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Artificial light at night as a driver of evolution across urban–rural landscapes

Gareth R Hopkins[1]*, Kevin J Gaston[2], Marcel E Visser[3], Mark A Elgar[1], and Therésa M Jones[1]

Light is fundamental to biological systems, affecting the daily rhythms of bacteria, plants, and animals. Artificial light at night (ALAN), a ubiquitous feature of urbanization, interferes with these rhythms and has the potential to exert strong selection pressures on organisms living in urban environments. ALAN also fragments landscapes, altering the movement of animals into and out of artificially lit habitats. Although research has documented phenotypic and genetic differentiation between urban and rural organisms, ALAN has rarely been considered as a driver of evolution. We argue that the fundamental importance of light to biological systems, and the capacity for ALAN to influence multiple processes contributing to evolution, makes this an important driver of evolutionary change, one with the potential to explain broad patterns of population differentiation across urban–rural landscapes. Integrating ALAN's evolutionary potential into urban ecology is a targeted and powerful approach to understanding the capacity for life to adapt to an increasingly urbanized world.

Light is fundamental to life on Earth. One constancy in the evolution of life has been the roughly 24-hour oscillation between a bright day, with a light intensity of around 1000–200,000 lux, and a dark night of between 0.0001–0.1 lux, depending on cloud cover and the lunar cycle (Gaston *et al.* 2014; Tierney *et al.* 2017). The vast majority of living organisms have daily and seasonal biological rhythms in key biological processes, such as reproduction (Helm *et al.* 2013; Gaston *et al.* 2014, 2017), that are fundamentally linked to the presence, intensity, and/or spectrum of natural light. The secretion and response of the photosensitive hormone melatonin documented in all higher taxonomic groups (Tan *et al.* 2010) is a key regulator of these biological rhythms, and melatonin is a powerful antioxidant with important fitness effects (Tan *et al.* 2010; Jones *et al.* 2015). The unprecedented global shift in the distribution, intensity, and spectra of artificial light at night (ALAN; Figure 1a) observed over the past century (Gaston *et al.* 2014; Kyba *et al.* 2017) has profoundly disrupted the light cycles perceived by many organisms, and thus the action of one of the most ancient and ubiquitous chemicals of life (Jones *et al.* 2015).

The biological impacts of ALAN, from the scale of molecules to ecosystems, have been well documented (eg Hölker *et al.* 2010; Gaston and Bennie 2014; Swaddle *et al.* 2015; Bennie *et al.* 2016). The degree to which ALAN masks natural daily and seasonal shifts in light is unprecedented in the history of the Earth. Its presence creates a mismatch for traits that inherently depend on natural variations in light patterns (Gaston *et al.* 2014, 2017), and it can directly disrupt behavior, social interactions, survival, reproduction, and physiology (see reviews cited above). ALAN therefore potentially exerts selective pressure on traits of organisms living in urban environments, where light at night is most prevalent; indeed, urban populations of plants and animals often differ genetically and phenotypically from their nearest rural counterparts (WebTable 1; reviewed by Evans 2010; Alberti *et al.* 2017; Johnson and Munshi-South 2017). Elements of urbanization that are thought to result in urban–rural differentiation include noise (eg interfering with acoustic communication; Parris *et al.* 2009), chemical pollution (eg selection for pesticide resistance in urban populations; Jones *et al.* 2012), air pollution (eg inducing mutations; Yauk *et al.* 2000; Somers *et al.* 2002), temperature (eg Thompson *et al.* 2016), and habitat fragmentation caused by roads (Holderegger and Di Giulio 2010). In contrast,

In a nutshell:
- Urban environments can alter the evolutionary trajectories of plants and animals
- Artificial light at night (ALAN) is a key element of urbanization, with increasingly recognized biological effects on organismal fitness, behavior, and movement
- These effects can alter natural selection, genetic drift, and gene flow, thereby leading to evolutionary differentiation of urban and rural populations of plants and animals
- Knowledge of how elements of urbanization like ALAN contribute to evolutionary change is essential for predicting the adaptive potential of populations and improving the management of urban biodiversity

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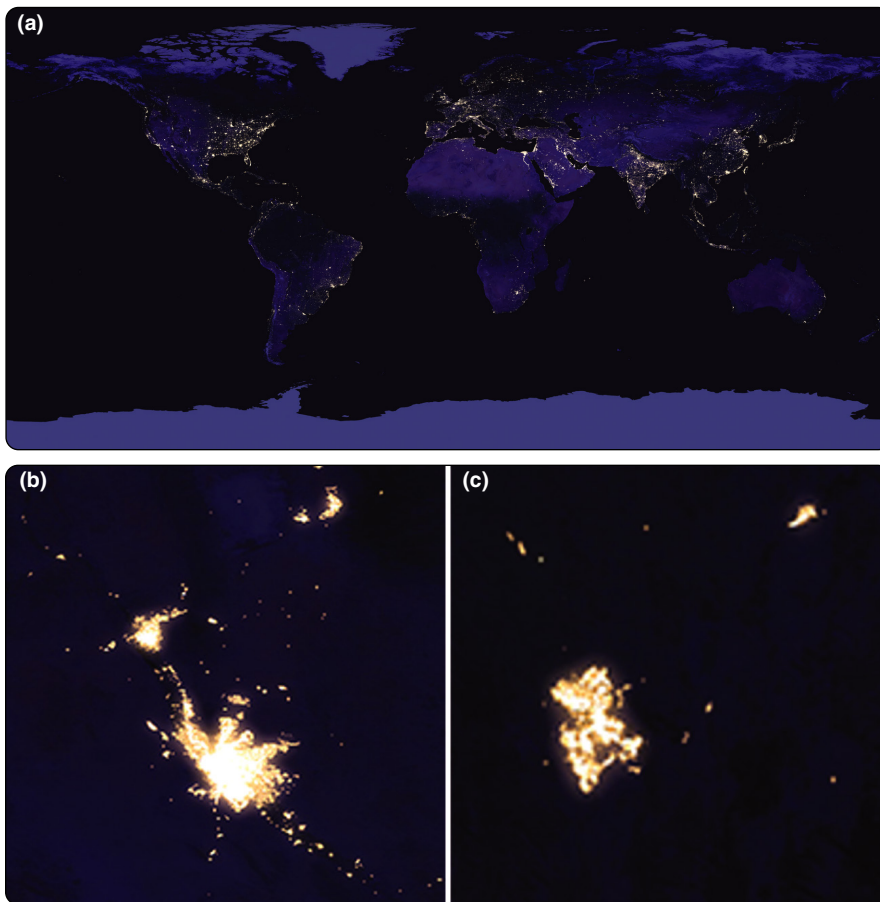
Figure 1. (a) The global distribution of artificial light at night (ALAN), as revealed by composite satellite images taken in 2016. (b) Examples of ALAN fragmenting the landscape along the Mexico–US border (left panel, showing Ciudad Juarez, Mexico; Las Cruces, NM; and Alamogordo, NM, along with smaller towns) and (c) in the area surrounding Canberra, Australia (right panel, showing Goulburn, New South Wales, at top right, along with various small towns). These Visible Infrared Imaging Radiometer Suite (VIIRS) satellite images show brightly lit areas in white or yellow, surrounded by darker, unlit areas. (Maps courtesy of the NASA Earth Observing Satellite Data and Information System [EOSDIS] Observation Group; https://go.nasa.gov/2PbhZSM).
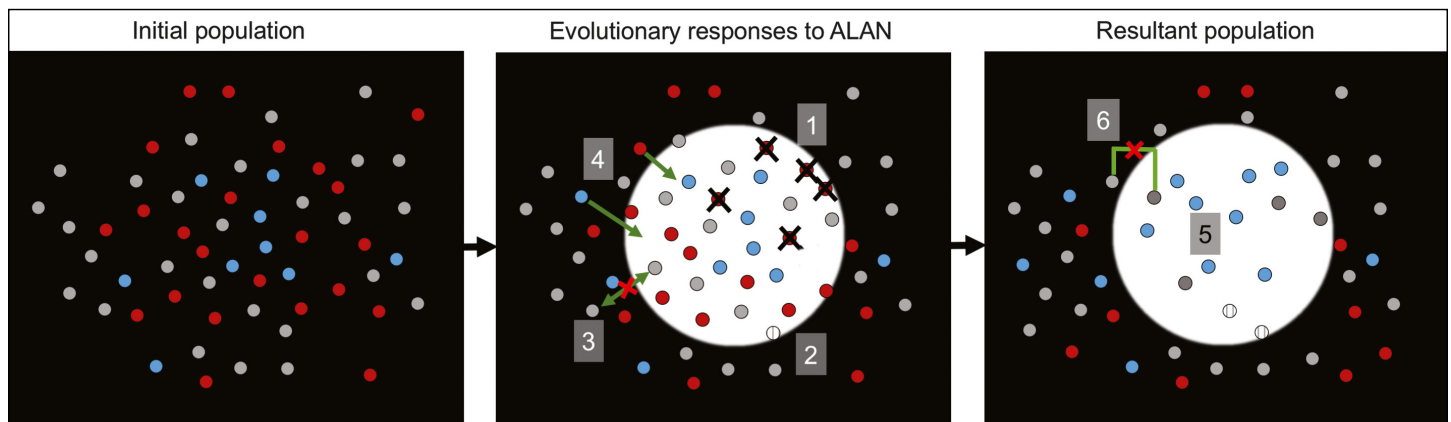
the broad capacity of ALAN to act as a driver of evolutionary change. We outline ALAN's relative potential as an agent of selection, fragmentation, and mutation, and recommend that a concerted research effort be undertaken to address this important topic in urban ecology.

Conceptual framework

Figure 2 illustrates our conceptual framework for the combined effects of ALAN-driven selection, fragmentation, and mutation leading to evolutionary differentiation between urban and rural environments. It should be noted, however, that not all the possible mechanisms of evolution are equally likely to produce genetic differentiation; for instance, ALAN is less likely to be a source of mutations, and rapid adaptive evolution is more likely to be the result of standing genetic variation than new mutations (Barrett and Schluter 2007). We focus on urban–rural comparisons, as these are often employed in genetic and phenotypic studies (Evans 2010; Alberti *et al.* 2017; Johnson and Munshi-South 2017). It is equally plausible that these patterns could apply to lit and unlit areas within an urban or suburban matrix, however, and where exactly on the urban–rural gradient ALAN will have the greatest evolutionary effects is likely be species- and city-specific.

A portion of a contiguous population (a population of animals is illustrated here for simplicity, but many of the principles could apply to plants either directly or indirectly through effects on pollinators and seed dispersers) occupies a large space on the landscape (Figure 2, left panel) that is subsequently lit by anthropogenic processes (Figure 2, center panel). This night lighting alters the behaviors and physiology of the animals within this environment and ultimately affects their fitness. The presence of lighting potentially imposes a strong, novel selection pressure ("1" in Figure 2) on a suite of traits in the illuminated habitat that is not present in the dark habitat. Light at night may also increase the frequency of mutations ("2" in Figure 2), creating genetic variation upon which selection can act.

The change in allele frequencies of the animals in the ALAN-affected area as a result of selection could be reinforced if animals fail to disperse across the light–dark boundary, thereby restricting gene flow ("3" in Figure 2). Conversely, local adaptation could be weakened by the flow of phototactic individuals into the lit population ("4" in Figure 2). Such attraction to light may be either adaptive or maladaptive (see below). If maladaptive, these individuals will be selected against. Genetic drift ("5" in Figure 2) may play a strong role in the resultant population (Figure 2, right panel) if its size has

the role that ALAN might play in explaining these evolutionary patterns has not been widely discussed (but see Swaddle *et al.* 2015; Alberti *et al.* 2017). In a recent review on urban evolution (Johnson and Munshi-South 2017), only one of the 192 studies (Altermatt and Ebert 2016) considered examined ALAN as a putative selection pressure promoting evolutionary change in urban populations. In addition to its potential role as a selective agent, ALAN also fragments the landscape (Figure 1b), altering the spatial patterns and movements of organisms (Gaston and Bennie 2014) in such a way that may influence patterns of gene flow and genetic drift. The combined effects of fragmentation with the ubiquity of ALAN in urban habitats provide potentially strong selection pressures for local adaptation and suggest that ALAN has a broad capacity to drive evolutionary changes in urban populations as compared to rural ones.

We offer a novel, potential explanatory perspective on the widely observed genetic differentiation between urban and rural populations of organisms across the landscape by highlighting

Initial population	Evolutionary responses to ALAN	Resultant population

Figure 2. Conceptual illustration of ALAN acting as a driver of evolutionary change. (Left panel) A hypothetical population composed of 60 individuals with one of three alleles (proportion = 2 gray to 1 red to 0.5 blue) for a particular trait living in a naturally dark at night environment. (Center panel) A section of the environment is artificially illuminated (white circle), imposing strong selection (1) against individuals with the red allele and eliminating them from the population (black "×" symbols). (2) Light might also have mutagenic effects (striped circles), introducing new variation into the population. Individuals with the gray alleles are repelled by light, and will therefore not cross the boundary, reducing gene flow both into and out of the population (3). This changes the frequency of gray alleles in the lit environment. Some individuals are attracted to lights, and join the lit population (4), which may be adaptive (blue) or maladaptive (red). Those maladapted individuals are quickly selected against. (Right panel) Genetic drift (5) then plays a stronger role in influencing evolution in the small (14 individuals) resultant population in the lit habitat. Finally, the resultant lit population is further isolated from the outside population by being phenologically mismatched (6), as light at night causes a change in seasonal reproductive timing (thus the different shade of gray). The final artificially lit population (right panel) now has a higher frequency of blue alleles, and a lower relative frequency of gray and red alleles than the source population (lit population proportion = 1 gray to 0 red to 2 blue; unlit population = 2 gray to 1 red to 0.5 blue), and evolution has occurred.

been reduced due to increased mortality, disruption of reproduction, and the potentially restricted movement of animals into and out of the lit environment. Finally, ALAN may alter the reproductive phenology of the animals, creating a difference in the optimal timing of reproduction in lit and unlit habitats that could generate temporal reproductive isolation of the two populations ("6" in Figure 2).

■ ALAN as a selective agent

ALAN may play a key selective role in trait differentiation in urban environments ("1" in Figure 2). Numerous life-history traits – ranging from body size to immune function, growth and development, and photosynthetic rates (WebTable 1) – vary between urban and rural populations of organisms. These traits have demonstrable links to circadian rhythms, and experiments have confirmed that these traits are susceptible to ALAN (WebTable 1).

ALAN may act directly as an agent of natural selection, for example against positive phototactic behavior (Gaston and Bennie 2014; Longcore *et al.* 2015; Rodríguez *et al.* 2017); in this case, animals attracted to light may be harmed or killed by colliding with the light source, by associated anthropogenic threats (eg hatchling sea turtles attracted to lights on roads), or by predators that specifically exploit phototactic prey attracted to lights (Perry *et al.* 2008; Rodríguez *et al.* 2017). As a consequence, selection should favor less pronounced phototaxis in light-polluted populations of potential prey animals. This evolutionary process has been documented for small ermine moths (*Yponomeuta cagnagella*; Figure 3a); individuals col-

lected during the larval stages from light-polluted urban areas and reared under a common-garden environment (where non-genetic variance could be minimized and controlled) were, when adults, less attracted to light than their rural counterparts (Altermatt and Ebert 2016).

ALAN indirectly affects a broader suite of traits through disruption of circadian rhythms. Photoperiod-dependent phenological traits, such as the timing of growth and reproduction, are the most likely candidate traits. Numerous studies have demonstrated phenological differences between urban and rural populations of plants and animals (WebTable 1), and both laboratory experiments and field studies have clearly shown the impacts of ALAN on plant and animal phenology (WebPanel 1; WebTable 1). Although this variation may be due to phenotypic plasticity, taxa-wide studies of both plants and animals have also demonstrated considerable degrees of heritable variation in phenology in response to different lighting regimes (WebPanel 1), suggesting that ALAN's role as an agent of selection may lead to evolutionary differentiation between populations. Regardless of whether the changes in reproductive phenology are genetic and/or plastic (WebPanel 1), they could promote mismatches in reproductive timing (Gaston *et al.* 2017) and social synchrony (Kurvers and Hölker 2015) between urban and rural populations (and/or between lit and unlit areas within an urban or suburban habitat), and potentially drive temporal reproductive isolation ("6" in Figure 2). In addition, sexual selection may drive reproductive isolation between populations through ALAN-induced shifts in the timing and efficacy of visual (Bird and Parker 2014) and acoustic (Baker and Richardson 2006; Da Silva *et al.* 2014; but see Da

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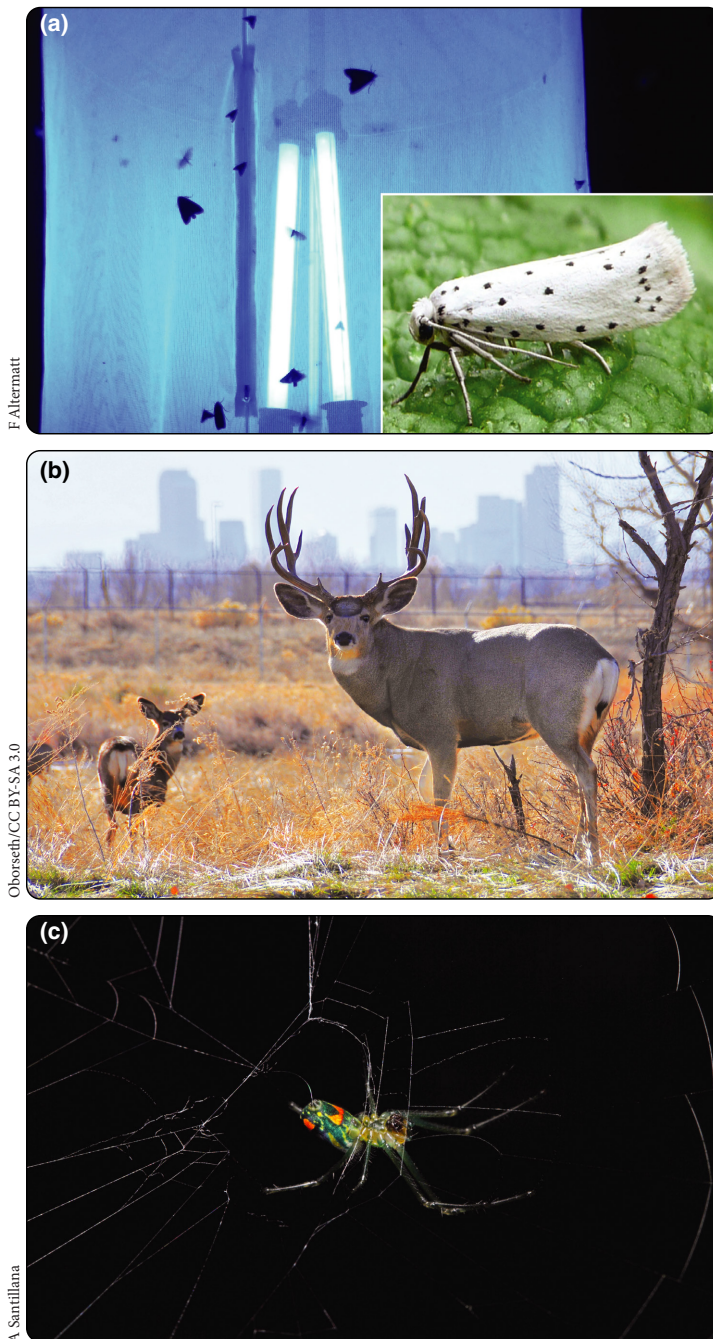
Figure 3. Examples where ALAN may play important roles in shaping urban evolution in animals. (a) Many moth species are highly attracted to lights at night, but small ermine moths (*Yponomeuta cagnagella*; inset) found in urban habitats have evolved to be less attracted to lights than their rural counterparts, probably due to selection against flight-to-light behavior in urban habitats (Altermatt and Ebert 2016). (b) Columbia black-tailed deer (*Odocoileus hemionus columbianus*) will not cross artificially lit habitat and will avoid dark areas immediately adjacent to lit habitat (Bliss-Ketchum *et al*. 2016), potentially restricting movement and gene flow between urban (lit) and rural (dark) populations. (c) Population densities of tetragnathid spiders, such as the orchard orb-weaver (*Leucauge venusta*), are 44% lower in artificially lit areas than in dark habitats (Meyer and Sullivan 2013). This large reduction in population size may make genetic drift an important factor influencing their evolution in urban habitats.

Silva *et al.* 2017) sexual signaling (WebTable 1; Kurvers and Hölker 2015). Moreover, urban–rural differences in traits that are less obviously affected by photoperiod, such as body size (WebTable 1), may nonetheless be shaped by ALAN; for example, exposure to even dim ALAN may cause changes in loco-motor activity, eating patterns, and growth rates of mammals (WebTable 1; Boldogh *et al.* 2007; Fonken *et al.* 2010). More generally, ALAN may disrupt seasonal cycles, which influence growth and developmental rates, and ultimately body size (WebTable 1). Natural and/or sexual selection could then act on ALAN-induced variation in these traits, leading to phenotypic differentiation between urban and rural populations.

◼ ALAN as a regulator of gene flow

ALAN-generated habitat fragmentation (Figure 1b) has important implications for genetic drift and gene flow, two important drivers of genetic differentiation at the landscape scale. ALAN has the capacity to affect gene flow directly in animals by selectively influencing organismal movement (Gaston and Bennie 2014) – of wild mammals (Figure 3b; Stone *et al.* 2009; Bliss-Ketchum *et al.* 2016), fish (Riley *et al.* 2013), aquatic insects (Perkin *et al.* 2014; Manfrin *et al.* 2017), and moths (Degen *et al.* 2016) – through attraction to or repellence by light, and indirectly in plants that may rely on these animals for seed and/or pollen dispersal (Bennie *et al.* 2016; Knop *et al.* 2017). The negative effects of urbanization on pollinators may result in an increased incidence of clonality in plants in cities (Johnson *et al.* 2015), which would result in changes to the genetic composition of urban plant populations. Animals that use light levels around sunrise and sunset or day-length as cues to initiate migratory activity may be particularly affected by ALAN (Gaston and Bennie 2014), given that these are the times when light has the strongest impact (Partecke and Gwinner 2007). For instance, blackbirds (*Turdus merula*) in urban habitats have evolved to be less migratory than their rural counterparts (Partecke and Gwinner 2007), although whether this is due to ALAN, temperature, or some other factor of urbanization remains unclear (Panel 1). The migration patterns of several bird (La Sorte *et al.* 2017), bat (Voigt *et al.* 2017), fish (Nightingale *et al.* 2006), and moth (McCormick 2005) species are disrupted by ALAN; such alterations in movement into and out of lit habitats may restrict gene flow ("3" in Figure 2), amplifying the effects of local adaptation while simultaneously limiting the influx of genetic diversity. Ultimately, genetic drift could become an important evolutionary force in affected habitats if fragmented populations become increasingly isolated and are reduced in size through a lack of dispersal and reduced immigration ("5" in Figure 2). For example, it has been suggested that ALAN-influenced gene flow followed by genetic drift promoted genetic differentiation of the Chagas-disease vector kissing bug (*Triatoma infestans*) in urban areas (Schofield *et al.* 1999), although this hypothesis has not yet been explicitly tested.

Panel 1. Disentangling the elements of urbanization

By definition, urban areas have high concentrations of a wide variety of potential stressors, including noise, impervious surfaces, temperature, heavy metals, salts, and chemical pollution (Swaddle *et al.* 2015; Johnson and Munshi-South 2017), which, in addition to ALAN, may influence evolutionary outcomes. A difficult challenge is determining their relative importance, as identifying the specific elements of urbanization that result in urban–rural differentiation is key to effective and targeted management. A multifaceted and integrated approach is necessary to achieve this goal; specifically, we recommend that researchers integrate as many of the following approaches and techniques as possible in their studies:

(1) Take a comprehensive approach in formulating hypotheses; the element of urbanization that might seem obvious in affecting a particular trait might not always be the primary driver, and numerous factors could influence the trait directly, indirectly, and interactively (eg McMahon *et al.* 2017);

(2) Measure as many factors of urbanization as possible in the field (eg light, noise, temperature, percent of impervious surfaces, chemical pollutants, and so forth), in as many cities as possible, and incorporate these into multifactorial mixed models to disentangle

significant from non-significant factors and test for interactions. Use a combination of measurement techniques, including remote sensing and on-the-ground directional sensors (eg Azam *et al.* 2016; Thompson *et al.* 2016; Casasole *et al.* 2017). The presence of a multitude of replicate cities around the world (Johnson and Munshi-South 2017), each likely varying in the relative importance of specific elements of urbanization, where geographically widespread species could be examined, make this multifactorial approach especially promising;

(3) Conduct controlled, common-garden experiments to isolate causal factors (Swaddle *et al.* 2015) and replicate these under field conditions to test competing factors (Holzhauer *et al.* 2015; Spoelstra *et al.* 2015; Thompson *et al.* 2016); and

(4) Move beyond overall genetic diversity measures (eg molecular measures of heterozygosity) to target specific candidate genes with known phenotypic links, and simultaneously test for both phenotypic and genetic variation in both the wild and in controlled experiments to link trait and allele frequencies (Thompson *et al.* 2016; Johnson and Munshi-South 2017).

ALAN as a promoter of genetic drift

ALAN has a direct and well-studied influence on mortality and may influence reproductive rates (WebTable 1; Gaston and Bennie 2014). How these demographic changes translate into reductions in population size that could make genetic drift an important driver of evolution in urban habitats is not well understood. ALAN has the potential to reduce population size and promote genetic drift by acting as an evolutionary and ecological trap (Hale and Swearer 2016; Manfrin *et al.* 2017). By attracting a subset of organisms maladapted to the presence of ALAN ("4" in Figure 2; Gaston and Bennie 2014; Manfrin *et al.* 2017), this could result in either a severe bottleneck (if attraction to lights is lethal) or founder effects in the illuminated population, which could further inflate the importance of drift in this habitat. Long-term increases in nighttime light pollution have been implicated as a possible cause of population declines in Macaronesian shearwaters (*Puffinus baroli*) in the Canary Islands (Rodríguez *et al.* 2012) due to the well-known (and often fatal) attraction of seabirds to ALAN (Rodríguez *et al.* 2017). Although such studies suggest a role for ALAN in reducing population size, causation is generally much more difficult to determine with certainty. Field experiments in which lights are added to previously dark habitats are yielding informative results for invertebrates and microbes; for instance, experimental additions of streetlights along a stream-reach in the US resulted in a 44% reduction in tetragnathid spider (Figure 3c) population density over the course of a year (Meyer and Sullivan 2013), and a long-term (five generations) mesocosm study of aphid populations exposed to ALAN in the UK demonstrated reduced population density of two species (*Megoura viciae* and *Acyrthosiphon pisum*) due to the bottom-up effects

of ALAN on their host plants (Sanders *et al.* 2015). This reduction in population density under ALAN treatments was also observed for the aphids' respective parasitoid wasps, *Aphidius megourae* and *Aphidius ervi* (Sanders *et al.* 2015). Abundance of freshwater mixotrophic and heterotrophic (but not photo-autotrophic) microbes in Germany also decreased after 5 months of experimental illumination in the field (Hölker *et al.* 2015). The well-known congregation of predators around artificial light sources (Perry *et al.* 2008; Rodríguez *et al.* 2017), and the fact that this increase in predator populations may be permanent for some taxa (ie not due simply to short-term nocturnal phototaxis; Davies *et al.* 2012, 2017; Manfrin *et al.* 2017), could lead to further reductions in the populations of many organisms through increased predation. Future research that links the effects of ALAN on fitness and organismal movement to demonstrated reductions in population size, genetic diversity, and genetic differentiation are required to clarify the relative importance of ALAN as a promoter of genetic drift in urban populations.

ALAN's possible mutagenic effects

The possible effects of ALAN in altering the genetic composition of populations by inducing mutations are currently unknown. Exposure to ultraviolet (UV) light in the laboratory (at concentrations greater than that found in most streetlights) is mutagenic to both fish and mice (Grunwald and Streisinger 1992; Pfeifer *et al.* 2005). Although UV light is present in certain types of commonly used streetlights (ie mercury vapor and metal halide; Lamphar and Kocifaj 2013), the intensities of and degree of exposure to these lights that are required

to induce mutations in the wild have yet to be determined. Because the potential effects of ALAN on mutation rates are likely to be highly wavelength-dependent, not all forms of ALAN would have the same mutagenic capacity. In particular, the current worldwide trend of replacing older lighting technologies with non-UV light-emitting diodes (LEDs) appears to further diminish this potential, and we therefore consider it unlikely that streetlights are an important cause of genetic mutations in urban environments.

One possible wavelength-independent mutagenic role for ALAN could be through its well-characterized action of suppressing melatonin, a powerful antioxidant (Jones *et al.* 2015). ALAN's suppression of melatonin might lead to increased mutation rates in urban environments through increased oxidative stress, as an accumulation of reactive oxygen species is linked to the impediment of cellular repair mechanisms and can result in increased mutations (Mikhed *et al.* 2015; but see Itsara *et al.* 2014). However, although the links between ALAN, melatonin, and oxidative stress are largely understood in theory (Colin-Gonzalez *et al.* 2015; Jones *et al.* 2015), empirical evidence is currently lacking (but see Escribano *et al.* 2014), especially in field populations (Casasole *et al.* 2017). Differences in mutation rates between urban and rural populations of animals have been documented in the field, but such variation is usually attributed to air pollution (Yauk *et al.* 2000; Somers *et al.* 2002). It is therefore unclear whether the differences in mutation rates between urban and rural environments can be attributed to any possible mutagenic effects of ALAN.

■ Challenges and opportunities

Key challenges remain in identifying the role that ALAN plays in influencing urban evolution. Several of these challenges, which present opportunities for interdisciplinary research, are summarized below:

(1) Investigate the genetic basis for phenotypic differentiation between urban and rural environments, and the key genotype × ALAN interaction for selected traits (WebPanel 1);

(2) Determine the population-level effects of ALAN. Past research has focused primarily on the biological effects of ALAN at the individual and community levels, whereas evolutionary effects at the population level have been largely overlooked;

(3) Understand how the spectral qualities of different types of ALAN may impact individuals, populations, and species interactions in ways that could influence evolutionary processes (Davies *et al.* 2017; Longcore *et al.* 2015; Spoelstra *et al.* 2015);

(4) Explore how spatial and temporal variations in ALAN influence evolutionary processes. In this paper, we assumed that ALAN is relatively homogenous and constant in urban habitats, but clearly this is an oversimplification; in reality, urban habitats are complex matrices of light and dark, with lights of different intensities and spectra rapidly switched on or off, and shaded by buildings, walls, and vegetation. Light also varies spatially (and not always linearly) along an urban–rural gradient, and therefore trying to predict where along this gradient light will have the greatest evolutionary effect is difficult and will most likely be species- and city-specific. The effects of ALAN may also vary with latitude, which causes variance in natural light–dark cycles (Da Silva and Kempenaers 2017). This variation may have important implications for (a) gene flow between and within populations and metapopulations; (b) fragmentation, effective population size, and genetic drift; and (c) selection strength;

(5) Disentangle ALAN from other elements of urbanization that could be responsible for evolutionary changes and examine the potential for interactions (McMahon *et al.* 2017) among urban stressors (Panel 1).

■ Conclusions

The dramatic rise in artificial nighttime illumination in urban areas around the world over the past century represents an unprecedented shift in the abiotic environment (Gaston *et al.* 2014). Arguably more than any other factor, light underpins the physiological mechanisms, rhythms, behaviors, and functionality of nearly all organisms, and is therefore fundamental to life on Earth. The direct links between urban environments, ALAN, and the prime importance of light argue for ALAN's role in influencing taxon-wide patterns of population differentiation across urban–rural landscapes. ALAN has a substantial capacity to alter evolution through its taxonomically broad effects on selection, reproductive isolation, gene flow, and genetic drift. Despite the current paucity of direct evidence of the evolutionary importance of ALAN, the large body of indirect evidence amassed to date strongly suggests that ALAN has an influential role in urban evolution.

Connecting the role of ALAN as a driver of evolutionary change with the extensive evidence of urban–rural population genetic differentiation (reviewed by Evans 2010; Alberti *et al.* 2017; Johnson and Munshi-South 2017), and successfully disentangling the effects of light from other elements of urbanization (Panel 1), remain important tasks that will require careful and concerted efforts by scientists across disciplines. Nevertheless, investigating the evolutionary impacts of ALAN provides an opportunity to address key questions in evolutionary ecology by integrating field measurements, experiments, and tests of both phenotypic and genetic differentiation across the urban–rural landscape (Johnson and Munshi-South 2017). Doing so will improve targeted management of the biological impacts of urbanization and provide a better understanding of how organisms adapt and survive in an increasingly urbanized and brightly lit world.

■ Acknowledgements

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