

Assessing the effects of artificial light at night on biodiversity across latitude – Current knowledge gaps

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Assessing the effects of artificial light at night on biodiversity across latitude – current knowledge gaps

Running title: Light pollution and biogeography

ABSTRACT

Aim: Exposure to artificial light at night (ALAN) is a risk factor for organisms. Considering the spread and increasing intensity of night brightness across the globe, and the key role of light at all biological levels, alterations of ecosystems are expected. Yet, we cannot predict the severity of the effects of ALAN in several biomes because little information is available outside the temperate zone. We reviewed current knowledge and identified traits that could be targeted to fill this knowledge gap in order to contribute to the elaboration of a biogeographical framework for the study of ALAN at the global scale.

Location: global

Time period: current and next decades

Method: We analysed the latitudinal variation of ALAN and focused on environmental factors that vary with latitude but that have been overlooked. We reviewed biological traits that exhibit latitudinal variation and depend on light and photoperiod and compiled information about the predicted changes of human demography and road networks across different world regions.

Results: Cloud cover amplifies ALAN far away from urbanized areas. Because of the increased frequency of overcast night skies, exposure effects may be stronger both at high latitudes and across a large fraction of the intertropical zone, though at different times of the year. Intertropical biomes host the largest fraction of global biodiversity. Although currently they are not the most exposed to ALAN, their human populations are growing, and urbanized areas and road networks are expanding. Hence, ALAN could have strong ecological consequences, with cloud cover as an aggravating factor.

Perspectives: Knowledge gaps currently limit our ability to predict the effects of ALAN in different biomes. Therefore, it will be important to start investigating the consequences of this novel environmental factor across the globe, in order to develop a relevant theoretical framework

Keywords: ALAN, light pollution, intertropical, latitude, global change, biogeography, exposure

1 ALAN as an emergent global risk for biodiversity

Habitat loss, climate change, pollution, invasive species, and overexploitation negatively affect a large part of the Earth's ecosystems, if not all of them (Millenium Ecosystem Assessment, 2005). Artificial light at night (ALAN) is emerging as another potential threat to biodiversity worldwide (Bennie *et al.*, 2015b; Davies & Smyth, 2018). ALAN is mainly generated by urbanized areas and transport infrastructures, and exposure happens either via direct lights or via skyglow. The latter is produced by the scattering of light by atmospheric particles and aerosols from distant sources. It can be detected dozens of kilometres away from a major source like a city by animals (Kocifaj & Lamphar, 2014; Aubé, 2015), whose sensitivity can be very high for nocturnal species (Kelber & Roth, 2006; Kelber *et al.*, 2017). ALAN now alters the natural photic regime across a large fraction of Earth (Cinzano *et al.*, 2001; Longcore & Rich, 2004). Recently, it has been estimated that 23 % of land surfaces between 60°S and 75°N are exposed to light polluted skies (Falchi *et al.*, 2016).

ALAN has been gaining attention from the scientific communities, authorities, and more generally societies. Concerns have initially sprung from astronomers that warned about the loss of quality of the nocturnal sky, and spread to other fields. New issues have been raised and expressed in reviews (Longcore & Rich, 2004; Navara & Nelson, 2007; Hölker *et al.*, 2010; Gaston *et al.*, 2013, 2015) and opinions (Nadis, 2002; Smith, 2009) for the last 15 years. ALAN generates a broad array of effects on animals, and as far as we know to a lesser extent on plants or micro-organisms (Hölker *et al.*, 2015; ffrench-Constant *et al.*, 2016; Bennie *et al.*, 2017). These effects range from the molecular (Honnen *et al.*, 2016) to the community (Rich & Longcore, 2006a; Hölker *et al.*, 2015; Bennie *et al.*, 2017), and ecosystem level (Lewanzik & Voigt, 2014; Sanders *et al.*, 2015; Knop *et al.*, 2017). As for the other major risk factors for biodiversity, ecosystem exposure to ALAN has been assessed at the global scale (Bennie *et al.*, 2015b; Davies *et al.*, 2016; Falchi *et al.*, 2016; Kyba *et al.*, 2017a; Guetté *et al.*, 2018). The field is expanding fast as revealed by the recent bloom of publications (Davies & Smyth, 2018). Nevertheless,no framework has been developed to predict whether and how the intensity of the effects caused by ALAN varies across the globe yet.

Photoperiod is crucial for many biological processes and ecological interactions. It is a major environmental cue that resets circadian rhythms and prime seasonal change in activity (Coppack & Pulido, 2004; Hut *et al.*, 2013). Photoperiod varies widely with latitude and this affects the importance of light as a cue depending on the location on Earth. Similarly, a general biogeographic rule is the occurrence of latitudinal biodiversity clines, the intertropical zone hosting more species than temperate or arctic environments (Willig *et al.*, 2003; Hillebrand, 2004; Mittelbach *et al.*, 2007). Exceptions have been observed (Willig *et al.*, 2003) but the statement holds true for vertebrates such as freshwater fishes (Abell *et al.*, 2008), birds, mammals, amphibians (Jenkins *et al.*, 2013), insects (Guenard *et al.*, 2012), and vascular plants (Kreft & Jetz, 2007). Surprisingly, while the major biodiversity hotspots are mainly located within the intertropical zone, we do not know whether the effects of ALAN in biodiversity are stronger at low than at mid or high latitudes.

From a literature survey on Scopus (accessed on 22/09/2019) using the combination of keywords (tropic* OR equat*) and “artificial light”, “artificial” AND “light”, or “light pollution”, we identified eleven references (Erkhert, 1976; Thakurdas *et al.*, 2009; Lewanzik & Voigt, 2014; Bennie *et al.*, 2015b; Dorado-Correa *et al.*, 2016; González-Bernal *et al.*, 2016; Gupta & Pushkala, 2016; De Freitas *et al.*, 2017; Gineste *et al.*, 2017; Rivas *et al.*, 2018; Frank *et al.*, 2019). Another search using the combination ("artificial light" OR "light pollution") AND "latitud*" accessed on Scopus on the same date yielded 59 hits. Four additional and partly relevant references were found. These were three reviews in which artificial lighting was not the main topic (Higuchi, 2010; Borniger & Nelson, 2017; Brelsford *et al.*, 2019), and one research paper on humans (Martín-Olalla, 2019). In comparison, a search using “light pollution” OR “artificial light”, and restricted to the Agricultural and Biological Sciences section yielded 233 relevant references. More information is certainly present but not necessarily in papers addressing directly ALAN as previously noted (Rich & Longcore, 2006b). Nevertheless, these figures highlight the publication bias between biomes and the fact that authors do not explicitly consider the biogeographical context.

Assessing the biological and ecological effects of ALAN at a global scale is now urgent. Yet, neither the systematic investigation of environmental factors varying at a biogeographic scale and

affecting the sensitivity of organisms to ALAN, nor the identification of the areas/ecosystems/biomes the most threatened now or in the near future, has been undertaken. We need a biogeographic framework to assess how the exposure risk for biodiversity varies across ecosystems or regions, and we present here the first attempt in that direction. We will focus on the latitudinal variation of environmental factors that affect the photic regime, summarize what biological processes vary with latitude, and provide a prospective view of the evolution of ALAN with a particular emphasis on the intertropical zone.

2 The geographical extent of ALAN and its effect on biodiversity

ALAN exposure at a given site depends on the distance to the light sources, their power and spectral composition (Luginbuhl *et al.*, 2014), the natural light regime (moon phase, visual barriers), and the atmosphere composition, including the presence and altitude of clouds. Cloud cover reflects artificial light downward and over large distances. For this reason, it has been identified as a major factor enhancing nocturnal light levels (Kyba *et al.*, 2011; Kocifaj & Lamphar, 2014). ALAN intensity, as measured by satellites, has kept increasing worldwide for the last decades, with local or regional variations (Falchi *et al.*, 2016), and changes were still recently detected over a short 5-year period for most countries (Kyba *et al.*, 2017a). All major ecosystems are now exposed (Bennie *et al.*, 2015b), including the intertropical zone (**Figure 1**). To highlight this point, we used the data from the last published World Atlas (Falchi *et al.*, 2016) and plotted the latitudinal distribution of ALAN in 5° bins. The highest mean values were observed between 30° and 40° in both hemispheres. The standard deviation was maximal for northern temperate latitudes. However, the largest variation occurred around 10°N which is explained by the large expanses of darker land in Africa and brightly lit areas in northern Venezuela, Southern India, and Malaysia. ALAN keeps on increasing in this area. Between 2012 and 2016, an elevation of upward radiance in the intertropical zone was detected at the country level (Kyba *et al.*, 2017a), while up to 35 % of the area covered by tropical ecosystems in Brazil experienced higher brightness at night between 2008 and 2012 (De Freitas *et al.*, 2017).

Insert Figure 1

Light intensities consistent with field measurements of ALAN alter the physiology of organisms, the behaviour of animals, and ecological processes. We will only outline the main traits and processes relevant to this article. For more extensive treatment, several review articles and book chapters have been published that can be referred to (Longcore & Rich, 2004; Rich & Longcore, 2006a; Perry *et al.*, 2008; Gaston *et al.*, 2013, 2015, 2017; Stevens & Zhu, 2015; Grubisic *et al.*, 2018; Owens & Lewis, 2018; Desouhant *et al.*, 2019). ALAN affects activity and time partitioning (Rich & Longcore, 2006a; Le Tallec *et al.*, 2013; Dominoni *et al.*, 2014; Da Silva *et al.*, 2015), orientation (Salmon, 2003; Pawson & Bader, 2014; Thums *et al.*, 2016), space use (Moore *et al.*, 2000; Stone *et al.*, 2009), foraging (Dwyer *et al.*, 2013; Cravens *et al.*, 2017; van Langevelde *et al.*, 2017), social interactions including sexual behaviour (Kurvers & Hölker, 2015; van Geffen *et al.*, 2015; Firebaugh & Haynes, 2016), and life-history traits (Van Geffen *et al.*, 2014). Foraging behaviour can be modified in opposite ways depending on the focal species (Dwyer *et al.*, 2013; Cravens *et al.*, 2017). At the sensory level, the effects of ALAN primarily depend on the spectrum and intensity of ambient light, and the photoreceptor characteristics (Endler, 1990). Individuals, in insects or amphibians for instance, can be attracted or repelled by unusual brightly lit areas (Hailman & Jaeger, 1974; Owens & Lewis, 2018), but more subtle process can be altered, like colour vision. Dim-light colour vision based on cones in insects and reptiles (Kelber & Roth, 2006), and rods in amphibians (Gomez *et al.*, 2009; Yovanovich *et al.*, 2017) has now been demonstrated. Therefore, the capacity of individuals to detect and select food items, or catch prey can be modified under ALAN because the contrast between the target and the background is altered.

Regarding **physiology**, ALAN is a major source of circadian disruption that generates metabolism, sleep and cognitive disorders, depression syndrome, and may increase risk of some cancers (Stevens *et al.*, 2013; Borniger *et al.*, 2014; Bedrosian *et al.*, 2015; Chellappa *et al.*, 2018). It inhibits the production of melatonin, a hormone that modifies stress response, mitochondria functioning,

oxidative stress, metabolism, and immune defence (Carrillo-Vico *et al.*, 2005; Tan *et al.*, 2010; Tallec *et al.*, 2016). Melatonin holds a central role in these processes because of its multifarious effects on circadian timekeeping and the regulation of biological rhythms (Hardeland *et al.*, 2011). The circadian variation of melatonin has been observed from bacteria to vertebrates (Tan *et al.*, 2010), and the effects of this molecule on clock genes have been demonstrated in vertebrates and arthropods. These molecular mechanisms likely date back at least to the cnidarian-bilaterian divergence (Peres *et al.*, 2014), which illustrates the taxonomic breadth of groups potentially affected by ALAN. The strength of the effects may depend on the diel activity patterns, with cathemeral species being probably less sensitive to changes in photoperiod than diurnal, nocturnal or crepuscular species. In plants, effects on physiological processes, including photosynthesis, and photoperiodism are expected (Aubé *et al.*, 2013; Singhal *et al.*, 2019). Individuals need to be relatively close to the light sources but physiological effects have been observed (Bennie *et al.*, 2016, 2017; ffrench-Constant *et al.*, 2016). The uncoupling between the thermal and photic cues caused by ALAN may affect the timing of seasonal processes like dormancy (Aubé *et al.*, 2013; Hut *et al.*, 2013; ffrench-Constant *et al.*, 2016; Solano-Lamphar & Kocifaj, 2018). However, the actual consequences for plant population largely remain to be investigated (Knop *et al.*, 2017; Macgregor *et al.*, 2019).

Because of the biological effects cited above, ALAN is expected to affect **ecological** processes like energy or nutrient fluxes or relationships in trophic networks (Longcore & Rich, 2004; Perkin *et al.*, 2011; Gaston *et al.*, 2013; Meyer & Sullivan, 2013; Bennie *et al.*, 2015a; Mathews *et al.*, 2015; Sanders *et al.*, 2015; Knop *et al.*, 2017; MacGregor *et al.*, 2017; Miller *et al.*, 2017). More generally, the synchronisation between the components of any interspecific interactions can be altered (Bennie *et al.*, 2015a; Helm *et al.*, 2017; Kronfeld-Schor *et al.*, 2017). Therefore, behavioural and physiological effects on individuals may scale up to the population, community and ecosystem level (Sanders & Gaston, 2018). Evidence of disruption on micro-organism, arthropod, and plant community has been provided (Meyer & Sullivan, 2013; Pawson & Bader, 2014; Hölker *et al.*, 2015; Bennie *et al.*, 2017; Knop *et al.*, 2017), but so far no evidence of large scale effects on ecosystems have been reported. Nevertheless, studies showing reduced efficiency of plant pollination by insects (Knop *et al.*, 2017;

MacGregor *et al.*, 2017) and bats (Lewanzik & Voigt, 2014), or increased predation on agricultural pest by insect (Miller *et al.*, 2017) suggest that large effects may occur in natural environments and agrosystems.

3 Natural factors modulating exposure to ALAN at the global scale

To understand how ALAN affects organisms and populations depending on their position on the globe, the geographical variation of factors that naturally determine the light-dark regime should be considered: photoperiod, lunar cycle, twilight, and climate. **Photoperiod** varies in a predictable way, with annual variation in daylength increasing with latitude, from about 0 % at the Equator to 100 % at the Arctic Circle.. In other words, photoperiod is more constant towards the Equator and more variable towards the poles.

Moonlight is the brightest nocturnal light source in pristine environments. The lunar cycle lasts 29.52 days and is synchronous at all latitudes. While Moon phase and Earth-Moon distance change, the former parameter contributes much more to the variation of illuminance. Natural maximal illuminance on Earth and under optimal conditions is 0.32 lux and in the intertropical zone only. Because of its orbital plane, the Moon can be seen at the sky zenith, where illuminance is maximal, only at locations lower than 28° latitude (Kyba *et al.*, 2017b). Thus, the Moon is less bright at higher latitudes. Illuminance lies typically within 0.05-0.2 lux at mid-latitude (Kyba *et al.*, 2017b). Brightness varies with season because of the change in the distance to the Sun and elevation. Moon elevation is higher in winter than in summer.

The variation in duration and intensity of moonlight cannot be used to determine the exact time or date. Yet, moonlight is more and more recognised as a major feature on the nocturnal environment for animals. Effects on activity, orientation, and communication have been observed in invertebrates and vertebrates (Dacke *et al.*, 2003; Grant *et al.*, 2009; Kronfeld-Schor *et al.*, 2013). In particular, moonlight is expected to suppress activity to reduce predation risk, especially in open habitat species.

194 This prediction was confirmed in amphibians (Vignoli & Luiselli, 2013) and all groups of nocturnal
195 mammals but primates for which higher activity during bright nights may reflect a better ability to detect
196 predators and forage (Prugh & Golden, 2014). One direct consequence of ALAN is that elevated
197 brightness tends to mask the natural photic variation as moonlight is attenuated against the skyglow
198 background (Davies *et al.*, 2013a).

199 **Twilight** is the transition between day and night when Sun drops under the horizon. It is split
200 into three periods that are characterized by the Sun declination and the colour of ambient light. During
201 the civil twilight the sun declination lies between 0 and 6°. Light level drops sharply during the nautical
202 twilight (declination 6-12°) and less quickly during the astronomical twilight (declination 12-18°).
203 Irradiance turns from a red dominant spectrum to a blue dominant spectrum (Johnsen, 2011). After
204 twilight, the irradiance spectrum of the sky depends on the Moon and other light sources. There is a
205 latitudinal cline in twilight duration that is shorter at lower latitudes (**Figure 2**). Some authors have
206 considered as "semi-darkness" the merged periods of twilight and lunar phases where at least 26 % of
207 the Moon is visible (Mills, 2008). Darkness is a relatively vague concept given the variable visual
208 capacity of species under dim light (Kelber & Roth, 2006). Nevertheless, the duration of natural semi-
209 darkness remains constant around 4.5h at the Equator and varies widely from 0h to 9h at 75°(Mills,
210 2008) and forms a gradient parallel to the photoperiod gradient. ALAN generates light levels in the same
211 range of those observed during natural twilight and can, therefore, extend the duration of this period.
212 Circadian rhythms which are reset with twilight. The rapid changes in light intensity and colour are
213 reliable cues to determine the onsets and the ends of activities like foraging or mating (Daan & Aschoff,
214 1975; Andersson *et al.*, 1998; Boulos & Macchi, 2005).

215 The importance of **cloud cover** in the global assessment of ALAN has probably been overlooked.
216 Clouds amplify light emitted from the ground, extend the photophase in light-polluted areas whereas
217 they mask celestial objects, dim their lights, and shorten the photophase in non-polluted areas. It is
218 important to keep in mind that global models of ALAN underestimate exposure at ground level because
219 they use upward radiance recorded from satellite images. The representation of a cloud-free world
220 elicited by these images may thus bias our perception of the phenomenon. The spatial extent of ALAN

during overcast nights is much broader (Kyba *et al.*, 2011; Kocifaj & Lamphar, 2014). A logical conclusion is that, all other factors being equal, the intensity, spread, and the annual number of days with high levels of ALAN should be related to the annual number of days with overcast skies, although rain or mist could strongly attenuate light transmission. Because cloud cover is crucial to determine the spatial extent of ALAN, it is important to consider how uneven its annual distribution on Earth is. A recent multi-year study of cloud cover mapped the average cloud fraction (number of pixels covered) across the World during the day and at night. **Figure 1** shows the latitudinal distribution of cloud fraction between July 2002 and April 2018 excluding seas and large lakes. Higher values were observed in the Arctic and subarctic regions and within the intertropical zone where cloud cover was particularly high in Central Africa, the Amazonian basin and Central America, India, and south-east Asia (King *et al.*, 2013). The annual variation in cloud cover is also the lowest for both areas. Owing to latitude and cloud cover, organisms in the intertropical zone often experience a stable photoperiod and on average a darker visual environment than in any other region on the globe. In the tropics, the variation in cloud cover is maximal and cloud cover low due to the presence of areas with arid or humid climates. Changes in the fraction of high clouds, and precipitation have been observed in the intertropical convergence zone but the expected trends for the next decades are still debated (Legates *et al.*, 2014; Mauritsen & Stevens, 2015; Norris *et al.*, 2016; Wodzicki & Rapp, 2016). Rainfall is also expected to decrease or increase depending on regional trends (Kitoh *et al.*, 2013; IPCC, 2014), and uncertainty is higher for rainfall than temperature models especially in the tropics (Corlett, 2012). Furthermore, a consensual prediction is a higher frequency of extreme rainfall events, largely in the form of storms shorter than a day (Westra *et al.*, 2014), which may not affect the annual number of overcast days. More robustness in climate models related to cloud cover and precipitation is needed to more precisely assess the exposure of ecosystems to ALAN across the Earth.

Insert Figure 2

4 Biological traits vary with latitude

Because of its influence on annual daylength variation, climate, and its current correlation with economic development, latitude is a key factor that is expected to modulate the sensitivity of populations to ALAN. We illustrate how the latitudinal variation in photoperiod influences variation in circadian rhythms, photoperiodism for major life-history traits like reproduction or migration (Hut & Beersma, 2011; Van Geffen *et al.*, 2014; Gaston *et al.*, 2017; Helm *et al.*, 2017), or the characteristics of sensory systems (Yammouni *et al.*, 2011). **Annual life-history events** are often synchronised with photoperiod so that organisms anticipate changes in forthcoming environmental conditions. Latitudinal variation in photoperiod determines changes in the timing of major events like migration, reproduction in birds, or diapause in insects. In birds, photoperiod is a major cue for the onset of gonadal maturation, moult, and migratory activity (Rowan, 1925; Gwinner, 1996; Dawson *et al.*, 2001; Coppack & Pulido, 2004; Bauer *et al.*, 2008). Great tits *Parus major* need longer days to initiate sexual maturation at mid-latitude than at higher latitudes, causing a cline in the onset of male gonadal maturation (Silverin *et al.*, 1993). The required daylength variation can be as small as 1h or less to initiate sexual maturation in temperate (Dawson, 2007) and subtropical species (Lewis *et al.*, 1974; Hau *et al.*, 1998; Coppack & Pulido, 2004). Photoperiod also largely contributes to induce diapause and to regulate voltinism in insects. Critical photoperiod for diapauses increases with latitude (Danilevskii, 1965; Bradshaw & Lounibos, 1977; Hut *et al.*, 2013) and the number of diapausing individuals with shorter daylength (Schmidt *et al.*, 2005; Hut *et al.*, 2013; Paolucci *et al.*, 2013). Photoperiod and local environmental conditions determine the number of generations per year, more generations being produced at lower latitudes (Altermatt, 2010). For instance, in the water strider *Aquarius remigi*, univoltinism is less frequent in southern populations, and change in growth occurred across a narrow range of 5° (Blanckenhorn & Fairbairn, 1995). In mammals, latitudinal variation in the timing of the breeding period was observed in the broadly distributed *Peromyscus* deermice and *Odocoileus* deers, and photoresponsiveness decreased with latitude in a mouse (Bronson, 1988).

Circadian clocks are found from cyanobacteria to plants and animals (Hut & Beersma, 2011). They generate endogenous circadian rhythms that synchronize physiological processes and activities of

organisms to the diel variation of environmental conditions. Light is the main cue used to reset circadian clocks, which explains why activity patterns and other behaviours change with latitude. In mammals, the occurrence of nocturnal and diurnal species is higher in the intertropical zone whereas crepuscular and cathemeral species are distributed at higher latitudes, thus reflecting the adaptation to larger variation in annual daylength and longer twilight periods (Bennie *et al.*, 2014). The photic regime of Arctic regions favours behavioural plasticity. For instance, populations of Reindeer *Rangifer tarandus* above 70°N lose their circadian rhythm of activity in summer and recover it in autumn and spring (Van Oort *et al.*, 2005), while the Arctic sandpiper *Calidris melanotos* undergo a drastic reduction of sleep during the mating period as a likely result of prolonged sexual activity under long days conditions (Lesku *et al.*, 2012). A large comparative study on shorebirds detected a latitudinal cline in incubation behaviour (Bulla *et al.*, 2016). The influence of photoperiod was lower at higher latitudes. Although the dataset is impressive, the study included temperate, boreal and arctic populations between 35° and 75°, and none from the intertropical zone. Latitudinal variation in diel activity patterns is observed at the intraspecific level too. In *Drosophila melanogaster*, ovoposition peaks at dusk at the beginning of the dark period. In a rare study ranging from 0° to 60°N, authors showed that the percentage of eggs laid during the dark period decreases from 80 % in Equatorial populations to less than 50 % in Northern Scandinavia (Allemand & David, 1976). Similarly, an earlier study showed that the onset and end of locomotor activity of five bird and three mammal species held in captivity at 47°N and 66°N varied more between days at higher latitude (Daan & Aschoff, 1975). Variation was reduced when species activity occurred during the civil twilight when light spectrum changes rapidly. Another study ranging from 37°N to 65°N across Europe found that the onset of dawn singing depended on latitude in some passerines. Under ALAN conditions, it was advanced for latitude-insensitive species only (Da Silva & Kempenaers, 2017).

Sensory systems experience circadian and seasonal regulation. In vertebrates, the expression of photoreceptors, and the detection of colour stimuli follow rhythms that are synchronized by photoperiod (Terman & Terman, 1985; Cahill & Beshare, 1995). In fishes (Shimmura *et al.*, 2017) and humans (Welbourne *et al.*, 2015) seasonal changes in colour perception occur. The visual system also varies with latitude. In fishes retinomotor movements are observed during which rods and cones move in

opposite ways across the retina depending on the time of the day (Yammouni *et al.*, 2011). Retinomotor movements during twilight track the changes in illumination and keep vision functional. They follow endogenous rhythms as demonstrated in individuals kept in the dark or exposed to light during the dark period. Fishes may rely more on changes in ambient illumination and less on endogenous oscillators at higher than at lower latitudes (Yammouni *et al.*, 2011).

5 A predictive biogeographical framework for ALAN is lacking

Beyond the characteristics of the light sources, exposure to ALAN depends on the time of the year, latitude, and climate. Logically, individuals should be less exposed during long-day periods than during short-day periods. **Figure 2** illustrates for three towns at low (6°N), medium (43°N), and high (64°N) latitude the monthly variation in sunrise and sunset, as well as the time of the astronomical sunrises and sunsets. Before astronomical sunrise and after astronomical sunset, the sun does not contribute to the ambient light level, and it is a conservative approach to determine when sky brightness will be for sure elevated beyond its natural value by ALAN, at least during moonless nights or under overcast skies. We represented the number of extra-lit hours due to ALAN before and after the astronomical twilight for two lighting scenarios. Lights are turned off at midnight in the first scenario, as an energy-saving measure, and remain turned on all night in the second. The pattern is the same for the two scenarios, but the number of extra-lit hours due to ALAN is larger for the second. At high latitude, there are no extra-lit hours for about 5 months, which period is used for breeding in many arctic species. One can predict the disruption to be mild or non-existent then. In contrast, ALAN duration is maximal during wintertime. Effects could be positive if artificial light allows longer foraging periods or negative if it raises activity and metabolic cost beyond sustainable levels for organisms. At low latitude, the extent of artificial lighting is constant throughout the year. Therefore, disruption may affect any life-history events regardless of annual timing. At mid-latitudes, the number of extra-lit hours is minimal around summer equinox, which often corresponds to the end of breeding for birds or amphibians, but is the main active period for insects or bats. The extension of ALAN is maximal in winter and the concern is the same as for arctic organisms with the addition that reproduction occurs in winter for some

mammals too. In temperate species, the seasonal effect of ALAN may be more diverse than at lower or higher latitudes and depend on the taxonomic group.

We have knowledge about the latitudinal variation of some traits and expectations about how exposure to ALAN may change across latitudes and seasons. Yet, we still do not know whether and how latitude determines the short or long-term responses of individuals and populations to ALAN. We make some propositions to go forward in that direction by pointing to candidate traits that would deserve more attention. We also make some predictions about the evolutionary responses that could be expected at different latitudes. Most physiological or behavioural traits are potentially affected but we can nevertheless identify some traits to address key issues, namely whether and how the strength of ALAN-induced effects varies with latitudes, if some periods of the year are more critical for biodiversity exposed to ALAN, and whether these periods change latitudinally. A major pending question is whether latitude can predict at least qualitatively the time taken by populations to develop responses to ALAN exposure.

As mentioned above, a longer photoperiod could have beneficial or detrimental effects on individuals in terms of time and energy budget. Thus, it is important to determine whether diurnal and nocturnal species respectively prolong or delay their activity period, and how they partition key activities like foraging or reproduction during a day. In this regard, light pollution may contribute to the stronger homogenizing effect of urbanization on nocturnal moths than on diurnal butterflies (Merckx & Van Dyck, 2019). The latitudinal effect on incubating bouts in shorebirds (Bulla *et al.*, 2016), where ALAN exposure was not assessed, or on the advanced onset of dawn singing in passerines (Da Silva & Kempenaers, 2017), illustrate which type of behaviour could be targeted. Focusing on activity alone may not unravel the complexity of the disruption process for organisms. The diel distribution of feeding bouts was altered in mice, resulting in obese individuals (Fonken *et al.*, 2010), while activity and metabolism were uncoupled in amphibians exposed to light at night (Touzot *et al.*, 2019). These lab studies highlight the need for analysing together activity and metabolic budgets or relevant proxies when other physiological measurements cannot be made. Because physiological constraints may be stronger at higher than at lower latitudes, short-term effects on survival may be quicker. More generally, we do

not know well how circadian clocks are affected by ALAN in most species. Even less do we know about how the clocks of populations located at different latitudes respond to novel photic regimes. Birds provide a good illustration of our limited capacity to predict the effects of ALAN in animals. Life-history traits like the onset of breeding, migration, dispersal, moult are important for individual fitness and population growth rate. They are all potentially affected by ALAN even in populations at low latitudes. The increase in the apparent daylength by ALAN may lead to maladaptive decision by desynchronizing the onset of biological events and the time window of optimal climate/trophic conditions. Desynchronization may affect the reproductive output and survival of individuals in resident intertropical species and migratory species. For instance, the extension of the photoperiod by ALAN could affect photorefractoriness, i.e. the loss of sensitivity to long days that prevents the initiation of spring migration and maturation. Slight changes in migration timing in a context of climate change may have negative consequences for bird populations. We simply do not know whether the sensitivity to the disturbance generated by ALAN depends on latitude and hardly what to predict. At the sensory level, ALAN is expected to affect the efficiency of visual tasks carried out at night or under crepuscular conditions like orientation (Somanathan *et al.*, 2008), or the selection of food sources (Kelber *et al.*, 2002), or mates (Gomez *et al.*, 2009). Adaptation to the light/dark transitions may be partly inefficient in populations that do not use photic cues to reset the circadian rhythm of their visual system (Yammouni *et al.*, 2011).

The novel pattern of annual daylength variation generated by ALAN may not be necessarily harder to overcome, at the evolutionary scale, than the colonization of higher latitudes for a species though. Latitudinal clines in activity illustrate the evolutionary potential of some populations to adjust to spatially heterogeneous conditions even over a few degrees of latitude (Blanckenhorn & Fairbairn, 1995). In the long-term, populations are expected to develop higher resistance to this novel disturbance (Hopkins *et al.*, 2018). For instance, urban populations of a moth developed a lower attraction to light than populations from less non-polluted areas (Altermatt 2018). A major issue is which response type should be favoured at different latitudes and what time scale is relevant for such changes to occur. The stability of the natural daylength and the ALAN period should favour adaptation to a longer photophase

at lower latitudes unless the physiological and ecological costs of plasticity are small (DeWitt *et al.*, 1998). In contrast, plastic phenotypes able to respond to varying daylength should be selected at higher latitudes. In this regard, it has been argued that individuals rely more on transitions between the light and dark period than on internal oscillators at higher latitudes, whereas the opposite pattern should be observed at lower latitudes (Gaston *et al.*, 2017; Helm *et al.*, 2017). Whether plasticity is adaptive in winter time, when the higher numbers of extra-lit hours may require a higher energetic demand, remains to be tested. We observed a limit to the studies on the latitudinal variation of biological traits. The behavioural and physiological clines observed at the interspecific or intraspecific level spanned a fraction of the latitudinal range between temperate and higher latitudes. Information about the transition between the intertropical and the temperate zones is lacking. However, such knowledge is necessary if we want to build a biogeographical framework robust enough to predict the latitudinal effect of ALAN. This publication bias has been noticed for the study of the evolution of breeding in mammals (Bronson, 1988). It is likely that the historical distribution of laboratories and the difficulty to identify species or groups of species spanning the entire latitudinal range, as well as the logistic constraint of these studies, account for the current situation. Up to now, only a few species distributed across the whole range like *D. melanogaster* have been tested (but see Bronson (1988) for mammals).

6 Prospective view about the geographical spread of ALAN: a concern for intertropical biomes?

The increase of ALAN essentially results from demographic growth and economic development, *i.e.* the greater use of electricity. World population is forecast to grow from 7.5 billion in 2017 to 9.8 billion in 2050 and over 11 billion in 2100 (United Nations Department of Economic and social affair Population division, 2017). Between 2017 and 2050, the intertropical region including Western, Middle and Eastern Africa should increase its population by 217 %. South-Eastern Asia, and the region including Central and Latin America (but excluding Argentina, Chile, and Uruguay), should grow respectively of 23 %

406 and 21 %. In comparison population in Europe and Eastern Asia should decrease by 4 % and Northern
407 America raise by 20 % (United Nations Department of Economic and social affair Population division,
408 2017). Larger use of lighting can also be predicted according to prospective studies that forecast the
409 expansion of urban areas and road networks. Roads generate light by their traffic, but they also facilitate
410 new settlements and the expansion of existing settlements. A recent study predicted an increase of 185
411 % of the global urban extent between 2000 and 2030 for the land category with the highest probability
412 of being urbanized (Seto *et al.*, 2012). In Africa a 590 % increase of urbanized areas is expected with a
413 concentration of this process in five areas, four of which are located in the intertropical zone.
414 Furthermore, the percentage of urbanization in 34 World major biodiversity hotspots is predicted to
415 triple during that period. The largest changes are expected in regions undisturbed by urban development
416 so far, and all concern inter-tropical areas (Seto *et al.*, 2012). Regarding road networks only 43 % of the
417 emerged land (except Antarctica and Greenland), were considered roadless, *i.e.* distant more than 5 km
418 from a road, in 2016 (Ibisch *et al.*, 2016), a distance at which a nocturnal light source is detected. In
419 tropical and subtropical countries, one-fifth of national parks is crossed by at least one main road (Caro
420 *et al.*, 2014)**.** Expansion of logging creates roads and gaps that are likely to increase exposure to light
421 in the vicinity of human settlements (Laporte *et al.*, 2007). Therefore, population growth, urbanized
422 land, and road networks are expected to keep growing in the next decades especially in areas of high
423 conservation value and in the intertropical zone (**Figure 3**).

424 International initiatives seeking to increase the access to electricity in developing countries are
425 welcome (see for instance www.AREI.org), but they may contribute to the increase of night brightness
426 in preserved environments. There is little doubt that a larger fraction of land in the intertropical zone
427 will experience higher levels of ALAN in the next decades. The increasing use of LEDs for outdoor
428 lighting may further deteriorate the nocturnal environment and generate more deleterious effects for
429 biodiversity than older technical solutions (Cajochen *et al.*, 2011; Davies *et al.*, 2013b; Pawson & Bader,
430 2014). For a given power, LEDs provide better lighting conditions than older sodium lamps because
431 they stimulate a broader range of the visual system of many organisms (Davies *et al.*, 2013b). In addition,
432 this cheaper technology tends to favour greater use of nocturnal light (Kyba *et al.*, 2017a). Countries in

the intertropical zone are developing their territory and will likely use the technology that is the most disrupting for biodiversity. By doing so, they will generate a more sudden change than the one experienced by wildlife earlier in other parts of the World. Such a rapid transition in lighting has been documented in Peru (Kyba *et al.*, 2017a). At a broader scale, an increase in nocturnal light was detected by satellites in the tropical/subtropical biomes. The proportion of the area that experienced higher brightness raised by 2 % between 1992-1996 and 2008-2012. The largest increase was observed for needle-leaf and mixed forests that occupy a restricted fraction of the total area but host rich endemic biodiversity (Bennie *et al.*, 2015b).

Insert Figure 3

7 Conclusion

We are clearly lacking a biogeographical framework to predict how species adapt or acclimate to ALAN and by which way. We do not know in which biomes ecological networks are the most sensitive to the elevation of nocturnal brightness, which ecosystems will be the most strongly exposed in the near future, and to which extent climate modulates exposure to ALAN at a given latitude. Only fragmentary information is available to generate testable hypotheses. Climate has probably a still unappreciated influence on the intensity of the biological and ecological effects of ALAN. In particular, more attention should be paid to the geographical variation in cloud cover. A higher sensitivity to change in nocturnal ambient light is expected in organisms from ecosystems where cloud cover is frequent because nocturnal light intensity is often low. Furthermore, within the same latitudinal range, areas where rain, fog, or mist is frequent may be less exposed than arid areas where moonlight is more present most of the nights, and negative effects on organisms and ecosystems may be milder. In forest, light exposure depends on the position of the organism relative to canopy. A large fraction of tropical forest biodiversity lies at the canopy level where individuals are more easily exposed to distant sources of ALAN. Under the canopy where the light level is very low, species are probably less exposed, but they could be highly sensitive

to small changes in light intensity. Species naturally living in forest edges, clearings, riparian or open habitats may be more exposed and suffer more from new lighting conditions. In this regard, roads or clearings in tropical forest generate a barrier effect, many organisms avoiding gaps as narrow as 30 meters (Laurance *et al.*, 2009)**.** The occurrence of ALAN in an otherwise dark environment could strongly enhance the barrier effect for these species (Lewanzik & Voigt, 2014).

Building a theoretical framework that describes how biogeographical factors modulate ALAN is a necessary step but it may not be sufficient. The spread of light at night co-occurs with the other drivers of biodiversity decline such as habitat fragmentation, chemical pollution, invasive species, that all generate stress for individuals. Negative synergistic effects of multiple stressors on organisms and populations are well known (Sih *et al.*, 2004). Climate change is likely the main global factor to focus on. A recent review highlighted the negative effects on animal fitness of changing climate under stable photoperiod (Walker *et al.*, 2019). The evolution towards a less frequent or less reflecting cloud cover would reduce exposure of organisms in terms of intensity and duration but also the size of the areas experiencing light pollution, compensating in a way the expansion of urbanized area. In contrast, more clouds are likely to enhance the biological and ecological effects of ALAN. Temperature, the main focus of attention of climate change, is also relevant. It modulates biological rhythms entrained by light (Underwood, 1989; Helm *et al.*, 2017), resets circadian clocks (Chen *et al.*, 2015), affects gene expression in insects and mammals (Helm *et al.*, 2017), alters the daily expression peak of melatonin in lower vertebrates (Mayer *et al.*, 1997), and induces seasonal shift from nocturnality to diurnality in insects and mammals (van der Vinne *et al.*, 2014; Helm *et al.*, 2017). The sensitivity of insects to warming is believed to be the highest in the intertropical zone because individuals are already close to their thermal tolerance threshold (Deutsch *et al.*, 2008). The annual covariation of temperature and photoperiod at a location determines an environmental envelope that enlarges in both dimensions with latitude (Hut *et al.*, 2013), as a result of increasing temperature and daylength range. Global warming changes one dimension of the envelope while ALAN changes the other dimension, giving rise to entirely new conditions with unknown consequences about the desynchronization of physiological and behavioural rhythms at the individual level, and the timing and intensity of interspecific relationships at

485 the ecological level (but see Miller (2017)). Effects are expected at any location on the globe but
486 predicting the outcome of the interaction remains difficult since temperature is rising faster at higher
487 latitudes (Hansen *et al.*, 2006) and light at night strongly changes the photic regime year-round at lower
488 latitudes.

489 The demographic and macro-economic projections for the next decades support the expansion of ALAN
490 across the World and particularly within the intertropical zone. Because synergies with other drivers of
491 global decline are not known so far, even if some may be anticipated, prevention and caution remain the
492 most appropriate approaches. We did not attempt a meta-analysis of the papers published on biological
493 rhythms or ALAN for species in the intertropical zone but it is no doubt that there are many less than
494 papers devoted to temperate or high-latitude species. The time is ripe to shift the balance and start
495 investigating the effects of ALAN at different latitudes. In particular, attention should be given to the
496 capacity of intertropical species to respond to the novel conditions generated by ALAN and climate
497 change. A good starting point could be to focus on groups originating from the intertropical zone. Habitat
498 loss, climate change, overexploitation have received so far the main attention in many areas for obvious
499 reasons. It should be acknowledged that ALAN might be a more insidious form of threat to local
500 biodiversity. Eco-tourism has been a major source of income for several countries and it is becoming a
501 major contribution for new ones particularly in countries benefiting from hotspots. It may also contribute
502 to accelerate the change of the photic environment at night. In this regard, a recent global study showed
503 that the increase in ALAN was much higher around protected areas than farther away (Guetté *et al.*,
504 2018). The demand for biodiversity will keep on growing with the global human population. A
505 cautionary message would be to remind that increasing population, infrastructures and facilities, and
506 more generally the use of electricity for nocturnal lighting may be harmful even in the most
507 environment-friendly areas that value biodiversity as a resource for their economic development.

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Data accessibility statement - Data be will made available in Repository upon acceptance of the manuscript

Figure 1 Mean latitudinal distribution of ALAN and cloud cover fraction (A and C) as measured from satellite images and their standard deviation (B, D). Data were binned in 5° categories. Only terrestrial areas have been included in the analysis. Seas and large lakes have been excluded. The grey band represents the intertropical zone. Original data reused with permission. For ALAN, the unit is relative and expressed as the ratio of the difference between the observed pixel value and the reference value of a natural sky (174 µCd/m²) to the reference value. Data source: Falchi et al. (2016), NASA, MODIS mission, and Giovanni only data system. For a global map of cloud cover fraction over the period 2002-2018, see Supplementary information.

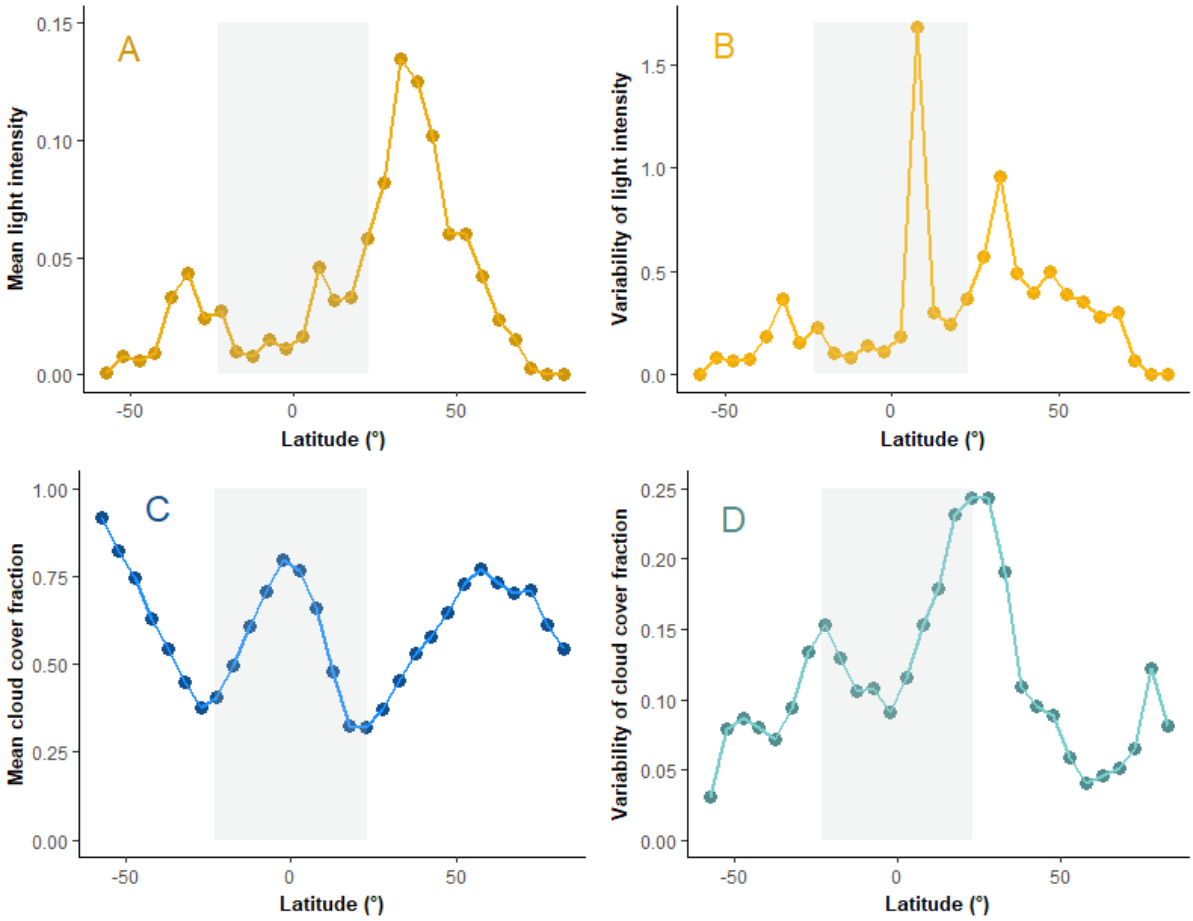
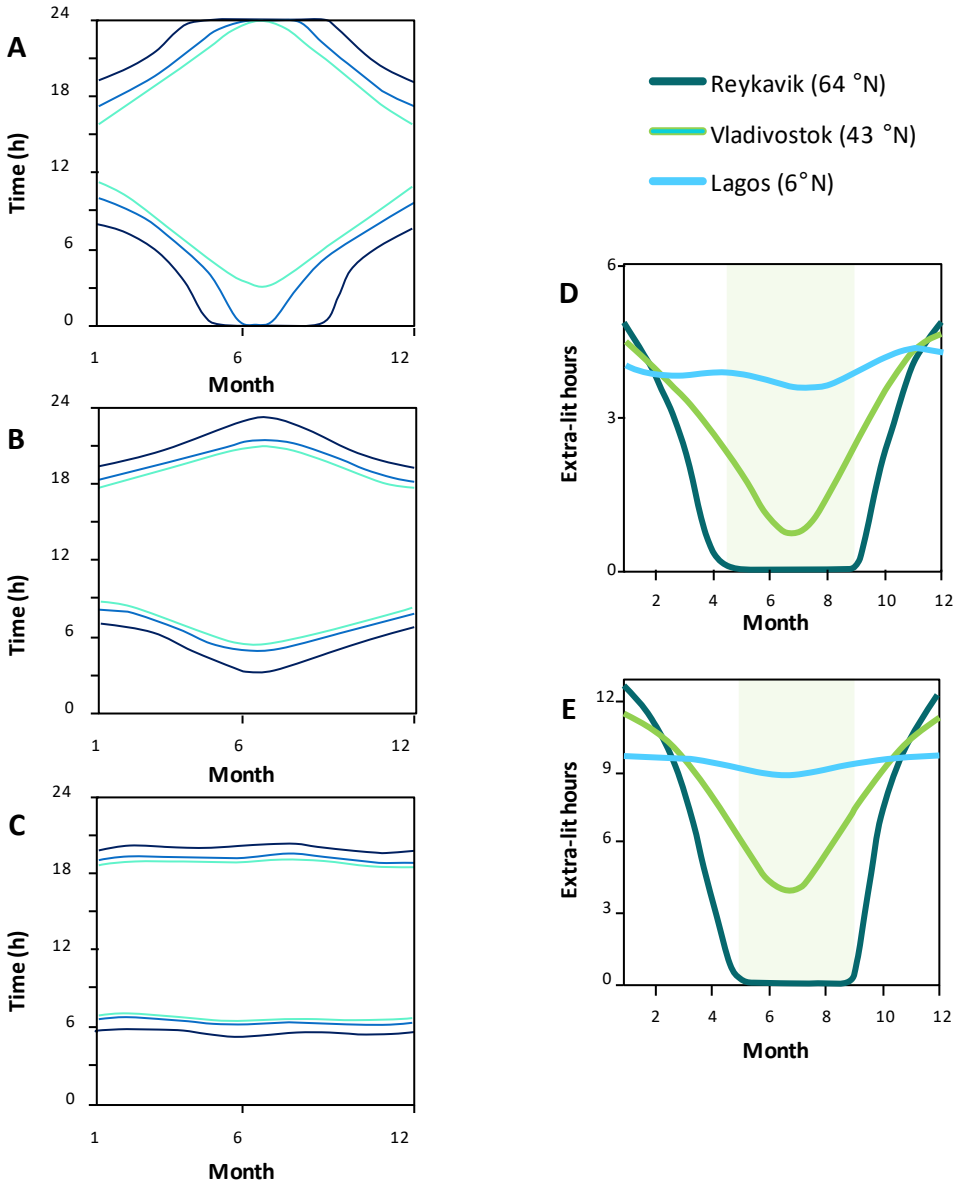
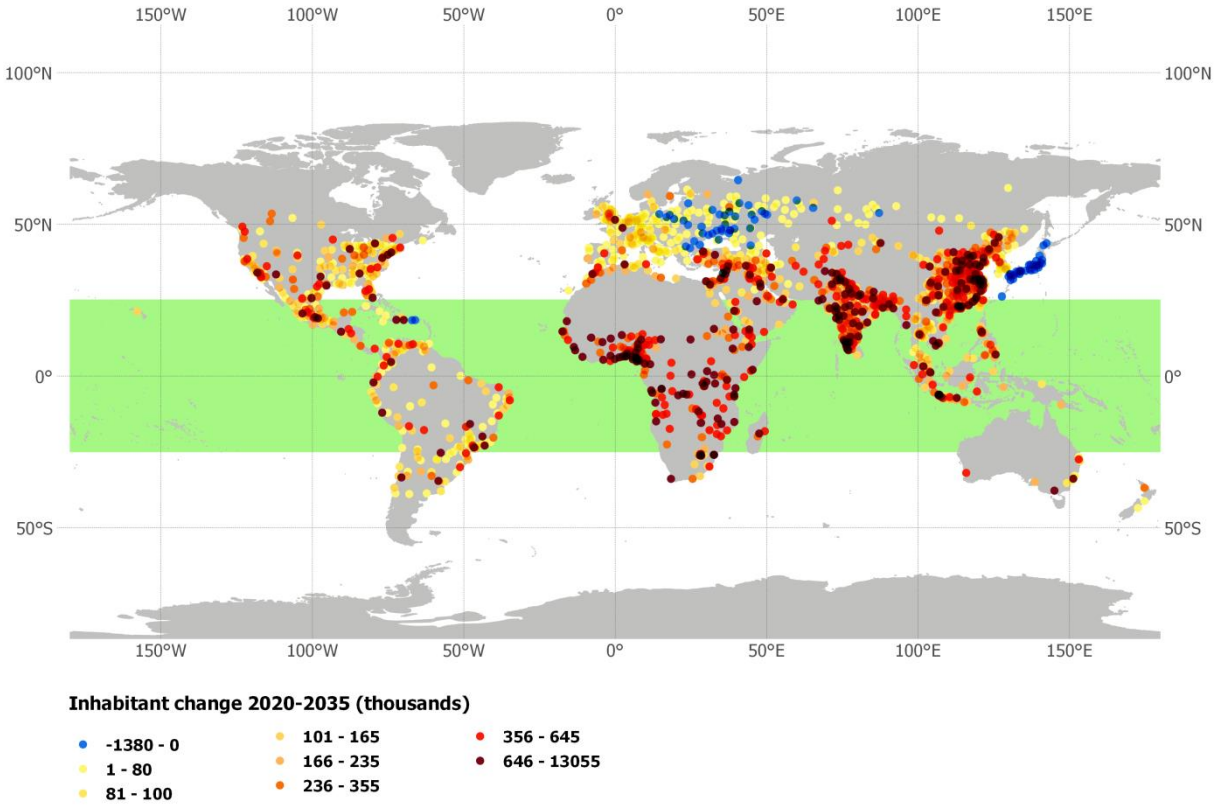


Figure 2 (A-C) Annual variation in twilight for three towns at low, mid, and high latitudes. Twilight represents the periods of the day when sun declination is between 0° and 18° below horizon. When the declination is lower, the sun does contribute to ambient light. The right column shows for two lighting scenarios the annual variation in the time period when ALAN elevates the ambient light level outside the twilight periods. Artificial lights are turned off at midnight (D) or stay turned on all night (E). Sources : https://www.esrl.noaa.gov/gmd/grad/solcalc/ ; https://earthsky.org/?p=235797.



973 **Figure 3** Expected change in Urbanization/demography between 2018 and 2030 (Source UNICEF,
974 United Nations). The green latitudinal band represents the intertropical zone.

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Supplementary Material S1 – Global cloud cover fraction