arrows indicate studied interactions, red arrows depict knowledge gaps. Text along the arrows summarizes (potentially) affected processes under ALAN conditions.

beneficial organisms. The combined expression of chemical and structural traits by the different plant parts, determines the composition of the phytobiome. Plant traits, however, are also plastic, and can respond to changes in abiotic conditions such as light status (Ballaré 2014), and biotic interactions with, for instance, mutualists, pathogens or herbivores (Agrawal 1999). Light has been shown to affect various plant traits (Poorter et al., 2019). Many responsive traits are related to leaf area or positioning, but also including rooting patterns, and chemical profiles (Folta & Carvalho 2015). For instance, when plants perceive a reduction in daylight via shading, they are often impaired in their defenses (Ballaré 2014; Ballaré & Austin, 2019). Moreover, providing supplemental light at night (albeit at high density levels), increases plant defenses (Ahn et al. 2015). However, it should be noted that most light studies are performed under high-density light, often in horticultural settings, and under natural or extended light cycles, and that these light conditions thus substantially differ from the light coming from most sources of ALAN. Given that many trait responses are (partly) mediated by photoreceptors, it is quite plausible that ALAN may also alter plant functional traits. However, empirical knowledge on the effect of ALAN on plant functional traits is currently lacking.

Plants produce sugars during the day through photosynthesis, and need to temporarily store this in the form of starch in aboveground tissues. This starch is in turn degraded at night, and transported to the root compartments, where it is stored in longer-term storage reservoirs (Stitt & Zeeman, 2012; Zeeman et al. 2010). These processes are tightly adjusted to optimize energy budgets under changing day length in the growing season (Sulpice et al. 2014). Light receptors play important roles in timing these processes, and ALAN has been shown to decrease nocturnal starch degradation in yellow poplar (*Liriodendron tulipifera*), and decrease starch levels during daytime, eventually leading to carbon starvation stress (Kwak et al. 2017).

ALAN and interactions in the phytobiome

Plants commonly interact with a multitude of antagonists as well as mutualists, above- as well as belowground (Heinen et al. 2018a). In addition, plants also serve as habitats for various organisms that do not directly interact with the plant itself, but that may strongly affect the presence or performance of those organisms that do interact with plant, via top-down forces (Power 1992). Predictability in diurnal light patterns has led to many organisms adapting to specific light conditions in different parts of the day. As a result, many species have become diurnal or nocturnal specialists. ALAN, by illuminating the dark hours, may severely disrupt these established diurnal patterns and hence cause direct effects on organisms of all trophic positions in the phytobiome, including the plants (Fig. 1). As the most fundamental component of the food chain, effects in plants, are likely to affect organisms in higher trophic positions. ALAN may also affect organisms indirectly, either mediated via plant-physiological responses to ALAN, or for instance by attracting or repelling their competitors or predators (Fig. 2A). In the following subsections I discuss how ALAN may have both direct and indirect effects on organisms in the phytobiome.

How does ALAN directly affect organisms in the phytobiome?

Many species in the phytobiome, most notably many insects and other invertebrate species, are strongly adapted to night or day conditions. The elimination of complete darkness may *directly* affect diurnal and nocturnal species, through an altered perception of diurnal patterns, phototaxis, or other forms of disorientation. This can for instance lead to behavioral and physiological responses in various insect species (Owens et al. 2020). Several recent works name ALAN as a significant threat to overall insect biodiversity (Boyes et al. 2020; Grubisic et al. 2018; Harvey et al. 2020; Hakami et al. 2020; Owens et al. 2020), but effects may be highly species-specific. This specificity becomes clear in a recent review by Owens et al. (2020), which discusses the strong but variable effects of ALAN on different insect groups. With regard to interactions occurring in the phytobiome, direct effects on insects can be expected to differ between trophic levels, i.e., between herbivores, predators and (hyper)parasitoids. Species within these groups express different degrees of mobility, which may lead to strong differences in terms of repellence by or attraction to light. Furthermore, the different trophic levels also differ in the degree of association with host plants, which may also lead to a differentiation in responses to ALAN. Below, direct effects of ALAN are discussed for the most important trophic guilds.

Herbivores - There are several mechanisms through which ALAN may affect herbivores directly. First, direct attraction or deterrence by ALAN has been shown as a behavioral response for various species of nocturnal insects with herbivorous larval stages, such as moths (van Geffen et al. 2015; Knop et al. 2017; Somers-Yeates et al. 2013; Fig. 2A). Furthermore, ALAN has been shown to interfere with mating in geometrid moths (van Geffen et al. 2015). Such behavioral responses in adults will determine local adult abundance of the affected species, and consequently may also determine infestation and damage pressure at the landscape level. Potentially, repellant effects on adults may lead to lower oviposition near ALAN sources. In contrast, attractant effects on adults may either lead to a higher oviposition near ALAN sources - or a complete lack of oviposition if the attractant effect is strong enough to keep the individuals at the light source, and away from their oviposition sites. Where an adult insect oviposits matters to

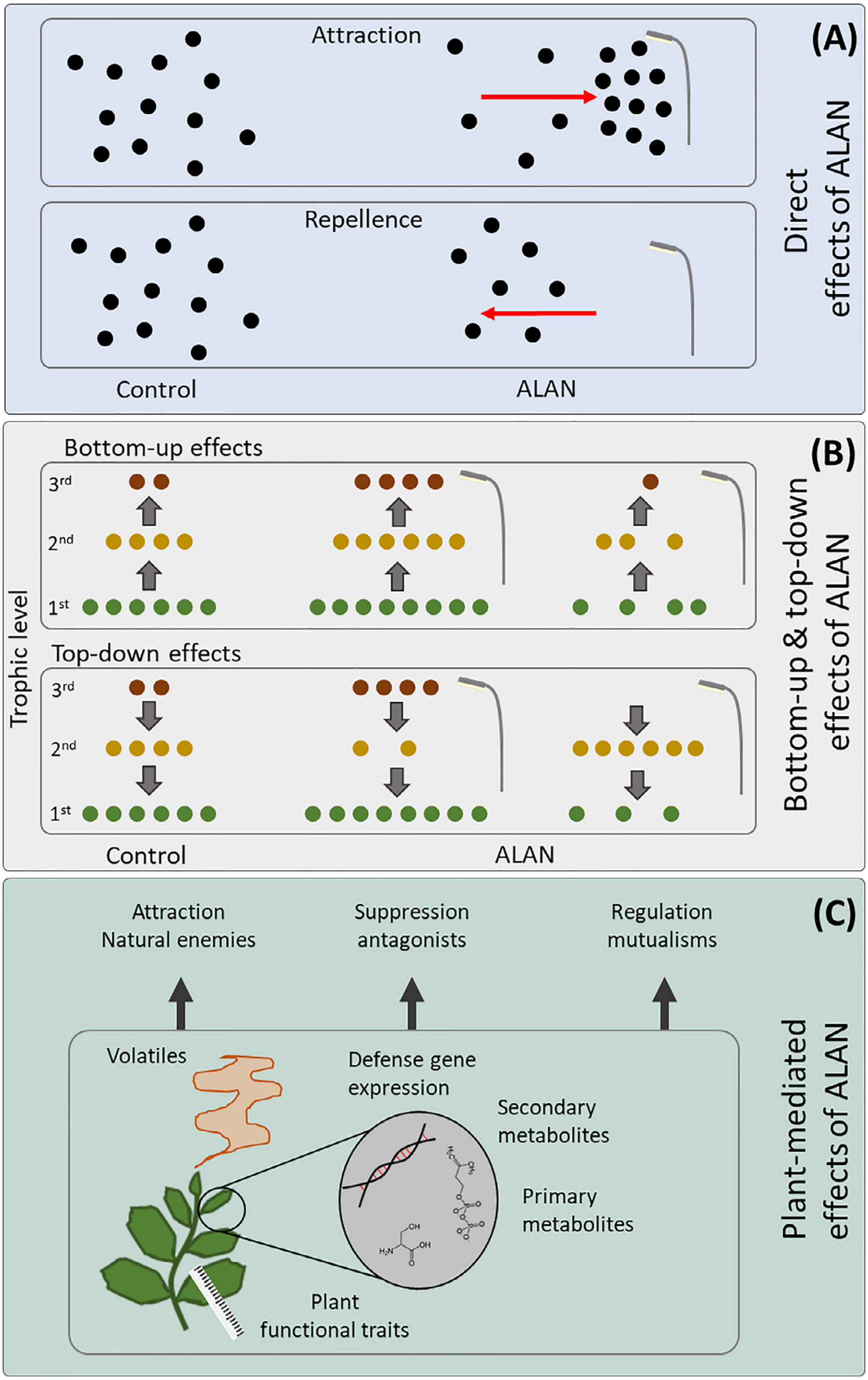

Fig. 2. Graphic representation of pathways through which ALAN may impact interactions in the phytobiome. Panel (A) depicts direct effects of ALAN, i.e., attraction and repellence by light sources, in which dots represent responding species, such as nocturnal pollinators, or ground-dwelling predators. Panel (B) depicts bottom-up and bottom-down effects of ALAN. A simplified food chain is presented for three hypothetical scenarios of how ALAN could alter bottom-up (upper box) and top-down (lower box) processes; under no ALAN conditions (left), under ALAN induced increases (e.g., attraction or increased population size) at the bottom or top end of the food chain (middle), or decreases (e.g., repellence or decreased population size) at the bottom or top end of the food chain (right). Dots represent the proportional number of individuals within the respective trophic level. Panel (C) depicts potential mechanistic plant physiological aspects that may be affected by ALAN, and are key regulators of interactions in the phytobiome.

the next generation, as most insect herbivores stay on or very close to the host plant that they were born on, as moving between plants is energetically costly and potentially dangerous (García-Robledo & Horvitz 2012). Therefore, the attraction or repellence of reproducing adults by ALAN may determine patterns of oviposition and larval occurrence in the landscape.

Second, herbivores often express different feeding behaviors over the course of 24 hours. For instance, several chewing herbivores feed exclusively during the daytime and rest at night, whereas other species are nighttime feeders that hide during the day. ALAN could potentially directly increase active (feeding) times of diurnal herbivores by prolonging the time that is perceived as daytime (Mcmunn et al. 2019). ALAN may reduce the perception of nighttime, which may greatly influence the feeding behavior of nocturnal herbivores. Interestingly, arionid slugs, which are generally nocturnal feeding herbivores, were found to be more abundant under ALAN than in the dark in one study, although how this affected herbivory levels, was not measured (van Grunsven et al. 2018). In another study, slugs did not respond to ALAN (Davies et al. 2012).

Natural enemies - ALAN may also have direct effects on natural enemies of herbivores, such as predators and parasitoids. For instance, positive phototaxis has been described in the literature for several families of the parasitic Hymenoptera (Chen et al. 2012, 2014; Chen et al. 2016; Luo & Chen 2016). Parasitic Hymenoptera are also common 'by-catch' for lepidopterists in nocturnal light traps (R. Heinen pers. obs.), which is another indicator that parasitoids may be attracted to light. One study by Sanders and colleagues (2015) assessed the effects of ALAN on broad bean (*Vicia faba*), three associated aphids (*Megoura viciae, Aphis fabae* and *Acyrthosiphon pisum*) and their parasitoids (*Aphidius megourae, Lisyphlebus fabarum* and *Aphidius ervi*, resp.). Although lower parasitoid abundance was observed in all three pairs, in the *A. fabae* - *L. fabarum* interaction, there were no detectable effects on aphid colony size that could explain the low parasitoid abundance. This may suggest that ALAN can also directly affect parasitism, potentially via a disruption of host search behavior or fecundity (Sanders et al. 2015). However, ALAN may also lead to an increased parasitism rate, as was shown in the *M. viciae* − *A. megourae* interaction in another study, likely through the perception of increased day length by the parasitoid, leading to longer search behavior (Kehoe et. al. 2020). Importantly, the positive effect of ALAN on parasitism gradually diminished with an increasing intensity of the ALAN source (Sanders et al. 2018). This suggests that above a certain light intensity, parasitoids may cease their search behavior, or, more likely, they become more attracted to ALAN.

Other groups of predatory arthropods, including beetles and spiders, have been shown to respond to ALAN as well (Allema et al. 2012; Davies et al. 2012; Manfrin et al. 2017; Mcmunn et al. 2019) although specific taxa show different responses in different studies. For instance, abundance of the mostly nocturnal group of predatory ground beetles may increase (Davies et al. 2012), or decrease (Manfrin et al. 2017), and one study reports that ALAN increased predation by *Pterostichus melanarius*, a common species of predatory ground beetle (Bennie et al. 2018). Higher predator activity may be due to increases in the number of (attracted) weakened or dead prey under ALAN (Eisenbeis et al. 2006; Manfrin et al. 2017). Furthermore, it has been observed in various spider species that they show preferences to build their webs under light (Heiling 1999), may be larger, and catch more prey under ALAN (Gomes 2020), likely also driven by an increased number of prey insects, that are attracted by the ALAN source. In one particular study, ALAN was shown to have a repellant effect on web-building behavior in individuals of *Steatoda triangulosa* spiders from rural populations, but no such effect was observed in urban *S. triangulosa*, suggesting that they may adapt to an illuminated world (Czaczkes et al. 2018).

Importantly, behavioral shifts in predators, caused by attraction or repellence to ALAN, may have strong effects on other trophic levels, such as herbivores or pollinators. The importance of potential 'indirect effects' should not be underestimated and will be discussed further below.

Pollinators - There is substantial evidence that indicates that ALAN can have strong attractive effects on pollinators, such as nocturnal Lepidoptera (van Geffen et al. 2015; van Langevelde et al. 2011). Many important pollinators are nocturnal, and it has been suggested that through light attraction, ALAN may interrupt pollination (Bennie et al. 2016; Macgregor et al. 2015). Pollinator abundance is elevated around streetlights, compared to the same height in unlit areas, but this pattern of abundance is reversed in vegetation (Macgregor et al. 2017). Notably, Knop and colleagues developed pollination networks in lit and dark environments that clearly reveal simpler networks, as well as a significantly lower number of flower visitation, as well as a lower number of developing fruits, in artificially lit environments than in dark environments (Knop et al. 2017). A recent study tested the effect of three different colors of streetlights on pollination in *Silene latifolia*, revealing no effects of light at the flower level, but negative effects, most notably of green light, at the ovule level, indicating that ALAN may affect pollination efficacy, and thus, plant fitness (Boom et al. 2020). It has also been shown that, although pollinators may be more active in lit sites, they are less efficient pollen transporters in lit areas (Macgregor et al. 2017).

How does ALAN indirectly affect organisms in the phytobiome?

'Bottom-up' and 'top-down' multitrophic effects - Several of the direct impacts of ALAN on groups described in the section above can lead to indirect effects on organisms from other trophic levels (illustrated in Fig. 2B). For example,

when ALAN locally suppresses natural enemies, this may lead to a lowered predation pressure, which may benefit herbivore populations. In turn, population increases in herbivores may have strong effects at the level of plants. Although literature on causal bottom-up and top-down relationships in the context of ALAN is scarce, there is some evidence of both from a small number of studies (Bennie et al. 2018; Sanders et al. 2018a; 2018b).

Plant-mediated indirect effects - ALAN-induced responses in plant traits, defenses and nutritional dynamics are all likely to result in changes in the way plants interact with their phytobiome, both locally and systemically, and both above- and belowground (Fig. 2C). Indeed, there is some evidence that aboveground insects can be affected by ALAN through changes in plant quality. For instance, *Acyrthosiphon pisum* had smaller colony sizes on *Lotus pedunculatus*, but only on plants that received amber light, and only in August. During this time, aphids tend to feed on flower heads, which were less abundant in the ALAN-treated plants. Another similar study reported suppressive effects of ALAN on the population sizes of two oligophagous aphid species (*A. pisum* and *Megoura viciae*), but no effects on a polyphagous species (*Aphis fabae*), colonizing *Vicia fabae* (Sanders et al. 2015). Although the literature abounds with studies on the effects of light quality and patterns on plant signaling, these mostly investigate either supplementation with high-density light, or effects of reducing daylight (i.e., shading effects). There are, however, some reports of supplementation with relatively low levels of light at night affecting root-knot densities in tomato plants, caused by the root-knot nematode *Meloidogyne incognita* (Yang et al. 2018; Yang et al. 2015). Notably, red light led to strong suppression and a marked upregulation of salicylic acid and expression of associated genes, suggesting that (red) light can alter plant defenses, leading to altered interactions belowground.

Indirect effects on the soil food web - It seems improbable that ALAN will have strong direct effects on soil food webs, as the soil is rather impermeable to light, and therefore the species within the soil community are unlikely to be directly exposed to light. However, as discussed in previous sections, the local abundances of several soil-dwelling predatory arthropod taxa (Allema et al. 2012; Bennie et al. 2018; Davies et al. 2012; Manfrin et al. 2017), as well as decomposer arthropod taxa (Davies et al. 2012) are directly affected by ALAN. It could therefore be that ALAN-induced shifts in abundance within such taxa may affect soil communities, but these are expected to be most pronounced in the very top layers of the soil, in which these taxa may be involved in interactions. Empirical studies examining how ALAN affects soil communities, either directly or indirectly, are severely lacking.

There is a clear knowledge gap when it comes to the specific effects of ALAN on plant signaling. A literature search on Web of Science and Google Scholar, using different combinations of the search terms “ALAN”, “light pollution”, “plant defenses”, “plant signaling”, and “herbivory”, yielded no relevant results. For the field to progress further, it is vital that ecologists and plant physiologists combine their skill sets to look at the effects of ALAN at the molecular and plant signaling levels, as this will be of great use in understanding its effects on ecological interactions.

How does ALAN affect the plant-associated microbiome?

Another area where knowledge is severely lacking is how ALAN affects the plant-associated microbiome. However, there are clear indications that light conditions can alter phyllosphere composition (Carvalho & Castillo 2018), which suggests that the plant microbiome is responsive to light. A recent study compared phyllosphere microbiomes on greenhouse and field plants grown in fall under artificial long-day regimes using different light types. Light type strongly affected the fungal microbiome, whereas bacterial microbiomes were unaffected (Alsanius et al. 2017), which suggests that different components of the microbiome may be differently affected. Furthermore, it has been shown that rhizosphere composition, and more importantly the activity of the rhizosphere microbiome, changes significantly from pre- to post-dawn circumstances, suggesting that the belowground microbiome can be affected through plant responses to light (Baraniya et al. 2018). Future work is needed to indicate whether and how ALAN may affect interactions between plants and microbes in the phyllo- and rhizosphere.

Discussion

The past decades have seen a strong surge in research on the effects of artificial light at night on a broad range of taxa. Surprisingly, the effects of ALAN on plants have been relatively little studied (as already indicated by Briggs in 2006 and again by Bennie and colleagues 2016, ten years later), and the effects of some forms on plants (particularly skyglow) have not been studied at all (but see Solano-Lamphar & Kocifaj 2018). Although it is quite clear that plant traits related to growth and defense, as well as starch dynamics in plants can be affected by light quality, virtually nothing is known about how the typical characteristics of ALAN − light of a generally low density - and occurring at night when plants naturally would experience darkness − will affect plant quality. It is likely that ALAN will affect plant quality and plant signaling and that this will affect plant-mediated interactions. Indeed, effects of ALAN on plant-insect interactions have been shown in a small handful of studies, mostly coming from the same research group. These studies have predominantly investigated piercing-sucking insects and it remains to be investigated how other herbivorous insects, such as chewers, leaf miners or galling insects are affected by ALAN. Other invertebrates, such as slugs have been shown to be affected by ALAN

(Grunsven et al. 2018). Although slugs are dominant herbivores in many ecosystems, how their response to ALAN translates to levels of herbivory is not well-understood. How ALAN impacts on microbes, either on or in the plant, above- or belowground, is not known. The role of the plant-associated microbiome in plant growth and its resulting impact on herbivores has received a lot of attention in the past few years (Hannula et al. 2021; Hannula et al. 2019; Heinen et al. 2018a; Heinen et al. 2018b), and understanding the functional implications of ALAN in the plant-associated microbiome will be an important avenue for future studies.

Several studies have investigated direct impacts of ALAN on non-herbivorous organisms associated with plants, such as ground-dwelling predators and nocturnal pollinators. It is evident that ALAN has the potential to disrupt plant-associated food webs, for instance via attraction or repellence that result in shifts in predator abundance (Bennie, Davies, Cruse, Inger, & Gaston, 2018; Davies, Bennie, & Gaston, 2012b). Such shifts at the top end of the food chain may have strong consequences for lower trophic levels (Fig. 2B). How shifts in phytobiome food webs alter plant growth and fitness is little understood. Although earlier studies reported effects of ALAN on pollinator abundance, it has only relatively recently been shown that these effects translate into effects on plant fitness (Macgregor et al. 2017; Boom et al. 2020). Longer-term studies are needed to assess how ALAN may affect plant growth and fitness, and how this will affect dispersal and plant community dynamics.

A recurring observation is that for many phytobiome-associated taxa the number of ALAN studies is very low, if there are any at all. This is a critical observation, as it makes it very difficult to assess whether there are any consistent patterns of ALAN-induced effects in the existing data, either through systematic literature review, or through meta-analysis (Sanders et al. 2021). In fact, from the existing data, it is often very hard to distinguish direct from indirect effects of ALAN on organisms. Literature is often limited to describing observations from studies, but to date provide little insight into the mechanisms behind them. Does an interaction between a plant and an herbivore change because of a change in behavior in the insect, or because of some physiological change in the plant, or both? We can often not be completely sure. To fully understand the breadth of effects of ALAN on plants and the phytobiome, ecologists should literally put a spotlight on plants and plant-mediated interactions. I have no doubt that ALAN has a much deeper impact on plant-mediated systems than we are currently aware of, and mechanistic insight into how ALAN impacts plant-mediated interactions is urgently needed.

The research conducted over the past two decades shows that ALAN has strong (and often detrimental) effects on many taxa. Nonetheless, the actions taken to mitigate the effects of light pollution is thus far limited (but see for instance The International Darksky Association, www.darksky.org). Light pollution is steadily increasing and is expected to keep doing so in the years to come. Unlike what is true for most other forms of pollution, the solution to the problem of light pollution is literally as simple as flipping a switch. Obviously, flipping the switch is often easier said than done. Lights are often installed for good reasons, including security and safety. Arguably, not all streetlights need to be present, and some be dimmed to lower levels or attached to motion sensors. A critical look at lightscapes could potentially reduce some of the negative impacts of ALAN on natural ecosystems in existing lit areas and minimize impacts in lit areas of the future (Spoelstra et al. 2015). Minimizing ecological light pollution should be integral in the way we design current and future urban and rural areas. As an example, Animal-Aided Design (Hauck & Weisser 2015) is aimed at making animals an integral part of building and landscape planning, so that the impacts of urbanization on wild animals may be reduced. In a similar fashion, we may design and optimize urban green spaces (including gardens, parks and road verges) in such a way that light pollution is minimized, whilst the feeling of security and safety for human users is maintained. To optimize lightscapes and mitigate their ecological impacts, it is vital that landscape and town planners, engineers, and ecologists work together in the future.

It is somewhat surprising to see how little (manipulative) research exists on the effects of ALAN on plants, plant physiology and plant-mediated interactions. Plant ecology and plant physiology are two enormous scientific disciplines. Why have the two fields hardly ever connected to study ALAN? Manipulative ALAN research can seem challenging for various reasons, including temporal and spatial aspects. It is difficult to maintain ALAN treatments and control treatments in the same space, as light will disturb dark controls. In fact, it is difficult to keep control treatments dark, especially in research greenhouse facilities, which are characterized by lots of light (and are also a typical source of light pollution). Multi-chamber climate room experiments can facilitate ALAN experiments. However, typically climate chamber light conditions do not operate within the ranges typical for ALAN (e.g., streetlights of 5-30 lux). External light fixtures can solve this relatively easily with dimmable (especially LED) light in all segments of the light spectrum being cheap and easily available. An additional experimental challenge arises with sampling of plant material (especially in the dark control treatments), but adequate preparation in the daytime and straight-forward sampling designs for the nighttime can make nocturnal sampling and the associated plant disruption very minimal. Just like in any research, most of the difficulties in ALAN plant phytobiome research can be overcome (R. Heinen, pers. obs.).

In summary, there has been a recent surge in scientific literature regarding the effects of ALAN on natural ecosystems, but plants are remarkably ‘underlit’. Most of the studies to date indicate effects of ALAN on phenological processes, such as flowering and bud burst (discussed in Briggs 2006; Bennie et al. 2016). However, a few recent studies, most of which are from one research group, also reveal how ALAN can influence bottom-up and top-down interactions in a multitrophic context. Furthermore, pollination can be severely disrupted by ALAN. Importantly, virtually nothing is known how light with the characteristics of ALAN (i.e., low intensity and occurring at night) affects plant physiology at transcriptomic or metabolomic level, and how this affects organisms in the phytobiome, such as microbes, herbivores and their enemies, or pollinators. It is about time that ecologists place a ‘spotlight’ on ecological effects of ALAN on plant-mediated interactions to get a full understanding of the ecological impacts, and understand mechanisms to be able to mitigate future impact.

Declaration of Competing Interest

There are no conflicts of interest related to this manuscript.

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