

Review



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

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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 spatially, but few revealed temporal alterations. There are biases regarding 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.

This article is part of the theme issue 'Light pollution in complex ecological systems'.

1. Introduction

Natural light cycles cue daily, monthly and annual activity patterns of species and have been a selecting force for adaptive visual, physiological, morphological and behavioural traits [1,2]. As many species are active for a limited portion of the 24 h cycle, they have specific traits that optimize fitness during their temporal niche [2,3]. An individual's temporal niche is defined by their predictable 24 h activity bout such as diurnality, crepuscularity and nocturnality. Species that occupy the same temporal niche are much more likely to interact in antagonistic (e.g. predator–prey) or mutualistic (e.g. plant–pollinator) interactions, but also amensalistic and commensalistic interactions. For instance, many prey species have evolved their activity patterns to reduce predation risk [4]. Although the theoretical construct of temporal niches dictating species interactions is in its infancy [2], the evidence is overwhelming that temporal partitioning facilitates coexistence between competitors, mutualists, and predators and their prey [3–5].

Unfortunately, the temporal niches that have dictated species activity patterns, their interactions and the associated traits involved in species interactions (e.g. vision, coloration), are being altered and destroyed by artificial light at night

(ALAN) [6]. This disruption of temporal niches globally is affecting species interactions in two ways. First, a change to the balance of naturally occurring species interactions due to shared temporal niches is occurring, where one species may have an adaptive advantage over the other, such as bats having increased foraging efficacy on flying insects under light-polluted skies [7]. Second, novel species interactions are occurring during altered temporal niches as certain species are having their temporal niche expanded (e.g. for crepuscular species under ALAN such as insectivorous birds in urban environments [8]), whereas other species are experiencing a contracted temporal niche, such as nocturnal rodents that are only active under very dim conditions [9]. In both scenarios, the evolved traits that are adaptive under one temporal niche may now become maladaptive and result in a shift in the coevolutionary relationship between two species [10].

ALAN is increasing both spatially and in intensity, with projections of 50% of global terrestrial area having ALAN exposure by 2052 [11–13]. With half of terrestrial ecosystems experiencing altered temporal niches from ALAN, it is imperative that we understand the ecological consequences of altered species interactions from ALAN [14]. Thus, our goals in this paper are to: (i) underscore that natural light cycles have shaped species interactions, as well as traits; (ii) review the alteration and destruction of natural light cycles relative to temporal niches and associated traits (e.g. vision, thermoregulation and coloration); (iii) provide a conceptual framework for the effects of ALAN on species interactions by exploring enhancements and reductions of species interactions due to the expansion and contraction of spatio-temporal niches; (iv) conduct a brief literature review from a literature database to highlight studies that show species interaction effects from ALAN; and (v) introduce techniques and methods to test hypotheses surrounding the consequences of ALAN on the spatio-temporal dynamics of species interactions.

2. Natural light entrains activity patterns and selects for specific traits

For thousands of years, humans have recognized that organisms exhibit predictable periodic behaviours corresponding to the timing of day and night, lunar phases and seasons [4]. Although time has only recently been a focus of niche partitioning [3,4], evidence is demonstrating that time is indeed an ecological niche variable that results in temporal niches [5,15]. The temporal niche can be defined as the time of day at which individuals display locomotor activity [2], such as diurnality (day-active), nocturnality (night-active), crepuscular (twilight-active) and cathemeral (predictably active and inactive during both day and night) [3]. However, it is crucial to understand that an individual's temporal niche is dependent upon specific behaviours and seasonality, for example, many migratory birds are mostly diurnal except during the annual migration, which is mostly a night-time behaviour [16]. Organisms have evolved daily activity patterns in response to predictable environmental variables (e.g. lighting, temperature and biotic community) via circadian rhythms that are entrained by light and temperature [2,3]. Thus, temporal niches such as day, twilight and night all have key biotic communities that interact with each other, and theoretically, each individual has adaptations for increasing fitness within their respective temporal niche [2,17,18].

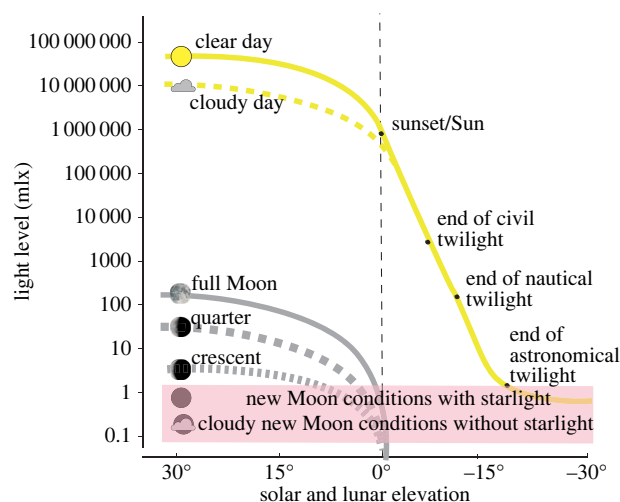


Figure 1. The absolute intensity of light in millilux resulting from solar and lunar elevation under natural conditions. When the Sun is less than 18° below the horizon, the altitude and phase of the Moon is the most important factor determining night-time light levels in natural settings. The dashed vertical line represents the horizon. Sun, cloud and lunar icons indicate each light condition. Yellow lines represent the solar altitude and grey lines represent lunar altitude. The pink bar represents the range of light at starlight conditions when both the Moon and Sun are under the horizon by at least 18°. Modified from Johnsen [21] and Jones *et al.* [22].

Temporal niches can range from a few minutes, such as twilight in the tropics, to hours, such as day and night or full Moon and new Moon. These temporal niches are all defined by the presence/absence/duration of natural light and, hereafter, we will focus on light as the driving factor of temporal niches, with the caveat that other crucial environmental factors correlate across these temporal niches, such as temperature [19]. Also, we focus on temporal niches that occur within the 24 h cycle of Earth and do not include seasonal changes in photoperiod. Photoperiod is an important factor affecting species distributions and biotic interactions and is greatly altered by ALAN, but is beyond the aims of our manuscript [20].

Irradiance is the amount of ambient lighting in an environment, and during a solar day it varies over nine orders of magnitude (0.0006–100 000 lx), changing with solar altitude, cloud cover and lunar illumination (figure 1) [23]. There are three broad timescapes during a solar day: daylight, twilight and nightlight, defined mostly by the amount of light (figure 1). However, owing to the physical nature of the atmosphere, the spectral composition of light varies across the solar day–night cycle, with daylight being mostly broadband (i.e. ‘white’ light), twilight comprising short and long wavelengths (i.e. purple) and nightlight consisting mostly of longer wavelengths (i.e. amber under moonlight and red under starlight). The significance of these timescapes for organismal behaviours and interactions cannot be understated [2,24,25]. For example, many flowers control scent emission and nectar production to attract pollinating day-active bees by light intensity [15,26]. Furthermore, the distance of diel vertical migration by zooplankton is directly controlled by light intensity, with some zooplankton not reaching the surface of the water column under light intensities brighter than starlight [27,28]. There are numerous cases of organisms cueing specific behaviours to changes in light levels across the solar day (see [12] for a full review).

The lunar cycle drastically alters nocturnal illumination owing to the moon reflecting approximately 0.0002% of solar radiation, resulting in night light intensities that range from 0.0006 lx (new Moon) to 0.2 lx (full Moon), depending on lunar phase and lunar altitude (figure 1) [12,21,29]. Although lunar illumination only contributes substantially to environmental lighting at night, many organisms cue their behaviours to night light levels dependent upon lunar illumination (see [12] for details). The impacts of lunar illumination on species and their interactions are complex and nuanced, but, at least in mammals, visually guided carnivores tend to minimize foraging outside of new Moon conditions, whereas visually guided prey tend to increase activity under moonlight [30]. Prey that relies upon non-visual sensory modalities for predator detection tend to be lunar phobic—i.e. inactive under moonlight [30]. Thus, moonlight is a key driver of animal behaviour and species interactions at night.

Countless adaptations have arisen from solar day and lunar light cycles, and here we briefly highlight visual, morphological and temporal adaptations that are likely to be affected by ALAN and result in altered species interactions. Visual adaptations have mostly been selected to optimize acquiring environmental information across the immense range of light intensities across the solar day. As many species are more active during one temporal niche than another, visual adaptations usually are the result of a trade-off between acuity (spatially, temporally and spectrally) and overall sensitivity—the ability to collect a requisite amount of photons to enable vision [31]. Visual systems across the animal kingdom are myriad and diverse [32], but some general patterns are evident. Nocturnal species usually have large tubular-shaped eyes, which have highly curved corneas, thicker lenses, larger photoreceptors and fewer types of photoreceptors (i.e. colour-blindness [33], but see [34–36]). In addition, many nocturnal taxa possess a tapetum lucidum, which is a reflective membrane behind the retina that increases photon capture, as well as neural and temporal summation across photoreceptors, which combine to increase the chances of a visual signal in dim conditions [1,32]. The eyes of diurnal species are usually characterized by smaller photoreceptors, more types of photoreceptors (resulting in better colour vision), more ganglion cells innervating photoreceptor cells, thinner lenses, a fovea resulting in high acuity, and—in vertebrates—fewer rods [1,32,37]. Thus, generally speaking, under bright daylight conditions the vision of animals evolved for nocturnal activity will be colour-blind, blurry, coarse and overstimulated, perhaps resulting in momentary blindness. In contrast, vision evolved for diurnal activity will be blind under dim starlight conditions.

As visual abilities are highly correlated with temporal niches due to light intensity, it is not surprising that visually linked traits such as coloration are also highly correlated with a temporal niche [38–40]. Animal coloration is important for deterring predators (e.g. crypsis and aposematism), foraging (e.g. crypsis and aggressive mimicry) and communication (i.e. mate choice and kin recognition) and, as such, nocturnal species have evolved coloration to increase contrast and are usually black and white, as in owls and non-butterfly moths, whereas diurnal species are generally more colourful, as in songbirds and butterflies [38,41]. Furthermore, it has recently been shown that temporal niches likely were involved in the evolution of sexual signals and warning signals, with ancestral diurnal clades evolving sexual signals and

ancestral nocturnal clades evolving warning signals [42]. Finally, daily changes in temperature are highly correlated with timescapes, resulting in numerous thermal adaptations enabling organisms to cope with hotter temperatures during the day and cooler temperatures at night [2]. Consequently, the role of light cycles cannot be underplayed when evaluating the mechanisms underlying species interactions and the consequences of ALAN.

3. ALAN alters and destroys natural light cycles responsible for temporal niches and nocturnal spatial niches

The night sky has become brighter owing to artificial light sources by approximately 10% every year for the last 10 years [13]. With brighter skies comes brighter nocturnal environments and the erasure of natural night lighting [12,43,44]. As reviewed above, natural night conditions range four orders of magnitude from starlight/new Moon of approximately 0.0006 lx to the full Moon directly overhead at approximately 0.2 lx [21]. Starlight conditions, due to the new Moon phase or the Moon being below the horizon, comprise approximately 50% of night-time hours, and thus, represent the most common night-time light condition [45]. Seymoure *et al.* [12] translated the 2016 *New world atlas of artificial night sky brightness* [43] to illuminance experienced on the Earth's surface due to light pollution and found that approximately 23% of terrestrial habitats never experience new Moon lighting conditions and approximately 5% are ten times brighter and experience perpetual crescent Moon illumination. It is important to note that, in both the *New world atlas of artificial night sky brightness* [43] and the Seymoure *et al.* translation, direct sources of light were not included; thus nocturnal light conditions were underestimated, resulting in many areas likely never experiencing quarter Moon conditions (0.01 lx, 100 times brighter than natural [11,13]).

The increase in nocturnal light conditions is concerning not only owing to the loss and degradation of the lunar light cycle [46], but also owing to the destruction of celestial cues that many species use for navigation and orientation, and owing to the addition of unnatural wavelengths (i.e. short wavelengths) of light [47–50]. Furthermore, ALAN not only affects the light cycles of the solar day and lunar month but also affects the Earth year light cycle by artificially increasing the photoperiod [51,52]. Consequently, many organisms exposed to artificial lighting exhibit phenological mismatch—the altered timing of regularly repeated phases in their life cycles—such as advanced migration of birds [53] and earlier budding in plants [54]. If humans continue to increase the extent and intensity of ALAN, especially with shorter wavelengths of light, the Earth will experience perpetual twilight. Perpetual twilight will match both the intensity and spectrum of natural twilight, likely masking all light-related nocturnal cues that numerous organisms rely upon for timing their activity to optimize evolved adaptations for a nocturnal lifestyle [55].

Not only does ALAN destroy natural photoperiods by extending perceived twilight owing to increased light levels, but also it drastically alters the spatial arrangement of light owing to direct light sources illuminating specific areas and casting shadows on other areas [56,57]. This is



Figure 2. Potential altered species interactions due to ALAN. (a) Dusk: crepuscular species such as bees may shift their activity and pollinate flowers later at night and/or earlier in the morning. (b) Early night: many nocturnal species, such as bats and rodents, may remain inactive at night under the presence of ALAN [9,66]. (c) Night: nocturnal species may aggregate around artificial light sources at night owing to non-homogeneous lighting, such as bats and moths aggregating around artificial light [67,68]. (d) Dawn: diurnal predators may extend their foraging to earlier in the morning owing to the presence of ALAN and thus increase predation on insects as a result of an extended temporal niche [69–71]. Illustration created by A. Portz. (Online version in colour.)

another avenue in which ALAN can disrupt species interactions—as certain species may be attracted to bright areas and lights [58–60], whereas other species may avoid artificially lit areas [61]. Furthermore, not only will ALAN be unequally distributed across a landscape both spatially and temporally, but different spectra of light will be cast upon the landscape owing to the myriad sources of artificial light (e.g. high-pressure sodium lamps, mercury vapour, metal halides and light-emitting diodes with numerous different colour temperatures) [62,63]. Thus, evolved species interactions may be altered owing to artificial lightscapes within a habitat resulting in one focal species occupying an artificially bright microhabitat and another species occupying a more natural, dark microhabitat.

4. Framework for ALAN effects on species interactions spatio-temporally

Most interactions between species occur when two species' temporal and spatial niches overlap, regardless of the type of interaction. Here we focus on direct antagonistic interspecific interactions, including predator–prey, herbivory, parasitism, parasitoids and mutualisms such as pollination and seed dispersal. In most cases of species interactions, the specific interaction occurs during a specific timescape that could be altered by ALAN. For example, *Lasioglossum*

texanum sweat bees emerge from nests during dusk in search of evening-primrose flowers (*Oenothera* spp.) to provision their nests with pollen, and on moonless nights will return to their nest before the end of nautical twilight owing to visual constraints [64]. *Oenothera* flowers open after sunset and remain open through the night, a behaviour dependent upon circadian rhythms entrained by light levels [65]. This specialized pollinator–plant interaction evolved under the natural darkness of the Chihuahuan Desert, resulting in visual adaptations and circadian behaviours. Perpetual twilight from ALAN could disrupt the circadian clocks and affect associated traits, resulting in a phenological mismatch between the co-dependent pollinator and flower; however, this temporal mismatch within a species interaction has not been tested. It is imperative to investigate not only how ALAN is structuring biotic communities but also how ALAN is disrupting evolved species interactions that rely upon numerous adaptations for specific temporal niches. With this in mind, we propose a framework for understanding disrupted, as well as novel, species interactions due to ALAN and spatio-temporal niches.

ALAN can affect species interactions in two main ways: (i) it can affect the species that interact during a temporal niche or (ii) it can alter the activity pattern/circadian rhythm of species, resulting in species occupying a novel temporal niche (figure 2). Additionally, ALAN is extending both day and twilight timescapes while reducing the night timescape

[72]. Crepuscular species, which occupy the twilight temporal niche, initially had a short bi-modal period of activity, dawn and dusk, whereas now these species experience much longer twilight periods and could be active longer, resulting in more interactions with other species. In addition, obligate nocturnal species that timed their activity during new Moon conditions may no longer experience their advantageous temporal niche or will have it drastically shortened in duration (figure 2). This is likely disadvantageous for prey species and mutualistic interactions that require the refugia of new Moon darkness; however, it is likely advantageous for predators, herbivores and parasites that depend on brighter conditions for their respective behaviours [19].

For those individuals that occupy the same temporal niche, regardless of whether it is a result of a naturally occurring shared temporal niche or of artificial light altering an individual's temporal niche, interactions with other species can be increased or decreased owing to the spatial composition of ALAN. Under patchy, non-homogeneous artificial light in the environment, photophobic species will have their nocturnal niche spatially constricted, as has been documented in rodents [9,73], bats [74] and insects [75,76], whereas photophilic species will be attracted by light sources in the landscape, such as bats [67], birds [77], spiders [78] and insects [59,79].

Following supposed temporal and/or spatial niche alterations due to ALAN, we propose a framework for approaching how ALAN affects species interactions. The framework consists of identifying the two main taxa (i.e. consumer and resource), the interaction type (e.g. herbivory, predation and pollination), whether the strength of the interaction (*sensu* [80]) is enhanced or reduced (i.e. under the impact of ALAN individuals of a given species pair would interact more often or more strongly, or less often or more weakly), and whether a temporal and/or spatial mismatch is occurring under ALAN. This is a simplified approach and fully understanding species interactions under ALAN will consist of knowing the effects on more than just two main taxa. However, owing to the paucity of studies directly testing the effects of ALAN on species interactions, this framework will enable future research to be comparable across studies, enabling comprehensive meta-analyses resulting in a much larger understanding of species interactions in the Anthropocene.

We applied this framework to a database on the effects of ALAN and movement, including search terms like foraging, flight or refuge as one part and a group of technical terms related to artificial lighting as the second part; see electronic supplementary material for complete search string. Within this database, we screened for studies that investigated species interactions explicitly, namely predator–prey, plant–herbivore, plant–pollinator, parasite/parasitoid–host, and other types of interactions typically included in investigations of species interactions and interaction networks [81,82]. Given that detritus and detritivores form an essential part of many, if not most food webs [83], and that effects of ALAN on detritivores have been documented already [84], we also decided to include these interactions in our analyses, although they technically do not represent an interaction between two species. Our screening resulted in 93 studies out of 1252 studies from the original database, retrieved from Web of Science on 21 December 2022. Subsequently, we applied our framework to determine the two main taxa, the interaction

type, whether the interaction was enhanced or reduced, and if temporal and/or spatial mismatch were induced. Through applying our framework, we further narrowed our subset of studies to 79, including 81 interactions owing to two studies investigating two different types of interactions simultaneously. Briolat *et al.* [85] looked at a predator–prey and a plant–pollinator interaction, whereas Giavi *et al.* [86] investigated both seed predation by a herbivorous insect and pollination success.

We want to emphasize that our literature review was not intended to represent a full systematic analysis. The rapidly developing literature on ALAN in general and its effects on species interactions in particular suggests it makes sense to wait a little more given how fast new studies covering previously uncovered organism groups are added (see results below). Furthermore, we are aware that (i) our approach of relying on a limited list of search terms related to movement ecology, as well as (ii) our reliance on the core database of the Web of Science alone, will not prevent the unintended exclusion of relevant studies. Moreover, our approach is unlikely to unravel issues like publication bias [87] or decline effects [88,89]. Nevertheless, we are confident that drawing from our movement ecology database provides a good overview of the field, particularly which species groups are best covered, and highlights the dynamics of this rapidly developing field.

5. Literature review of expansion and contraction of spatio-temporal niches involved in species interactions by ALAN

The effects of ALAN on species interactions are only beginning to be quantified and understood, as our review revealed that 94% (75 out of 79) of studies researching species interactions were published since 2014 and over 58% (46 out of 79) of studies were published in the last 3 years (figure 3a; electronic supplementary material, data). Thus, it is likely that our knowledge of the consequences of ALAN on species interactions will greatly increase within the next decade.

Of the 79 articles in the movement and ALAN database that studied species interacting, 56 were focused on predator–prey interactions, 11 on herbivory, six on pollination, five on detritivory and then only one article each for frugivory/seed dispersal, parasite–host and parasitoid–host interactions (figure 3b; electronic supplementary material, data). The species studied were diverse, albeit biased with respect to bats and insects, also including crustaceans, arachnids, molluscs, angiosperms, protists and all major classes of vertebrates (figure 3c,d; electronic supplementary material, data). Not all of the 79 studies showed a change in species interactions; only 54 showed that interaction strength was affected by ALAN. There were an almost equal number of studies showing reductions and enhancements of interactions, with 29 and 28 studies for enhancement and reduction, respectively. Two studies found that enhancement and reduction of species interactions were dependent upon species, even within the same taxon: bats [90,91].

Reductions in species interactions occurred across interaction types including predator–prey (12), herbivory (6), detritivory (4), pollination (3) and frugivory (1). The taxa

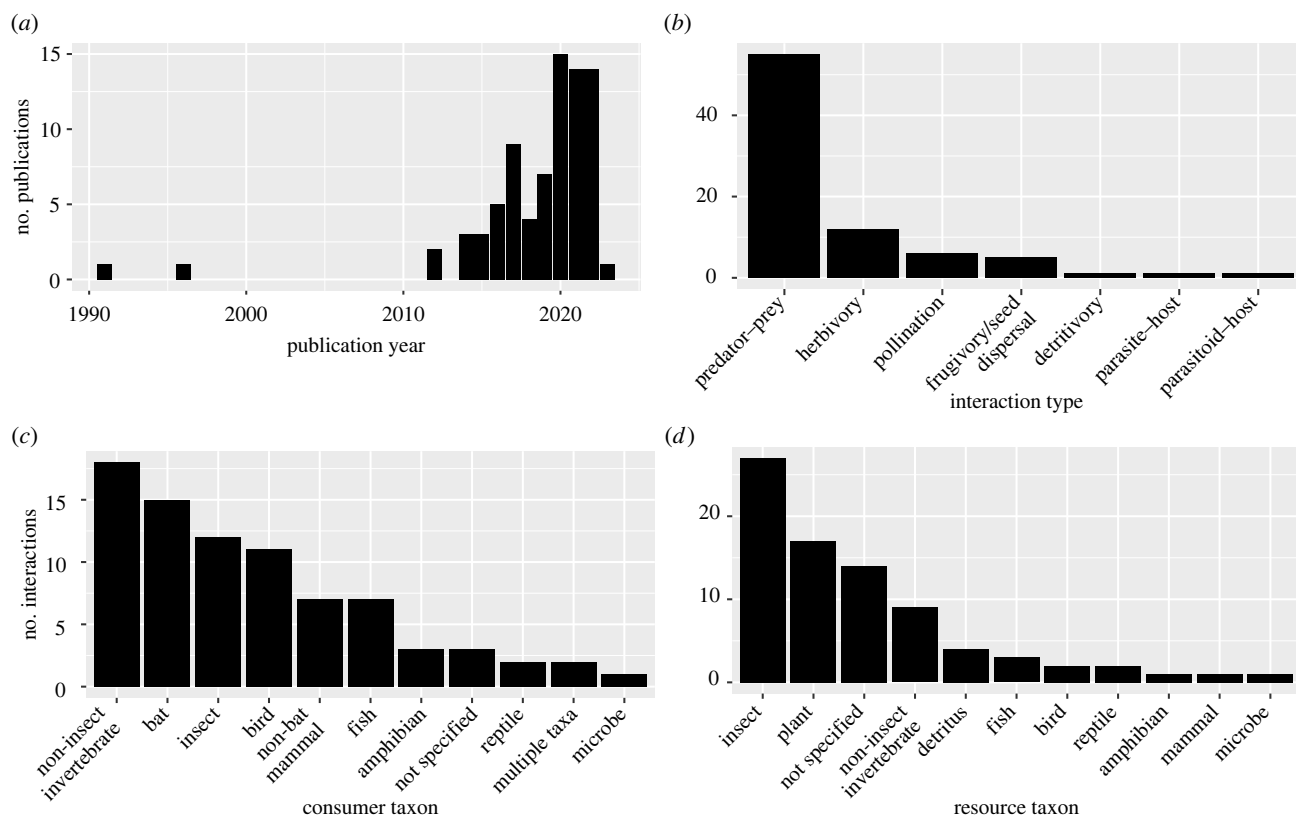


Figure 3. Findings from the literature review on species interactions and ALAN. (a) The number of publications on species interactions and ALAN by year. (b) The number of interactions by interaction type. (c) The number of interactions by taxa for consumer species. (d) The number of interactions by taxa for resource species. Note: (a) is based on 79 publications as Giavi *et al.* [86] and Briolat *et al.* [85] both included two separate interaction investigations, and (b–d) are based on 81 separate investigations.

involved in these reduced interactions were diverse, although dependent upon interaction type. Consistent with the overall findings of detritivory, only amphipods were shown to have reduced foraging/shredding on detritus. Not surprisingly, pollination was only shown to be reduced in insects, specifically moths and their respective pollen sources. Alterations to herbivory occurred with insects, molluscs and mammals. Of the predator–prey interactions, both predators and prey were very diverse in representation, ranging across chiropterans, molluscs, crustaceans, asteroids, fish, arachnids, rodents and birds as predators. The prey consisted of insects, crustaceans, molluscs and sea turtle hatchlings.

Reductions resulted mostly from at least one, if not both, of the species exhibiting photophobic behaviour and avoiding ALAN. For example, Macgregor *et al.* [92] found that moth abundance was halved at lit sites and more concerningly that moths travelling through lit areas had significantly smaller pollen loads. All reductions in detritivory were a result of amphipod photophobic behaviours—amphipods exposed to ALAN remained within their shelters and did not shred detritus at night [84]. Frugivory on pepper plants decreased under ALAN, even within dimly illuminated areas, in Sowell's short-tailed bat (*Carollia sowelli*) owing to a reduction in foraging by the bats [93]. Eckhardt & Ruxton [94] found that insects, albeit dead insects within bird feed, had higher nocturnal predation rates away from direct light sources, and they suggest that this is due to nocturnal insectivores avoiding lit areas. One exception to photophobic behaviours driving the reduction in species interactions was found in herbivory on the greater bird's-foot-trefoil (*Lotus pedunculatus*) by pea aphids (*Acyrtosiphon pisum*), which was not due to photophobia by aphids, but instead due to decreased flowering density of plants under ALAN [95].

Just as reductions resulted mostly from photophobic species, enhancement was due to photophilic species. Enhancements were demonstrated for herbivory (2 studies), and for parasite–host (1 study), parasitoid–host (2 studies), pollination (2 studies) and predator–prey (22 studies) interactions. Interestingly, many taxonomic groups showed both reduced and enhanced species interactions, indicating that the effects of ALAN on species interactions are very species- and context-specific. For example, Cravens *et al.* [91] found that many bat species increased foraging behaviour under ALAN whereas other bat species decreased foraging. The majority of species interactions that were enhanced were due to predator–prey interactions between birds and bats as predators and insect prey (figure 3). Although studies varied across methods and species, the overall trend was similar: many bats increased foraging activity under ALAN and had greater consumption of their insect prey, likely owing to increases in prey abundance [91,96]. It appears that ALAN may be tipping the balance of the evolutionary arms race between bats and moths. Bailey *et al.* [97] found that eared moths, which detect bat echolocation under natural conditions but not artificially lit conditions, had greater predation rates by bats under ALAN. Further enhancements included Australian garden orb-web spiders (*Hortophora biapicata*) selecting web foraging sites in ALAN-rich areas, resulting in higher prey capture rates [78]. Tetragnathid spiders were also positively affected by ALAN [98,99]. ALAN sites had 51% more tetragnathid spiders than dark controls, and prey capture rates were 139% greater in ALAN mesocosms, owing to an 818% increase in the abundance of emergent aquatic insects under ALAN [98]. Avian predation on insects was enhanced by ALAN as owls sought out lit areas and changed their diets to be more

invertebrate-rich, specifically with insects that were attracted to lights [100]. Increases in predator–prey interactions were not limited to terrestrial habitats; predation on aquatic crabs and aquatic invertebrates by vertebrate predators was greatly increased by ALAN [84,101,102].

Although predator–prey interactions were a main focus of enhanced species interactions due to ALAN, several studies found increases in herbivory, parasitism and pollination. The great pond snail, *Lymnaea stagnalis*, had numerous effects from ALAN exposure, including delayed reproductive development and behaviours. ALAN also increased foraging rates at night on lettuce while reducing movement compared with controls [103]. Giavi *et al.* [86] found seed-predacious moths (*Hadena* sp., Noctuidae) selected plants that were adjacent to light sources and thus these plants had the highest seed predation compared with direct light sources or controls. ALAN also increased haemosporidian parasites in dark-eyed juncos, *Junco hyemalis*, [104] as well as increased foraging for pyralid moth hosts by diurnal parasitoid wasps, *Venturia canescens*, during the night [105]. Macgregor *et al.* revealed that plants had higher pollination rates under constant night-time lighting compared with dark controls and partial-night-time lighting, likely due to higher pollinator attraction [106,107].

(a) Temporal mismatches

There were seven cases of temporal mismatch, which is not surprising as most studies focused on species that occupied the same temporal niche. Furthermore, it is possible that several studies may have missed shifts in temporal niches owing to studying non-specific taxa and thus not identifying the normal chronobiology of the resource taxa, for example, insects and zooplankton. Most studies involved predator–prey interactions; however, one investigated the effects of ALAN on a diurnal pollinator, a species of yucca moth (*Tegeticula maculata*) and its host plant, the chaparral yucca (*Hesperoyucca whipplei*) [107]. This study found that although *T. maculata* was diurnal in control plots, yucca in areas with high levels of skyglow had greater rates of pollination and fruit set [107]. Another study documented changes in foraging timing in a diurnal parasitoid wasp (*V. canescens*), which under the influence of ALAN searched for its pyralid moth host (*Ephestia kuehniella*) at night [72]. ALAN has also disrupted temporal niches and associated species interactions in predator–prey contexts. In all five studies documenting a shift in temporal niches involved in predator–prey interactions, vertebrates were the predators. Several species of diurnal birds, including northern mockingbirds (*Mimus polyglottos*), blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*), expand their foraging bouts on insects into the night or begin before twilight when exposed to ALAN [108–110]. Another case of temporal niche expansion was found in the common wall gecko (*Tarentola mauritanica*), which interestingly was dependent upon lunar illumination. Geckos increased foraging under both moonlight and ALAN and relied on ALAN to increase foraging activity during new Moon conditions [69]. Diurnal jumping spiders, *Platycryptus undatus*, also have been shown to extend foraging on insect prey into the night under ALAN [70]. Finally, only one case of temporal niche contraction was reported within the literature. The least horseshoe bats (*Rhinolophus pusillus*) emerged 14 min later under lit conditions compared with dark control

conditions, and even more concerning is that only 10% of bats emerged under light exposure [66].

(b) Spatial mismatches

There were almost four times (27) as many studies finding spatial mismatches between species due to ALAN as the seven studies finding temporal mismatches. The lack of temporal mismatch studies is likely an artefact of study designs for investigating ALAN on species interactions as many studies investigated the presence or absence of consumers and resources under ALAN. However, the lack of temporal mismatch evidence could be indicative of spatial mismatch occurring more often; more research is needed. Most cases of spatial mismatch were due to photophobia or photophilia in one of the species but not both. For example, the nocturnal and endangered rodent, Stephen's kangaroo rat (*Dipodomys stephensi*), exhibited photophobia, was less likely to forage in lit patches and would only fully deplete resource patches under dark conditions [9]. Also, the burrowing owl (*Athene cunicularia*) altered spatial use across the landscape depending upon light sources, with owls preferring lit sites, resulting in the consumption of different prey from owls in dark control sites [100].

As with the other species interaction effects, most cases of spatial mismatch were found in predator–prey interactions, (15/27) and then herbivory (7/27), detritivory (4/27) and finally pollination (2/27). However, as there were 56 studies investigating predator–prey interactions, only 26% of predator–prey interactions demonstrated a spatial mismatch, whereas 63% of herbivory (7/11), 33% of pollination (2/6) and 80% of detritivory (4/5) demonstrated cases of spatial mismatch. Nineteen of the 27 cases of spatial mismatch had the interaction strength reduced, whereas six cases demonstrated enhanced species interactions due to spatial mismatch and two cases showed that the species altered their spatial distribution, but were not able to determine if the interaction was strengthened or reduced. Finally, there were only three studies that showed both temporal and spatial mismatch, all of which were predator–prey interactions that involved vertebrates as the predators. Eleonora's falcons (*Falco eleonorae* [110]) and wall geckos (*T. mauritanica* [69]) extended foraging into the nocturnal niche on migratory birds and insects, respectively, near artificial light sources, thus enhancing the predator–prey interaction both temporally and spatially. Luo *et al.* [66] is the one study that found predator–prey interactions between bats and insects were reduced both spatially and temporally under artificial light owing to bats avoiding both spaces and times with light pollution. We do not believe that these three studies demonstrate that spatial and temporal mismatches between species due to ALAN are rare, but instead, demonstrate that few studies have investigated temporal and spatial mismatch of species interactions under ALAN owing to research biases and the lack of methods and equipment to accurately and effectively quantify species interactions in the presence of ALAN.

6. Next steps, tools, techniques and future directions

Overall, the evidence is clear that ALAN is affecting species interactions in myriad ways; however, the literature is too

sparse currently to make broad conclusions about the impacts of ALAN on species and their interactions within biotic communities. However, there are a few generalizations that can be made from past research. Previous literature is biased towards terrestrial predator–prey interactions focused on predacious bats and birds and is lacking investigations on seed dispersal, parasitism and parasitoids. It also appears that ALAN leads to enhanced species interactions just as often as it reduces species interactions, with closely related species showing different effects [91]. Additionally, species interaction research is lacking depth and breadth regarding direct effects of ALAN on species interactions across time and space, as many studies reviewed did not assess direct effects between species, nor did the studies quantify temporal and spatial alterations of species behaviours. Finally, very few studies connected traits and species' natural histories to the effects of ALAN on interactions, though see [85]. Thus, the field is ripe with opportunities to further expand our understanding of the consequences of ALAN on species interactions across space and time.

Over the last few decades, great strides have been made across three different and complementary methods that now enable us to test hypotheses surrounding ALAN and species interactions: site-based sensors [111,112], individual-based sensors [52] and remote sensing of light at night [24]. As we are advocating for researchers to contain hypotheses surrounding temporal and spatial mismatches in their studies, two factors must be included: time and space. Fortunately, site-based sensors and individual-based sensors include spatio-temporal information. Site-based sensors such as camera traps, passive acoustic monitoring, lidar and radar are powerful and robust tools to quantify the time (in seconds) and space of organisms (in centimetres or metres depending upon the method) in the field [113]. However, in most cases, site-based sensors are limited in their ability to capture species interactions, but instead only enable testing for spatial and temporal overlap in occupancy between two species [114], whereas individual-based sensors such as data loggers and accelerometers allow direct measurements of species interactions. By coupling these site-based sensors and/or individual-based sensors with light loggers or remote sensing of ALAN, researchers can directly quantify how ALAN is disrupting the natural movement and utilization of both space and time across numerous individuals and species.

A few other site-based approaches have developed immensely over the last decade and provide numerous applications to quantifying spatio-temporal distributions of animals under ALAN. Weather surveillance radar will mostly be informative at the landscape scale [115], whereas techniques with lidar are now enabling researchers to quantify and track individuals at the submetre scale. Insects can be identified down to species, sex and life stage in certain contexts across a few-kilometre range [116,117]. As lidar techniques develop, fluorescently labelled insects will be able to be tracked across ALAN sites, resulting in endless applications of real-time quantification of direct species interactions [113,118]. Finally, even traditional techniques for documenting species diversity, such as pitfall traps, have greatly improved enabling researchers to passively quantify communities over temporal scales and now include better spatio-temporal resolution [119]. Time-sorted pitfall traps now enable researchers to quantify predator–prey and pollinator–plant interactions through molecular identification of gut contents and pollen load quantification, respectively [113,119].

A golden age of animal tracking is upon us owing to advancements in animal biotelemetry devices, such as GPS tags, enabling collection of accurate and precise data on individual-based movement at high frequencies and over long periods of time [120–122]. Biotelemetry devices and light loggers continue to decline in size, weight and cost, and increase in accuracy, precision and longevity, enabling many species to be tracked relative to light levels using passive and active telemetry [52,123,124]. Increases in remote data transfer are further enabling higher frequency and accuracy in the monitoring of animal movements spatio-temporally [122]. New generations of tracking devices even allow communication between instruments on different individuals, enabling novel insights into species interactions such as predator–prey [125] or commensalisms. Ideally, studies should combine GPS tags, light loggers and accelerometers to gain full insight into the specific location, light level and specific behaviours of individuals interacting with heterospecifics. Accelerometers have also greatly improved, resulting in understanding specific predator behaviour such as prey strikes in snakes [126] and swallowing of prey in fish [127], as well as activity patterns and antipredator behaviours in prey species [128–130]. Thus, the techniques are available and improving rapidly, which we hope will facilitate further research into the consequences of ALAN on numerous species interactions.

Methods, techniques and equipment for ecologically relevant measurements of light at night continue to improve. There have been several reviews and methods papers highlighting best practices for quantifying light at night in different realms [23,131–134]. Just as with quantifying species interactions, there are numerous appropriate approaches for quantifying ALAN with ecologically relevant metrics [132]. A few guidelines and caveats should be followed for future research on species interactions and light. First, light has several properties that likely affect species interactions, including intensity, spectrum, polarization and flicker. We urge researchers to quantify and/or control these properties as much as possible in their investigations, especially when introducing experimental light into an environment [132]. Second, as Aulsebrook *et al.* [131] stress, researchers must know the limitations of their equipment and methodologies pertaining to light levels. It is very unlikely that dark conditions have zero photons, but instead is much more likely that a measurement of zero reflects the photon detection limit of the equipment [21]. Third, remote sensing via satellite imaging of ALAN is a powerful tool for understanding light pollution at the landscape and continental level [12,43]. However, satellite imaging is not a realistic surrogate for understanding point sources of light in an organism's viewshed [132]. We urge researchers to include both remote sensing techniques (i.e. satellite measurements) and on-the-ground measurements of ALAN to fully understand the light environment in which species are interacting.

7. Conclusion

As ALAN continues to increase, resulting in brighter and shorter nights [11,13], interactions among species are altered, resulting in cascading effects in ecosystems worldwide [19,60]. Our literature review demonstrates that there is considerable evidence that nocturnal illumination affects individuals within their biotic community. However, the burgeoning literature on ALAN and

species interactions is scattered and lacks a unifying framework. We hope that our work here will facilitate productive investigations into the underlying spatio-temporal mechanisms resulting in altered interactions among species. Many questions remain, for example are the effects of ALAN consistent across different species interactions and in which contexts is ALAN destabilizing trophic systems? As biodiversity, and the ecosystem services supported by it, are directly tied to species interactions, it is crucial to understand the impacts of ALAN on the spatio-temporal dynamics of interspecific interactions.

Data accessibility. All data reported within this review are available within the electronic supplementary material including the data frame of the 79 studies investigating species interactions: <https://doi.org/10.6084/m9.figshare.c.6837630> [135].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. B.S.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, validation, visualization, writing—original draft, writing—review

and editing; A.D.: conceptualization, writing—review and editing; F.H.: conceptualization, supervision, writing—review and editing; G.K.: conceptualization, data curation, formal analysis, investigation, methodology, resources, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

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