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# Let there be light to interact

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Light plays a crucial role in ecological dynamics, both as a consumable resource and as an environmental factor. Prokaryotic and eukaryotic photoautotrophs use light as an energy source for photosynthesis, which forms the basis of food chains and determines the flow of energy and matter in ecosystems. Light availability and quality can influence resource complementarity and species coexistence, as well as the stoichiometry of primary producers and the transfer efficiency of food webs. In addition, light serves as an important source of information for organisms, influencing their activities and interactions with the environment. Light shapes biotic interactions, including competition, predator-prey relationships, and mutualistic and antagonistic relationships between photoautotrophs and heterotrophs. Anthropogenic activities affect these photoecological processes, with largely unknown consequences. Hence, understanding the ecological role and control of light is essential for understanding the functioning of ecosystems and biogeochemical cycles.

## KEYWORDS

light, ecological niche, ecological stoichiometry, light induced behavior, light cycles, light pollution

## Introduction

While photosynthesis was not an initial metabolic pathway of early life on Earth and light is not a prerequisite for life *per se* (Shih, 2015; Ralser et al., 2021), the perception of light is already a vital trait of a vast number of prokaryotes (Williams, 2016). It is necessary for the evolution of pathways to obtain energy for metabolic processes from light. As either a consumable resource and/or an environmental factor structuring life, light is part of the ecological (Hutchinsonian) niche (Hutchinson, 1978) of most species on Earth. Niche requirements for resources and environmental factors shape the interactions of organisms with their environment and thus ecological dynamics and biogeochemical cycles. Consequently, light is one of the key drivers of such processes (Figure 1): light as a resource underlies the global ecological and biogeochemical consequences of carbon fixation by photoautotrophs since the invention of photosynthesis (Ozaki et al., 2018). Moreover, light as an environmental factor can trigger the behaviour of organisms on a global scale, such as the diel vertical migration (DVM) of marine zooplankton moving between the surface and deeper water layers (Bandara et al., 2021).

## Light affecting ecological dynamics as a consumable resource for photoautotrophs

Prokaryotic and eukaryotic photoautotrophs use light as an energy source to split molecules, most commonly H<sub>2</sub>O, to obtain electrons to reduce carbon dioxide to organic molecules (Messinger and Shevela, 2011). These processes are typically at the base of so-called food chains or food webs - man-made maps of interactions between organisms - that determine the flow of energy and matter to higher trophic levels (May, 1974; Pimm et al.,

1991). In a broader sense, the ecology of food webs is therefore largely influenced by being driven by photo-ecological processes. Even the voracious energy demands of modern human populations are largely met by light-driven biotic processes. Fossil fuels such as petroleum are largely the result of photosynthetically produced organic biomolecules that are one hundred or more million years old (Ourisson et al., 1984) and which have not yet been recycled back to carbon dioxide.

Consumable resources are necessary for the survival, growth and reproduction of individuals. Consumption of a resource by one individual precludes its availability to another individual, leading to intra- and interspecific competition for resources and evolutionary adaptations (Begon et al., 2006). As a resource, light can be considered both quantitatively (high light, low light) and qualitatively (bundles of different wavelengths). This holds true especially in aquatic environments. Phytoplankton moving up and down the water column experience a much greater variation in background colour than land-based plants. As a result, differential sensitivity to different wavelengths has evolved (Stomp et al., 2007a; Kehoe, 2010; Falkowski and Raven, 2013).

Photosynthetic active radiation (PAR) consists of wavelengths from approximately 400–700 nm (McCree, 1972) and the selective use of certain wavelengths within the resource bundle by phytoplankton can allow resource complementation and hence species coexistence (Stomp et al., 2007b). In addition, resource complementarity may also be a mechanism underlying relationships between biodiversity and ecosystem functioning, such as higher resource use efficiency of highly diverse phytoplankton communities that use the PAR spectrum more efficiently (Striebel et al., 2009).

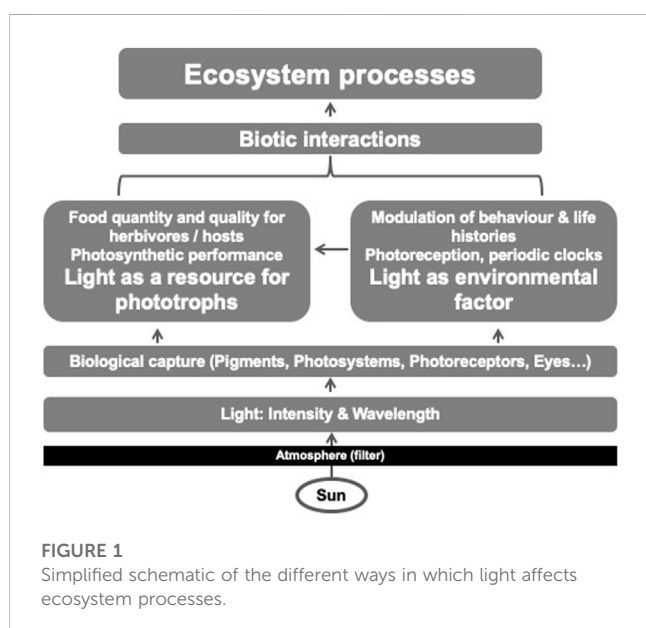
Too much of the resource light can have detrimental effects, while too little does not allow for a positive net energy balance through photosynthesis. Therefore, a variety of responses are known to optimise light use related traits (Poorter et al., 2019). In addition to such ecophysiological processes at the individual level, there are also food web effects of varying light levels. Light can affect the

stoichiometry of primary producers, mainly their carbon to nutrient ratio (Elser et al., 2000). This can theoretically lead to the so-called “energy enrichment paradox”, where an increase in light resources can have a negative effect on the transfer efficiency of the food web, as described for plankton food webs (Diehl, 2007). The mechanistic basis of this paradox is that an increase in light, and hence photosynthesis, can lead to an increase in the carbon to nutrient ratio of phytoplankton biomass (Dickmann et al., 2006), which affects food quality for higher trophic levels (Urabe et al., 2002). Higher trophic levels may experience a shift from carbon to nutrient limitation. Such a shift can result in lower production at higher trophic levels despite an enrichment of resources (more light) at the base of the food web (Urabe and Sterner, 1996).

In addition to the energy enrichment paradox mentioned above, light-driven shifts in the biomass stoichiometry of flexible primary producers can have a variety of other implications for ecological dynamics on land and underwater (Güsewell, 2004; Elser et al., 2010). Spatial and temporal light distribution and environmental light-nutrient ratios also influence terrestrial vegetation successional patterns, driving vegetation structure and biodiversity along successional dynamics (Tilman, 1985; Matsuo et al., 2021). Early successional communities are often characterized by thriving at high light to nutrient ratios, whereas the opposite is true for late successional species. Such light-dependent dynamics have far-reaching consequences, as the composition and hence functional characteristics of vegetation determine to some extent the functional and species composition of higher trophic levels (Russo et al., 2023).

Light as a resource shapes biotic interaction between photoautotrophs (mainly through competition) and between photoautotrophs and heterotrophs, either in the form of predator-prey relationships (e.g., by affecting the quantity and quality of food for herbivores as described above) or in complex mutualistic and antagonistic relationships. Examples of mutualistic relationships include spatially intimate phototroph-bacteria (Cirri and Pohnert, 2019), phototroph-ciliate (Dziallas et al., 2012), phototroph-fungi (Ahmadjian, 1993) or phototroph-animal relationships (Venn et al., 2008), where partners provide resources to each other in both directions. For example, algae can provide photosynthetic products in the form of dissolved organic carbon sources to associated bacteria, which in turn provide essential nutrients to the algae, such as fixed nitrogen or vitamin B12 (Croft et al., 2005; Thompson et al., 2012). The importance of the photosynthetic processes of coral-associated dinoflagellates for tropical reefs and their impact on biogeochemical cycles is undisputed and well documented (Roth, 2014; van Oppen and Medina, 2020). Light as a resource can also strongly regulate the important symbiotic nitrogen fixation of endosymbiotic bacteria of terrestrial plants (Taylor and Menge, 2018; Ottinger et al., 2023), with far-reaching consequences for food web processes and biogeochemical cycles. Resource availability can influence such mutualistic interactions (Hom and Murray, 2014), which are often better characterised by functioning along a mutualistic-antagonistic transition gradient (Sachs and Wilcox, 2006; Drew et al., 2021).

Combinations of phototrophic and heterotrophic nutritional pathways are not restricted to combinations of different phototrophic and heterotrophic species forming a holobiont. Both pathways can also occur within a single species, for



example, carnivorous plants obtaining additional nutrients by feeding on animals (Těšitel et al., 2018), or algae combining photosynthesis with heterotrophic pathways, either by using organic carbon sources in addition to CO<sub>2</sub>, either dissolved or specific (Flynn et al., 2013). In addition, heterotrophic feeding can also serve as a source of nutrients from particulate matter. Aquatic environments are mostly light-limited and highly nutrient-depleted. As a result, a large number of marine and freshwater phytoplankton species are so-called mixotrophic species, operating along a gradient from predominantly autotrophic to predominantly heterotrophic (Flynn et al., 2013; Stoecker et al., 2017). Light as a resource can influence the proportion that each of the two pathways contributes to the overall carbon budget (Ptacnik et al., 2016). Assuming that approximately 50% of global carbon fixation in aquatic environments is by phytoplankton (Field et al., 1998), it is clearly important to understand the ecological role and control of mixotrophic nutrition (Mitra et al., 2014). In addition to large-scale carbon cycling, the abundance of mixotrophs within phytoplankton and their individual level of mixotrophy can also influence biomass stoichiometry and food quality, and thus transfer efficiencies within aquatic food webs (Katechakis et al., 2005; Vad et al., 2020).

## Light as an environmental factor shaping biotic interactions

Light can be converted into thermal energy and is an important source of heat for poikilotherms, which depend on external heat supply to determine their activities and thus their interactions with their biotic and abiotic environment. A large number of poikilothermic organisms have evolved mechanisms to efficiently absorb light, such as specific colouration (Clusella-Trullas et al., 2007), which is often flexible in response to temperature (Zhang et al., 2020). Absorbed light can also be re-emitted at longer wavelengths by a living organism, a common phenomenon known as biofluorescence, which is known from aquatic and terrestrial habitats (Lamb and Davis, 2020). Potential functions of biofluorescence include processes such as communication (Marshall and Johnsen, 2017) or sexual selection (Hausmann et al., 2003), which affect biotic interactions. Blue light-induced fluorescence of phytoplankton chlorophyll can convey information about population density at the microscale level and regulate resource uptake (iron) in diatoms (Liu et al., 2021).

Most obviously, however, light contains rich and complex information that is very useful for exploring the environment through photosensitive morphological structures (photosensing), allowing a more or less complex picture of the visual environment to be formed and enables appropriate responses to it (photoregulation, Nilsson et al., 2022). These processes allow ecological interactions such as the identification and evaluation of other organisms for intra- or interspecific interactions such as interference competition, sexual reproduction, determining suitable prey, escaping predators, shaping predator behaviour, synchronising the timing of reproduction, etc. A famous example of such a light-induced behavioural process operating on a large scale is the Diel Vertical Migration (DVM). It is the world's largest synchronised movement of organisms (plankton) and occurs in the open water (pelagial) of marine and freshwater systems (Bandara

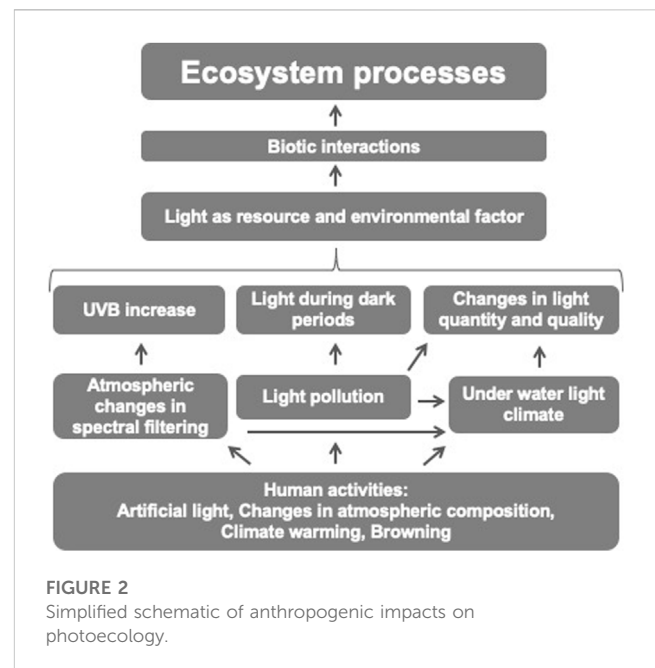


FIGURE 2  
Simplified schematic of anthropogenic impacts on photoecology.

et al., 2021). Organisms such as zooplankton migrate into deep and therefore dark water layers during the day and return to surface waters at night. Light is either an ultimate or proximate factor controlling DVM. It can act as a proxy for a dangerous environment where visual predators such as large numbers of fish are active, resulting in a high mortality risk for their food, the zooplankton. Light can also act as an ultimate cause of DVM, such as in high altitude lakes where high UV levels in the upper water layers force zooplankton to perform a diel vertical migration to escape the risk of UV damage (Rhode et al., 2001). Light and light-driven cycles control the behaviour and activity patterns of a wide range of organisms, with major consequences for the dynamics of biotic interactions such as predation or competition. Such light-driven processes can operate even during the polar night (Berge et al., 2020), modulated by lunar and auroral components at very low light levels (Cohen et al., 2021). At the base of aquatic and terrestrial food webs, photosynthetic dynamics (such as photosynthetic light absorption) are regulated by photosensing required to detect light direction or diurnal/seasonal irradiance cycles, such that light as an environmental factor regulates the uptake of the resource light (Haeder et al., 2009; Forbes-Stovall et al., 2014; Jaubert et al., 2017; Schuback and Tortell, 2019). In an antagonistic bacteria-algae relationship, bacteria can destroy the primitive visual system of the green alga *Chlamydomonas*, preventing phototactic behaviour important for resource uptake (Hotter et al., 2021). Prokaryotes can also link light perception to control of motility use, thereby optimising light use efficiency for photosynthesis (Wilde and Mullineaux, 2017). For example, in non-phototrophic prokaryotes, light can regulate virulence (Bonomi et al., 2016) and thus interactions with their host organisms, which affect population and food web dynamics.

In environments lacking sufficient sunlight for visual orientation, such as the deep sea or nocturnal habitats, a large number of dark-active organisms have evolved the ability to actively produce light, known as bioluminescence (Widder, 1999; Haddock

et al., 2010). Such biogenic light production can be used to attract prey, mates for reproduction, intraspecific synchronisation or to confuse predators (Widder, 2010; Ellis and Oakley, 2016; Verdes and Gruber, 2017; Wainwright and Longo, 2017). Bioluminescence is far from being an exotic phenomenon, as shown by a study that examined a marine water column from the surface to the deep sea, where bioluminescence was observed in a large number of organisms across a large variety of phylogenetic groups. Bioluminescence is considered to be a common and important ecological trait in the dark (Martini and Haddock, 2017).

## Anthropogenic impacts on photoecology

In addition to the large diversity of organisms mentioned above that are able to produce their own light to attract mates or prey, or to confuse predators, humans have also developed increasingly complex cultural skills to produce light. This has allowed humans to become independent of natural day-night cycles and to extend activities that rely on vision to 24 h a day. However, the use of artificial light sources has not only allowed humans to extend vision and related activities to any time of day in any place on Earth; it is also visible to other organisms, both mobile and sessile, disrupting their natural light cycles (Rodrigues-Comino et al., 2023). Darkness, usually defined as light below a critical and individual-specific threshold, can play a similarly important role for ecological traits (feeding, reproduction) as light itself (Gerrish et al., 2009). These disturbances of the dark period can affect a wide range of ecological processes (Gaston et al., 2013; Sanders et al., 2021) (Figure 2). Light pollution can have far-reaching indirect effects on wildlife through its interactions with other environmental factors (Bennie et al., 2016). For example, artificial light at night (ALAN) can attract insects, disrupting their natural behaviour and leading to changes in insect populations. This in turn can affect the foraging behaviour of insectivorous birds and bats, leading to potential declines in their populations (Longcore and Rich, 2004). Similar far reaching impact can be seen in aquatic primary producer systems, where ALAN decreases biomass and alters community composition (Grubisic et al., 2017). Such processes affect biodiversity and associated ecosystem services (Hölker et al., 2021).

Human activities not only increase the spatial and temporal availability of light, disrupting a wide range of ecological processes, but also cause shifts in atmospheric chemistry. These shifts affect the atmospheric filtering of electromagnetic radiation from the Sun and thus the spectral composition of light at the Earth's surface (Figure 2). A well-known example is the anthropogenic depletion of atmospheric ozone, which can result in a lower retention efficiency of the atmosphere for ultraviolet radiation (UVB) and hence higher levels of UVB reaching the Earth's surface (Solomon, 1999). UVB radiation is known to have adverse effects on terrestrial (Caldwell et al., 1998) and aquatic organisms (Bancroft et al., 2007), with important implications for population and community dynamics and far-reaching consequences for ecosystems (Mostajir et al., 2000). Although the Montreal Protocol (1987) regulating the production and consumption of ozone depleting

substances has led to an improvement of the ozone layer (Barnes et al., 2021), global climate change may cause it to deteriorate again. For example, aerosols originating from increasing wildfires have the potential to negatively impact the ozone layer (Solomon et al., 2023). In addition smoke from wildfires can result in direct changes of light quantity and light quality, for example, smoke selectively absorbs UV radiation, which can for example, have consequences for DVM in lakes (Williamson et al., 2016).

However, beside human-induced shifts in atmospheric composition, human-induced shifts in the spectral composition of underwater light also affect ecological dynamics (Figure 2). Increased transport of terrestrial carbon into aquatic systems due to global change leads to browning of water, resulting in shifts in light quantity and quality (Blanchet et al., 2022). As a result, browning can alter phytoplankton dynamics in terms of production and community composition, with far-reaching consequences for higher trophic levels (Soulié et al., 2022).

Furthermore, global change is affecting stratification and mixing of water columns. There is no clear direction of this shifts on a global scale. Warming of surface waters due to global change can lead to earlier and stronger stratification of water columns, characterised by decreasing mixing depths of upper water layers (Woolway et al., 2021; Sugimoto, 2022). In temperate seasonal regions, stratification in lakes also starts earlier, which can lead to earlier development of phytoplankton blooms in spring (Peeters et al., 2007), potentially leading to so-called match-mismatch scenarios between phototrophs and their herbivore consumers, where the timing of food availability to consumers is no longer synchronized with their seasonal dynamics (Winder and Schindler, 2004). However, climate change can also result in wind driven intensification of upper-ocean turbulence (Young and Ribal, 2019; Li et al., 2020; Sallee et al., 2021). Independent in which direction stratification and mixing depth shifts, phytoplankton suspended in the mixed layer of oceans and lakes thereby experience changes in both light quantity and quality. For example, a decrease in mixing depth results in a higher proportion of red light within the available PAR in the mixed layer, favoring cyanobacteria. Such shifts can potentially disrupt food web transfers to higher trophic levels due to the potential toxicity or poor food quality of large numbers of cyanobacteria (Stockenreiter et al., 2021).

Another aspect of global change that affects light properties for ecological dynamics is shorter ice seasons in temperate and polar regions, which shifts light availability for ecosystems, potentially leading to earlier and longer growing seasons for phototrophs, with the potential for light-driven tipping points. For example, earlier ice loss in polar regions is likely to cause extensive regime shifts, with endemic shallow-water invertebrate communities being replaced by algae, reducing coastal biodiversity and fundamentally altering ecosystem functioning (Clark et al., 2013).

## Conclusion

In summary, the few selected examples described above, illustrate just how many ways light shapes the interaction between organisms and their environment; from being a resource for metabolism that influences growth, life history,



and population and community dynamics, to being an environmental factor necessary to create a visual environment, or acting as a cue to structure daily and seasonal routines (Figure 1). Common to all is that light influences interactions between individuals and their biotic and abiotic environment, and thus ecological dynamics and biogeochemical cycles. Directed and undirected human-induced changes in light dynamics, as part of recent global changes, therefore affect a wide range of ecological processes (Figure 2). Modern tools in the toolbox of ecologists and environmental biologists allow the study of such processes at unprecedented resolution, providing mechanistic insights through, for example, new molecular approaches and increased causality through modern experimental capabilities. Thus, photoecology and environmental photobiology (Haeder, 2004) are core research areas that contribute to the mechanistic understanding and conservation of the unique dynamics of life on Earth.

## Author contributions

HS: Conceptualization, Writing—original draft, Writing—review and editing. MS: Conceptualization, Visualization, Writing—review and editing.

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