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### Theme issue

### 'Light pollution in complex ecological systems'

compiled and edited by Myriam R. Hirt, Darren M. Evans, Colleen R. Miller and Remo Ryser

Light pollution, or excessive artificial light in our environment, is increasingly recognised as a major driver of environmental change and a growing topic of concern. Research has shown that different species react in unique ways to artificial light at night, making predictions about how these effects play out in entire communities of species difficult to determine. Understanding and reducing the negative effects of light pollution on our ecosystems is pressing work, especially as the world continues to change. This collection of studies aims to dive deeper into how light pollution affects the natural environment. Here, papers investigate light pollution ecology at various environments and scales, from single processes to whole communities, to better understand the relationship between light pollution, ecological balance, and human influence. The ultimate goal is to gain insights to help maintain a balanced ecosystem in our ever-brightening world.

# Artificial light at night: a global disruptor of the night-time environment

Salvador Barát and Fabio Falchi

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#### Abstract

Light pollution is the alteration of the natural levels of darkness by an increased concentration of light particles in the night-time environment, resulting from human activity. Light pollution is profoundly changing the night-time environmental conditions across wide areas of the planet, and is a relevant stressor whose effects on life are being unveiled by a compelling body of research. In this paper, we briefly review the basic aspects of artificial light at night as a pollutant, describing its character, magnitude and extent, its worldwide distribution, its temporal and spectral change trends, as well as its dependence on current light production technologies and prevailing social uses of light. It is shown that the overall effects of light pollution are not restricted to local disturbances, but give rise to a global, multiscale disruption of the night-time environment.

# Impacts of artificial light at night on the early life history of two ecosystem engineers

Svenja Tidau, Fraser T. Brough, Luis Gimenez, Stuart R. Jenkins, Thomas W. Davies

### Abstract

Sessile marine invertebrates play a vital role as ecosystem engineers and in benthic-pelagic coupling. Most benthic fauna develop through larval stages and the importance of natural light cycles for larval biology and ecology is long-established. Natural light-dark cycles regulate two of the largest ocean-scale processes that are fundamental to larvae's life cycle: the timing of broadcast spawning for successful fertilization and diel vertical migration for foraging and predator avoidance. Given the reliance on light and the ecological role of larvae, surprisingly little is known about the impacts of artificial light at night (ALAN) on the early life history of habitat-forming species. We quantified ALAN impacts on larval performance (survival, growth, development) of two cosmopolitan ecosystem engineers in temperate marine ecosystems, the mussel Mytilus edulis and the barnacle Austrominius modestus. Higher ALAN irradiance reduced survival in both species (57% and 13%, respectively). ALAN effects on development and growth were small overall, and different between species, time-points and parentage. Our results show that ALAN adversely affects larval survival and reiterates the importance of paternal influence on offspring performance. ALAN impacts on the early life stages of ecosystem engineering species have implications not only for population viability but also the ecological communities that these species support.

# Artificial light at night (ALAN) causes shifts in soil communities and functions

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Abstract

Artificial light at night (ALAN) is increasing worldwide, but its effects on the soil system have not yet been investigated. We tested the influence of experimental manipulation of ALAN on two taxa of soil communities (microorganisms and soil nematodes) and three aspects of soil functioning (soil basal respiration, soil microbial biomass and carbon use efficiency) over four and a half months in a highly controlled Ecotron facility. We show that during peak plant biomass, increasing ALAN reduced plant biomass and was also associated with decreased soil water content. This further reduced soil respiration under high ALAN at peak plant biomass, but microbial communities maintained stable biomass across different levels of ALAN and times, demonstrating higher microbial carbon use efficiency under high ALAN. While ALAN did not affect microbial community structure, the abundance of plant-feeding nematodes increased and there was homogenization of nematode communities under higher levels of ALAN, indicating that soil communities may be more vulnerable to additional disturbances at high ALAN. In summary, the effects of ALAN reach into the soil system by altering soil communities and ecosystem functions, and these effects are mediated by changes in plant productivity and soil water content at peak plant biomass.

# Artificial light at night decreases plant diversity and performance in experimental grassland communities

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### Abstract

Artificial light at night (ALAN) affects many areas of the world and is increasing globally. To date, there has been limited and inconsistent evidence regarding the consequences of ALAN for plant communities, as well as for the fitness of their constituent species. ALAN could be beneficial for plants as they need light as energy source, but they also need darkness for regeneration and growth. We created model communities composed of 16 plant species sown, exposed to a gradient of ALAN ranging from 'moonlight only' to conditions like situations typically found directly underneath a streetlamp. We measured plant community composition and its production (biomass), as well as functional traits of three plant species from different functional groups (grasses, herbs, legumes) in two separate harvests. We found that biomass was reduced by 33% in the highest ALAN treatment compared to the control, Shannon diversity decreased by 43% and evenness by 34% in the first harvest. Some species failed to establish in the second harvest. Specific leaf area, leaf dry matter content and leaf hairiness responded to ALAN. These responses suggest that plant communities will be sensitive to increasing ALAN, and they flag a need for plant conservation activities that consider impending ALAN scenarios.

# Insect communities under skyglow: diffuse night-time illuminance induces spatio-temporal shifts in movement and predation

Alexander Dyer, Remo Ryser, Ulrich Brose, Angelos Amyntas, Nora Bodnar, Thomas Boy, Solveig Franziska Bucher, Simone Cesarz, Nico Eisenhauer, Alban Gebler, Jes Hines, Christopher C. M. Kyba, Myles H. M. Menz

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#### Abstract

Artificial light at night (ALAN) is predicted to have far-reaching consequences for natural ecosystems given its influence on organismal physiology and behaviour, species interactions and community composition. Movement and predation are fundamental ecological processes that are of critical importance to ecosystem functioning. The natural movements and foraging behaviours of nocturnal invertebrates may be particularly sensitive to the presence of ALAN. However, we still lack evidence of how these processes respond to ALAN within a community context. We assembled insect communities to quantify their movement activity and predation rates during simulated Moon cycles across a gradient of diffuse night-time illuminance including the full range of observed skyglow intensities. Using radio frequency identification, we tracked the movements of insects within a fragmented grassland Ecotron experiment. We additionally quantified predation rates using prey dummies. Our results reveal that even low-intensity skyglow causes a temporal shift in movement activity from day to night, and a spatial shift towards open habitats at night. Changes in movement activity are associated with indirect shifts in predation rates. Spatio-temporal shifts in movement and predation have important implications for ecological networks and

ecosystem functioning, highlighting the disruptive potential of ALAN for global biodiversity and the provision of ecosystem services.

### Part-night exposure to artificial light at night has more detrimental effects on aphid colonies than fully lit nights

Robin Heinen, Oriana Sanchez-Mahecha, T. Martijn Bezemer, Davide M. Dominoni, Claudia Knappe, Johannes Kollmann, Anton Kopatsch, Zoë A. Pfeiffer, Michael Schloter, Sarah Sturm, Jörg-Peter Schnitzler, A. Corina Vlot and Wolfgang W. Weisser

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#### Abstract

Artificial light at night (ALAN) threatens natural ecosystems globally. While ALAN research is increasing, little is known about how ALAN affects plants and interactions with other organisms. We explored the effects of ALAN on plant defence and plant–insect interactions using barley (*Hordeum vulgare*) and the English grain aphid (*Sitobion avenae*). Plants were exposed to 'full' or 'part' nights of 15–20 lux ALAN, or no ALAN 'control' nights, to test the effects of ALAN on plant growth and defence. Although plant growth was only minimally affected by ALAN, aphid colony growth and aphid maturation were reduced significantly by ALAN treatments. Importantly, we found strong differences between full-night and part-night ALAN treatments. Contrary to our expectations, part ALAN had stronger negative effects of ALAN on plant defences are indirect, and regulated via direct disruption of aphid colonies rather than via ALAN-induced upregulation of defences. Mitigating ecological side effects of ALAN on plant defences.

### Nearby night lighting, rather than sky glow, is associated with habitat selection by a top predator in human-dominated landscapes

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#### Abstract

Artificial light at night (ALAN) is increasing in extent and intensity across the globe. It has been shown to interfere with animal sensory systems, orientation and distribution, with the potential to cause significant ecological impacts. We analysed the locations of 102 mountain lions (*Puma concolor*) in a light-polluted region in California. We modelled their distribution relative to environmental and human-disturbance variables, including upward radiance (nearby lights), zenith brightness (sky glow) and natural illumination from moonlight. We found that mountain lion probability of presence was highly related to upward radiance, that is, related to lights within

approximately 500 m. Despite a general pattern of avoidance of locations with high upward radiance, there were large differences in degree of avoidance among individuals. The amount of light from artificial sky glow was not influential when included together with upward radiance in the models, and illumination from moonlight was not influential at all. Our results suggest that changes in visibility associated with lunar cycles and sky glow are less important for mountain lions in their selection of light landscapes than avoiding potential interactions with humans represented by the presence of nearby lights on the ground.

# A framework for untangling the consequences of artificial light at night on species interactions

Brett Seymoure, Anthony Dell, Franz Hölker and Gregor Kalinkat

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Abstract

Although much evidence exists showing organismal consequences from artificial light at night (ALAN), large knowledge gaps remain regarding ALAN affecting species interactions. Species interactions occur via shared spatio-temporal niches among species, which may be determined by natural light levels. We review how ALAN is altering these spatio-temporal niches through expanding twilight or full Moon conditions and constricting nocturnal conditions as well as creating patches of bright and dark. We review literature from a database to determine if ALAN is affecting species interactions via spatio-temporal dynamics. The literature indicates a growing interest in ALAN and species interactions: 58% of the studies we analysed have been Published since 2020. Seventy-five of 79 studies found ALAN altered species interactions. Enhancements and reductions of species interactions were equally documented. Many studies revealed ALAN affecting species interactions and ALAN—most studies investigated predator—prey interactions with vertebrates as predators and invertebrates as prey. Following this literature review, we suggest avenues, such as remote sensing and animal tracking, that can guide future research on the consequences of ALAN on species interactions across spatial and temporal axes.

# How artificial light at night may rewire ecological networks: concepts and models

Dirk Sanders, Myriam R. Hirt, Ulrich Brose, Darren M. Evans, Kevin J. Gaston, Benoit Gauzens and Remo Ryser

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Abstract

Artificial light at night (ALAN) is eroding natural light cycles and thereby changing species distributions and activity patterns. Yet little is known about how ecological interaction networks respond to this global change driver. Here, we assess the scientific basis of the current understanding of community-wide ALAN impacts. Based on current knowledge, we conceptualize and review four major pathways by which ALAN may affect ecological interaction networks by (i)

impacting primary production, (ii) acting as an environmental filter affecting species survival, (iii) driving the movement and distribution of species, and (iv) changing functional roles and niches by affecting activity patterns. Using an allometric–trophic network model, we then test how a shift in temporal activity patterns for diurnal, nocturnal and crepuscular species impacts food web stability. The results indicate that diel niche shifts can severely impact community persistence by altering the temporal overlap between species, which leads to changes in interaction strengths and rewiring of networks. ALAN can thereby lead to biodiversity loss through the homogenization of temporal niches. This integrative framework aims to advance a predictive understanding of community-level and ecological-network consequences of ALAN and their cascading effects on ecosystem functioning.

### Does artificial light at night alter moth community composition?

Kylee Grenis, César Nufio, Gina M. Wimp and Shannon M. Murphy

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Abstract

Ecological studies investigating the effects of artificial light at night (ALAN) have primarily focused on single or a few species, and seldom on community-level dynamics. As ALAN is a potential cause of insect and biodiversity declines, community-level perspectives are essential. We empirically tested the hypothesis that moth species differentially respond to ALAN and that these responses can cause shifts in community composition. We sampled moths from prairie fragments in Colorado, USA. We tested whether local light sources, sky glow, site area and/or vegetation affected moth community diversity. We found that increased sky glow decreased moth abundance and species richness and shifted community composition. Increased sky glow shifted moth community composition when light and bait traps were combined; notably this result appears to be driven entirely by moths sampled at bait traps, which is an unbiased sampling technique. Our results show that ALAN has significant effects on moth communities and that local light sources have contrasting effects on moth community composition compared to sky glow. It is imperative that we better understand the contrasting effects of types of ALAN to comprehend the overall impacts of light pollution on biodiversity declines.

### Long-term exposure to experimental light affects the grounddwelling invertebrate community, independent of light spectra

Kamiel Spoelstra, Sven Teurlincx, Matthijs Courbois, Zoë M. Hopkins, Marcel E. Visser, Therésa M. Jones and Gareth R. Hopkins

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#### Abstract

Our planet endures a progressive increase in artificial light at night (ALAN), which affects virtually all species, and thereby biodiversity. Mitigation strategies include reducing its intensity and duration, and the adjustment of light spectrum using modern light emitting diode (LED) light sources. Here, we studied ground-dwelling invertebrate (predominantly insects, arachnids, molluscs, millipedes, woodlice and worms) diversity and community composition after 3 or 4 years of continued nightly exposure (every night from sunset to sunrise) to experimental ALAN with three different spectra (white-, and green- and red-dominated light), as well as for a dark control, in natural forest-edge habitat. Diversity of pitfall-trapped ground-dwelling invertebrates, and the local contribution to beta diversity, did not differ between the dark control and illuminated sites, or between the different spectra. The invertebrate community composition, however, was significantly affected by the presence of light. Keeping lights off during single nights did show an immediate effect on the composition of trapped invertebrates compared to illuminated nights. These effects of light on species composition may impact ecosystems by cascading effects across the food web.

### Spectral composition of light-emitting diodes impacts aquatic and terrestrial invertebrate communities with potential implications for cross-ecosystem subsidies

Elizabeth Parkinson and Scott D. Tiegs

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Abstract

Resource exchanges in the form of invertebrate fluxes are a key component of aquatic-terrestrial habitat coupling, but this interface is susceptible to human activities, including the imposition of artificial light at night. To better understand the effects of spectral composition of light-emitting diodes (LEDs)—a technology that is rapidly supplanting other lighting types—on emergent aquatic insects and terrestrial insects, we experimentally added LED fixtures that emit different light spectra to the littoral zone and adjacent riparian habitat of a pond. We installed four replicate LED treatments of different wavelengths (410, 530 and 630 nm), neutral white (4000 k) and a dark control, and sampled invertebrates in both terrestrial and over-water littoral traps. Invertebrate communities differed among light treatments and between habitats, as did total insect biomass and mean individual insect size. Proportional allochthonous biomass was greater in the riparian habitat and among some light treatments, demonstrating an asymmetrical effect of differently coloured LEDs on aquatic-terrestrial resource exchanges. Overall, our findings demonstrate that variation in wavelength from LEDs may impact the flux of resources between systems, as well as the communities of insects that are attracted to particular spectra of LED lighting, with probable implications for consumers.

### Light pollution of freshwater ecosystems: principles, ecological impacts and remedies

Franz Hölker, Andreas Jechow, Sibylle Schroer, Klement Tockner and Mark O. Gessner

### Abstract

Light pollution caused by artificial light at night (ALAN) is increasingly recognized as a major driver of global environmental change. Since emissions are rapidly growing in an urbanizing world and half of the human population lives close to a freshwater shoreline, rivers and lakes are ever more exposed to light pollution worldwide. However, although light conditions are critical to aquatic species, and freshwaters are biodiversity hotspots and vital to human well-being, only a small fraction of studies conducted on ALAN focus on these ecosystems. The effects of light pollution on freshwaters are broad and concern all levels of biodiversity. Experiments have demonstrated diverse behavioural and physiological responses of species, even at low light levels. Prominent examples are skyglow effects on diel vertical migration of zooplankton and the suppression of melatonin production in fish. However, responses vary widely among taxa, suggesting consequences for species distribution patterns, potential to create novel communities across ecosystem boundaries, and cascading effects on ecosystem functioning. Understanding, predicting and alleviating the ecological impacts of light pollution on freshwaters requires a solid consideration of the physical properties of light propagating in water and a multitude of biological responses. This knowledge is urgently needed to develop innovative lighting concepts, mitigation strategies and specifically targeted measures.

# The impacts of artificial light at night on the ecology of temperate and tropical reefs

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#### Abstract

Despite 22% of the world's coastal regions experiencing some degree of light pollution, and biologically important artificial light at night (ALAN) reaching large portions of the seafloor (greater than 75%) near coastal developments, the impacts of ALAN on temperate and tropical reefs are still relatively unknown. Because many reef species have evolved in response to low-light nocturnal environments, consistent daily, lunar, and seasonal light cycles, and distinct light spectra, these impacts are likely to be profound. Recent studies have found ALAN can decrease reproductive success of fishes, alter predation rates of invertebrates and fishes, and impact the physiology and biochemistry of reef-building corals. In this paper, we integrate knowledge of the role of natural light in temperate and tropical reefs with a synthesis of the current literature on the impacts of ALAN on reef organisms to explore potential changes at the system level in reef communities exposed to ALAN. Specifically, we identify the direct impacts of ALAN on individual organisms and flow on effects for reef communities, and present potential scenarios where ALAN could significantly alter system-level dynamics, possibly even creating novel ecosystems. Lastly, we highlight large knowledge gaps in our understanding of the overall impact of ALAN on reef systems.

# Scaling artificial light at night and disease vector interactions into socio-ecological systems: a conceptual appraisal

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#### Abstract

There is burgeoning interest in how artificial light at night (ALAN) interacts with disease vectors, particularly mosquitoes. ALAN can alter mosquito behaviour and biting propensity, and so must alter disease transfer rates. However, most studies to date have been laboratory-based, and it remains unclear how ALAN modulates disease vector risk. Here, we identify five priorities to assess how artificial light can influence disease vectors in socio-ecological systems. These are to (i) clarify the mechanistic role of artificial light on mosquitoes, (ii) determine how ALAN interacts with other drivers of global change to influence vector disease dynamics across species, (iii) determine how ALAN interacts with other vector suppression strategies, (iv) measure and quantify the impact of ALAN at scales relevant for vectors, and (v) overcome the political and social barriers in implementing it as a novel vector suppression strategy. These priorities must be addressed to evaluate the costs and benefits of employing appropriate ALAN regimes in complex socio-ecological systems if it is to reduce disease burdens, especially in the developing world.

# Mitigating the impacts of street lighting on biodiversity and ecosystem functioning

#### Darren M. Evans

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#### Abstract

Street lights are not only a major source of direct light pollution emissions, but stock has been transitioning to light-emitting diode (LED) technology in many parts of the world, resulting in increases in the blue part of the visible spectrum that is more harmful to biodiversity and human health. But LEDs can be modified more easily than conventional sodium lamps by adjusting their intensity, spectral output and other features of street light systems. In this Opinion piece, I provide an updated overview of street light mitigation strategies and contend that research in this area has been slow. I show how experimental lighting rigs that mimic real street lights can be used for mitigation testing, since invertebrate behaviour, abundances and interactions can respond quickly and measurably. I demonstrate how advances in network ecology that use species interaction data can provide much-needed assessments of the impacts of street lights on biodiversity and ecosystem functioning, and ultimately provide new tools and metrics for biomonitoring. I acknowledge the limitations of measuring local, short-term responses of biodiversity and identify promising avenues for collaborating with industry and government agencies in new or existing road lighting schemes, to minimize the negative long-term impacts at marginal cost.