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Forum

Combined light pollution and night warming as a novel threat to ecosystems

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Artificial light at night (ALAN) and night-time warming (NW) are a combined threat altering the night-time environment and the behaviour and physiology of organisms. Impacts on fitness and the nocturnal niche have knock-on effects for ecosystem structure and function. Understanding the way both stressors interact is critical for making ecological predictions.

Impact of ALAN and NW on night-time ecology

The extensive spread of ALAN from a variety of human light sources is eroding natural light cycles across the world [1], and climate change, urbanisation, and loss of vegetation cover are increasing NW faster than daytime warming [2]. Around 30% of vertebrates and at least 60% of invertebrates are estimated to be nocturnal, suggesting that a high proportion of biodiversity relies on night-time conditions for their activity, and is therefore susceptible to the currently underappreciated impact of **night-time stressors** (see Glossary). However, the night is also important for diurnal organisms, as it marks their recovery periods. Paradoxically, **night-time ecology** has remained poorly documented [1]. Central to our understanding of the combined impacts of ALAN and NW is how they jointly shape the nocturnal niche, thereby allowing some species to extend their activity into the night while other species are being excluded.

Potential for interactive effects

Among night-time stressors, NW has strong potential of interaction with ALAN in changing the night-time environment and affecting both diurnal and nocturnal organisms' physiology and activity patterns with consequences for fitness, survival and the functional role of species within communities. Such changes are likely to cause cascading extinctions and biodiversity loss; for example, through trophic network rewiring and increased niche overlap. The interaction of the two stressors is concerning, and their net combined effect on organisms depend on their (co)-variations in space and time and their respective frequency (spatial or temporal recurrence), amplitude (effect strength), direction (positive or negative effect on fitness), as well as the additive, **synergistic** or **antagonistic** potential of the response towards both stressors [3]. Therefore, it is first necessary to link species' **response traits** to the combined impact of ALAN and NW on the use of the nocturnal niche, and the night-time as refuge and for recovery. **Effect traits** at multiple scales and levels of biological complexity will help to predict knock-on effects on ecological communities estimated for each species or functional group.

Species are affected differently by these covariations depending on their functional ecology, such as their activity patterns (nocturnal, crepuscular, or diurnal) and the timing of critical biological processes [2]. They are also affected differently at different stages of their developmental cycle, since nocturnal stressors covary differently on seasonal time scales. Some developmental stages may not be sensitive to one of the two stressors and therefore not to their combined effect (e.g., buried larvae or seeds may not respond to light). The two stressors are more likely to coexist in urban than in rural environments, where a few studies have been able to distinguish the effect of urban heat islands from that of ALAN [4]. Tropical communities may respond even more strongly as they are sensitive to daylight changes [5] and are already close to their thermal tolerance limits. Lastly, marine and terrestrial environments far from cities are likely to be less exposed to the combination of these night-time stressors. However, the riparian, lake, and coastal aquatic environment is subject to

Glossary

Antagonistic effect: type of nonadditive effect where the combined effect of two or more factors is less than the sum of their individual effects, with either positive (reduction in harm or vulnerability of one stressor by the other) or negative (reduction in fitness benefits) outcomes.

Effect trait: any trait that reflects the effects of an organism on environmental conditions, or community or ecosystem properties (e.g., high predatory activity under warmer or increased light conditions). There can be an overlap between response and effect traits, depending on the functions studied.

Environmental filtering: effect of the environment that locally selects a subset of species from the regional species pool. Through fitness effects the environmental conditions impact survival and local community assembly.

Night-time ecology: also known as nocturnal ecology, can be defined as the set of biological events occurring during the night, whether they are related to periods of behavioural or physiological activity or rest. It directly concerns time partitioning but logically extends to ecosystem function, community dynamics and the general nocturnal environmental conditions.

Night-time stressor: also known as nocturnal stressor, is any natural or anthropogenic variable that causes a quantifiable change, irrespective of its direction (increase or decrease), in a biological response. Night-time stressor specifically occurs during the night, but has consequences that can transcend the night period.

Photoperiod: periodic change in light conditions over various time scales (e.g., day–night cycles, seasonal cycles) to which animal and plant photoperiodism respond through physiological and behavioural reactions.

Response trait: any trait that explains the response of organisms to changes in environmental conditions (e.g., capacity or incapacity to see at night). They predict which species will be excluded and which ones will respond with a shift in their functional role.

Synergistic effect: type of nonadditive effect where the combined effect of two or more factors is greater than the sum of their individual effects, with either positive or negative fitness or ecosystemic outcomes.

Thermoperiod: periodic change in temperature conditions over various time scales (e.g., day–night cycles, seasonal cycles) to which animal and plant photoperiodism respond through physiological and behavioural reactions.

extensive ALAN [1], which, combined with progressive warming of the water temperature, can for example increase the vulnerability of coastal zooplankton to combined stressor effects [5].

Only a few studies have directly tested the combined effect of ALAN and warming (Table 1). Insights for potential interactive effects can be drawn on those studies demonstrating singular effects of either night-time stressor on similar biological processes. Both stressors are causing similar responses, even if their respective pathways often differ, and therefore are likely to have additive or nonadditive combined effects on the night-time ecology. For example, in plants, photosynthesis, respiration, carbohydrate metabolism, biomass, leaf expansion, flowering dates, and susceptibility to herbivore attacks are affected by the two stressors [11,12]. Important ecosystem functions such as pollination respond to both ALAN [13] and NW [2]. Similar to ALAN, NW can shift predator activity patterns, population growth, species interactions and functional response in food webs [6]. Both ALAN and NW can prevent recovery from diurnal heat stress; for example, in the English grain aphid *Sitobion avenae* [14]. In many organisms, biological clocks are influenced by both the **photoperiod** and the **thermoperiod** [8,10], which both ALAN (even at skyglow levels) and NW disturb.

Stressor impact pathways

ALAN and NW act jointly at different time scales through mutually nonexclusive pathways. First, **environmental filtering** leads to a change in the local species pool through filtering of especially sensitive traits. Secondly, phenotypic plasticity allows some organisms to take advantage of new night-time conditions, or

Table 1. Summary of the available literature on the combined actions of ALAN and NW, whether it describes a direct and intended evaluation of these combined effects (the experiments were designed to test them), or an indirect evaluation (the study was focused on the interaction with global warming but not specifically NW)

Context	Taxa	Disrupted function	Type of interaction	Mechanism	Refs
Direct evidence for a combined effect of NW and ALAN					
Spatial covariation in night-time warming and ALAN	Insects (aphid: *Acyrthosiphon pisum*, ladybirds: *Coccinella septempunctata* and *Coleomegilla maculata*)	Predation rates (prey–predator interaction)	Synergistic	Ladybirds can take advantage of warmer night temperatures under ALAN. However, the nonadditive effect may vary among predator species	[6]
Change in photoperiodic and night temperature regimes, combined with ALAN	Insects (aphid: *Megoura viciae*, parasitic wasp: *Aphidius megourae*)	Parasitism rates (host–parasitoid interaction)	Synergistic	ALAN intensifies the effect of longer daylength on the increase in parasitism rates during warmer nights	[7]
Indirect evidence					
Evolutionary responses to urban areas with both heat island and ALAN effects	Insects (lepidopterans: *Pieris napi* and *Chiasmia clathrata*)	Phenology (timing of diapause induction)	Potentially additive	Diapause is delayed through genetic shift in urban populations, mostly due to urban heat islands, but ALAN may contribute as a diapause-averting cue	[8]
Plastic responses to urban areas with both heat island and ALAN effects	Insects (diptera: *Sarcophaga similis*)	Phenology (timing of diapause induction)	Synergistic	The strong effect of ALAN on preventing diapause is exacerbated by warming	[4]
Increasing ALAN exposure interaction with climate warming	Plants (trees: *Aesculus hippocastanum*, *Alnus glutinosa, Betula pendula, Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur* and *Tilia cordata*)	Phenology (leaf budding and flowering date)	Antagonistic	ALAN inhibits the advance effect of warming on plant phenology	[9]
Increasing warming and light pollution exposure in coastal ecosystems	Plankton (copepod: *Pseudodiaptomus incisus*)	Life-history traits (development time, body size, clutch size, hatching success)	Synergistic	Light pollution leads to stronger reductions in life-history traits values at warm temperatures	[5]
Increasing ALAN exposure, interaction with temperature and predictions for the future	Plants (>700 species of deciduous woody plants)	Phenology (leaf budding and leaf colouring)	Additive	ALAN and warming advance breaking leaf bud date.	[10]
			Non-additive	ALAN accelerate the warming-induced delay in leaf colouring in current climate, but slow down or even reverse such delay as the climate warms	

temporarily avoid the negative effects of the stressor combination. Finally, there is evolution in response to the new nocturnal pressures. The latter two processes lead to shifts in species niches and/or specific traits thereby changing the functional role of species within their communities.

Main predictions from species functional ecology

The potential for synergy or antagonism between ALAN and NW is substantial for some traits or combination of traits with high sensitivity to either or both stressors. The most relevant to consider mechanistically are diel activity pattern (circadian rhythms), hunting mode, foraging habit, resting period, habitat preference, and light and temperature sensitivity, with complex group-specific outcomes on fitness (Figure 1). Both stressors can lead to marked changes in a species' traits and temporal niche space, for example by changing predator or prey activity patterns.

ALAN exposure can allow for a diurnal predator to forage at night, but if they additionally need higher temperature for their activity in the night, only increasing nighttime temperatures at the same time can fully unlock the nocturnal niche and extend its hunting window (positive synergistic effect) [6,7]. Some organisms that were limited by low night temperatures or lighting at night will benefit from the combination of NW and ALAN [2] and expand or shift their temporal niche. Miller *et al*. [6] reported such synergistic impacts, which only benefited ladybug species using visual cues to hunt on prey, while the other ladybug species responded to NW, with ALAN providing no additional advantage.

However, diurnal organisms extending their activity into the night due to ALAN potentially experience reduced quality and duration of resting periods, exhaustion through the inability to find shelter, and an accelerated metabolic rate due to NW (antagonistic effect), leading to either

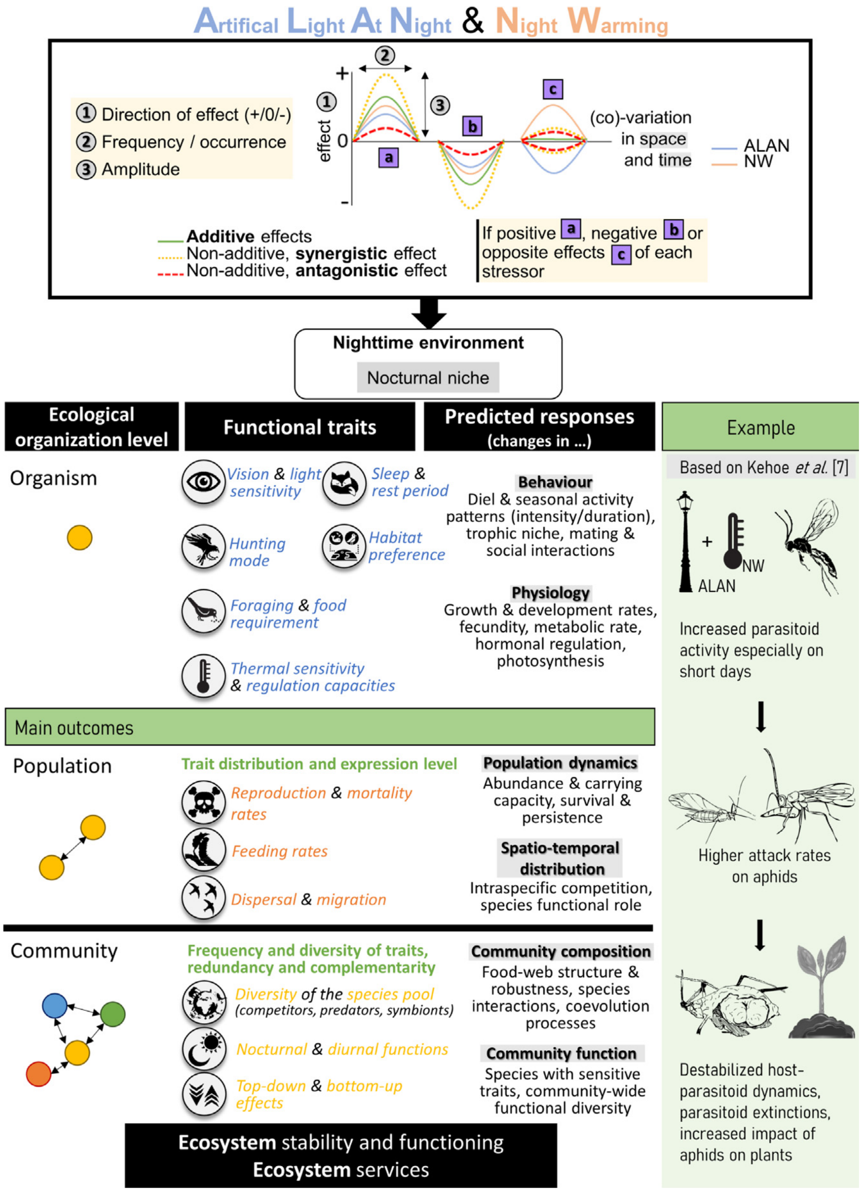

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Figure 1. Mechanistic framework to understand the combined effects of artificial light at night (ALAN) and night-time warming (NW) on organisms and ecosystems. The combined night-time stressors can act additively, synergistically, or antagonistically. The respective effect sizes of the combined stressors can vary in amplitude, frequency or occurrence as the stressors covary in space and time, with either a positive effect, a negative effect, or an opposite effect of both stressors, independently. They can have neutral, positive or negative net combined effects on organisms depending on the stressor–response relationship, thresholds, and tipping points. The assumption is made of an equal impact of ALAN and NW, but one stressor may prevail over the other and drive the net combined impact. A species may also respond to one of these stressors but not to the other or to their interacting effects. Behavioural and physiological responses at the organism level and changes in traits at the population and community level will ultimately impact ecosystem functioning. In addition, particular traits and functions are likely to be the most impacted by the combined stressor effects. For example, aphid parasitoids increase their activity with ALAN, but only when nights are warmer, and this synergistic effect is the strongest on short day conditions (seasonal modulation) [7]. The combined ALAN and NW effect translates to higher attack rates on aphids. At the community scale (plant–aphid–parasitoid), the destabilised host–parasitoid dynamics may have consequences on top-down regulation of aphids impact on plants.

positive or negative net fitness consequences depending on the amplitude of each stressor effect. In addition, if activity is expanded to the night, this can result in overexploitation of the environment or exposure to new predators, or to cold temperatures if there is a mismatch in the covariation between stressors, and lead to population declines. We can expect a substantial increase in niche overlap between different groups of species (diurnal, nocturnal, and crepuscular), making their niches more similar with consequences for coexistence. Diurnal organisms that do not switch activity periods could still be affected, because if rest periods (sleep or nonphotosynthetic phase) are disturbed by NW, this has potential harmful long-term consequences in terms of activity during the day (e.g., increased rest during the day) and fitness [14]. Strictly nocturnal organisms, which may prefer a cool habitat and rely on visual discretion at night, will likely be negatively affected by the interaction between ALAN and NW. Reduced activity at night would have severe fitness consequences for them, with less opportunities to find resources and mates.

Consequences for ecological communities

Both night-time stressors can change the way species interact, as shown for prey–predator [6] and host–parasitoid systems [7], which can impact communities, ecosystem functions, and stability (Figure 1). A shift in activity patterns to exploit the nocturnal niche for diurnal predator species will lead to the overexploitation of prey species and cascading effects across food webs. Further, disruption of nocturnal pollinators through ALAN and NW exposure can destabilise plant-pollinator networks with knock-on effects on plant fitness and survival [2,13] (e.g., Chiroptera–Cactaceae interactions, nocturnal pollination by moth or Coleoptera). The net combined effects will depend on the distribution of response traits within the community and on asymmetric responses between interacting species, with some species emerging as winners and others as losers [12].

One of our main predictions is that the stressors are likely to remove any species with sensitive traits (e.g., flight to light behaviour or light avoidance). This can significantly shift the presence and distribution of functional traits within communities, potentially leading to cascading effects through top-down or bottom-up cascades. The net impact of combined ALAN and NW is driven by (i) their filtering effect at the community level; (ii) change in biotic interactions; and (iii) vulnerability of communities to these changes. Predictions are achieved by linking nocturnal ecology to the underlying response and effect traits in nocturnal species assemblages and making the relevant links to diurnal species and their activity patterns.

Unveiling the implications and path forward

In a world where wildlife is becoming more nocturnal to escape anthropogenic disturbances during the day [15], it is crucial to consider the combined impact of ALAN and NW, which is widespread and increasing. What is striking and complicates our predictive capacity is that while we have substantial knowledge about ALAN impacts, we still know little about the consequences of NW, or the combination of these two nocturnal stressors. We also need to distinguish the effects of NW in general from those of overall warming. ALAN and NW strongly covary and act on similar processes thereby changing the use of the nocturnal niche, leading to shifts in functional ecology, niche occupancy and overlap, and also likely work in concert with other stressors such as noise and other kind of pollution.

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Declaration of interests

No interests are declared.

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