Anthropogenic light disrupts natural light cycles in critical conservation areas

*Brett M. Seymoure[1,2], Rachel Buxton[2], Jeremy White[1], Carlos Linares[2], Kurt Fristrup[3], Kevin Crooks[2], George Wittemyer[2], and Lisa Angeloni[1]

[1]Department of Biology, Colorado State University, Fort Collins, CO 80523
[2]Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523
[3]Natural Sounds and Night Skies Division, National Park Service, Fort Collins, CO 80525

*Corresponding author: brett.seymoure@colostate.edu

Note: This manuscript is currently in review at a peer reviewed journal and thus the data generated from this work are not publicly available. If interested in the data, please contact Brett Seymoure for options of data sharing.

Anthropogenic lighting drastically alters nocturnal environments, threatening a wide range of species by disrupting light regimes that regulate fundamental biological processes such as reproduction, foraging, and predator defense[1,2]. We translate satellite measures of anthropogenic light radiating from the earth to a biologically relevant measurement – the amount of light scattered back to the earth (horizontal illuminance). Anthropogenic light exceeding the natural level produced by stars, galactic light, and airglow on a clear moonless night (i.e., new moon conditions) affects 22.9% of the Earth's terrestrial surface, as well as 51.0% of Key Biodiversity Area units, 77.1% of Global Protected Area units, and approximately 20% of the most biodiverse areas for mammals, birds, and amphibians. Thus, due to anthropogenic sources, these environments experience at least double the levels of natural illuminance during half of the night hours in a year. To facilitate biological interpretation of these levels of anthropogenic illuminance observed globally[3,4], we undertook a systematic literature review of animal responses to changing nocturnal light levels. Known biological effects from the current anthropogenic illuminance levels range from behavioral and physiological alterations to increased mortality, which have been documented in 117 species from 23 orders and 8 classes. These findings provide a biological perspective on global light pollution, and they identify regions where reductions in anthropogenic illuminance would yield the greatest benefits for conserving biodiversity.

Diel and seasonal light patterns synchronize physiological and behavioral rhythms of most organisms on Earth, regulating fundamental biological processes[5–7]. Furthermore, animals have evolved diverse visual systems to facilitate optimal behavior under natural light cycles[8]. Humans have substantially altered light environments[6]. Prior studies demonstrated global increases in anthropogenic illuminance within protected areas and high biodiversity areas[9–12]. Yet, the assessment of the scattering of upwelling light back to the Earth's surface, known as skyglow, has been overlooked until recently[12,13]. Skyglow conceals celestial cues for migratory animals[14] and, as it affects areas that are otherwise distant from anthropogenic disturbances[12,13,15], its biological effects can permeate into otherwise well-protected systems[12]. Moreover, skyglow has increased faster than global human population for several decades[16].

The New World Atlas of Sky Brightness[13] provides a global map of skyglow, measured as zenith sky luminance. We translated zenith sky luminance into predictions of ground illuminance using a radiance transfer model of skyglow[17] validated with analyses of all sky monitoring data within US National Parks (Methods, Extended Data Fig. 1, Supplemental Data 1). Translating upward radiance measured by satellites into ground illuminance caused by skyglow enables direct connection of the most spatially extensive form of light pollution to extensive studies of photobiology[2].

The lunar cycle is a crucial cue for numerous organisms ranging from corals to bats[5,18]. Thus, we express anthropogenic ground illuminance in categories of equivalent lunar phases, ranging from new moon to full moon. Lunar illuminance spans four orders of magnitude. We also utilize these orders of magnitude to organize our systematic survey of the photobiology literature. To document levels of anthropogenic exposure, we use ranges that equate to levels of new moon (approx. 0.1 to 1 mlux), (crescent (approx. 1 to 10 mlux), quarter (approx. 10 to 100 mlux), and full (greater than 100 mlux)[3,19] moon phases (Methods). The most widespread level of anthropogenic illuminance, and our primary focus, is anthropogenic illuminance within new moon levels, thus causing at least a doubling of natural illuminance. Anthropogenic light exposure below new moon levels we designate as minimal.

We found that anthropogenic light at night has considerably altered the global nightscape. Our analysis shows 22.9% of terrestrial environments consistently experience anthropogenic new moon illuminance or higher, and 5.5% experience at least perpetual crescent moon illuminance (Fig. 1). To investigate the extent of skyglow in areas important for biodiversity conservation, we analyzed the extent of anthropogenic illuminance for terrestrial land that encompassed the top 25% most biodiverse area for mammals, birds, and amphibians[20] (Fig. 2; Methods). Globally, exposure to anthropogenic light at least as bright as anthropogenic new moon levels affected 21.7% of amphibian, 19.1% of bird, and 17.0% of mammal biodiverse areas (Fig. 2). Threatened species[20] experienced greater exposure to anthropogenic illuminance, with threatened amphibians, birds, and mammals exposed to at least anthropogenic new moon conditions in 37.5%, 24.9%, and 23.9% of their biodiverse areas, respectively (Fig. 2). Amphibian species, which are primarily (93%) active at night and frequently (32%) threatened with extinction[21], were exposed to the highest levels, with 5.8% (6.9% threatened) of their biodiverse areas at anthropogenic crescent moon levels or higher (Fig. 2A). At least 1000 km^2 of biodiverse areas for mammals, birds, and amphibians experienced continuous anthropogenic full moon illuminance or greater, a level that occurs in less than 5% of natural nighttime hours (Fig. 2). Thus, species of concern have large areas affected by skyglow, with potentially adverse effects for persistence and recovery.

We also assessed the extent of artificial illuminance in important terrestrial and marine conservation areas using Key Biodiversity Areas (KBAs)[22] and the World Databases on Global Protected Areas (GPAs)[23]. We extracted median illuminance within each KBA and GPA unit and found that 51.0% of KBA units and 77.1% of GPA units had anthropogenic illuminance at or above new moon (Fig. 3A-B, Extended Data Fig. 2). Many areas had even greater exposure, with 17.0% of KBA units and 32.8% of GPA units having median anthropogenic illuminance as least as bright as crescent moon. The largest KBAs and GPAs had minimal anthropogenic illuminance, and thus only 6.1% of total KBA area (Fig. 3A) and 9.0% of total GPA area (Fig. 3B) had anthropogenic illuminance at new moon or brighter (Supplemental Data 2 and 3). Terrestrial KBAs and GPAs had more exposure than their marine counterparts (Extended Data Fig. 2). 53.5% and 77.5% of terrestrial KBA and GPA units, respectively, experienced at least anthropogenic new moon illuminance, compared to 39.9% and 54.2% of marine KBA and GPA units, respectively. Likewise, 16.4% and 13.8% of the total area of terrestrial KBAs and

GPAs experienced at least anthropogenic new moon illuminance, compared to 5.3% and 1.9% of marine KBAs and GPAs (Extended Data Fig. 2).

Anthropogenic illuminance in KBAs varied with geographic region, with the greatest illuminance in Europe (~60% of area experiencing anthropogenic illuminance at new moon levels or higher) and the Middle East (~43%; Fig 3C). The lowest anthropogenic illuminance was in marine KBAs (100% of area at minimal levels), Oceania (99.9% of area at minimal levels), and Australasia (98.8% of area at minimal levels) (Fig. 3C). Note that although we report no anthropogenic illuminance in the strictly designated marine KBA region, other KBAs include marine area and were exposed to anthropogenic illuminance along or near shorelines (Fig. 1, Extended Data Fig. 2), which are sensitive areas for coastal species like shorebirds, sea turtles, fishes, and corals[18].

The biomes of GPAs differ in topography, aridity, precipitation, and vegetation structure, which can affect exposure to skyglow[24,25]. Amongst the 16 terrestrial biomes, Mediterranean chaparral, which is one of the most densely populated biomes[26], had the highest proportion of GPA area experiencing anthropogenic illuminance at new moon levels or higher (64%) (Fig. 3D). Much of the Mediterranean biome is coastal, where severe consequences from anthropogenic light have been documented for marine biota[18]. Except for aquatic and ice biomes, all had a proportion of GPA area experiencing anthropogenic quarter moon lighting or higher, with temperate broad leaf forests having the most area (0.2% of area) and tundra having the least area with anthropogenic quarter moon exposure (less than 0.0001% of area) (Fig. 3D). The aquatic biome experienced anthropogenic crescent moon in 0.2% of area, and ice was the only biome with all of its GPA area experiencing minimal anthropogenic lighting (Fig. 3D).

Anthropogenic illuminance in GPAs also varied with IUCN designation[23]. Both wilderness areas (IA) and protected areas with sustainable use of resources (VI) had the smallest proportion of area illuminated at or above new moon levels (2.8% and 2.4%, respectively), whereas protected landscapes and seascapes (V) had the largest proportion of area illuminated at these levels (17.3%; Extended Data Fig. 3A). GPAs with all other designations had less than 10% of their area illuminated at or above anthropogenic new moon levels. Both tropical and polar GPAs had some area exposed to anthropogenic new moon illuminance or greater (3.6% and 2.0% of area, respectively), whereas temperate GPAs had greater exposure, with 19.0% of the area experiencing at least anthropogenic new moon conditions and over 3% experiencing at least crescent moon conditions (Extended Data Fig. 3B).

To interpret the biological importance of these global levels of exposure to anthropogenic illuminance, we conducted a systematic literature review of organismal responses to light at night (Methods). We compiled results from studies examining the effects of illuminance levels up to nautical twilight, which exceeds the brightest full moon conditions, spanning the anthropogenic illuminance levels we observed across the globe (Methods). We found studies demonstrating effects of light at night on 117 species from 23 orders across 8 classes of both arthropods and chordates (Fig. 4A). These studies showed that changes in light levels affected foraging, movement, activity patterns, vigilance, mating and reproduction, community and population metrics, predation and mortality, physiology and development, and vocal behavior (Fig. 4B, Extended Data Table 1). Although the studies were not evenly distributed across light levels, impacts were demonstrated across the range of illuminance, with 77 species affected by levels between full moon and nautical twilight illuminance (between 100 mlux and 3,000 mlux), 25 species affected by illuminance between quarter and full moon levels (between 10 and 100 mlux), and 18 species affected by levels between crescent and quarter moon illuminance (between 1 and 10 mlux). Twenty-eight species altered their activity patterns, foraging, and vigilance at light levels in our new moon category (<1 mlux), with five cases of elevated mortality for prey species (Supplemental Data 5). For example, new moon levels initiate foraging in tropical sweat bees[27] and stimulate courtship displays in fireflies[27]. Crescent moon levels alter circadian rhythms in hamsters[28]. Quarter moon and brighter levels alter numerous predator-prey interactions in invertebrates and vertebrates[29] (Fig. 4, Supplemental Table 1). Although the literature on the effects of anthropogenic light is not comprehensive, the taxonomic and ecological breadth of impacts reflects the importance of light at night. Anthropogenic light at night impacts numerous and critical nocturnal behaviors, physiological processes, and community interactions.

Our literature review revealed a wide range of effects of nighttime light on a diversity of animal taxa. Pervasive exposures to anthropogenic illuminance at levels known to alter biological processes constitutes a substantial threat to protected natural areas. Skyglow is an unintended consequence of lighting. Skyglow can be meaningfully reduced and community lighting objectives can also be achieved through improvements in design and use of emerging technologies. Solid state lighting and advanced lighting controls can deliver reduced costs, energy usage, and greenhouse gas emissions[16,30]. Reimagining lighting implementations with advanced technology can enhance human communities at night and substantially diminish a global, chronic stressor to ecosystems.

Data Availability

All data will be accessible to the public via CSU library once the manuscript is published.

Acknowledgements

This research was funded through a partnership with the Natural Sounds and Night Skies Division (NSNSD) of the US National Park Service. We appreciate the expert advice and data sharing of the NSNSD, especially discussions with Dan Duriscoe and Sharolyn Anderson. Tessa Parrish, Alynn Karnes, and Danny Irwin contributed to data collection for the literature review. All sky monitoring data were collected by NSNSD, and we thank Dan Duriscoe, Chad Moore, Bob Meadows, and Davyd Betchkal for their measurements.

Author Information

Contributions: B.M.S., R.B., and J.M.W. designed the research with contributions from G.W., K.C., L.A., K.F., and C.R.L. B.M.S. and C.R.L. led the literature review; R.B. led the geospatial analysis with contributions from J.M.W.; and J.M.W. led the luminance to illuminance conversion research. B.M.S. led the summary analysis and wrote the manuscript main text with contributions from G.W., K.C., L.A., and

K.F.; and B.M.S, J.M.W. and C.R.L. wrote the methods and supplemental information with contributions from R.B., G.W., K.C., L.A., and K.F.

Author Information

Reprints and permissions information is available at www.nature.com/reprints. The authors have no interests to declare. Correspondence and requests for materials should be addressed to Brett.Seymoure@gmail.com.

Figure Legends

Figure 1: Global anthropogenic illuminance map. The anthropogenic illuminance (i.e., light produced only by skyglow) in lux at a resolution of 852 m^2, excluding south of 60S (mostly Antarctica) and north of 80N (mostly Arctic Ocean) where no anthropogenic light data are available. The anthropogenic light levels include: minimal (<0.1 mlux), New Moon (0.1 to 1 mlux), Crescent Moon (1 to 10 mlux), Quarter Moon (10 to 100 mlux), and Full Moon (greater than 100 mlux). Note that these values measure anthropogenic illuminance and thus are additive to the natural levels experienced by the Earth's surface due to natural sources of light (e.g. starlight, celestial bodies like the Milky Way, airglow, and zodiacal light).

Figure 2: The extent of anthropogenic illuminance in biodiverse areas (the terrestrial land that encompassed the top 25% most speciose area for each taxon). Bars represent the artificially illuminated log area at each light level in biodiverse areas for amphibians (A), birds (B), and mammals (C). Black bars represent all species and grey bars represent IUCN threatened species. Numbers within bars indicate the percentage of area. Areas with minimal illuminance had no anthropogenic lighting or lighting at very low levels (<0.1 mlux).

Figure 3: The extent and levels of anthropogenic illuminance within Key Biodiversity Areas (KBAs) and Global Protected Areas (GPAs). The number and area of terrestrial and marine KBAs (A) and GPAs (B) exposed to each light level. C) The area of KBAs exposed to each level for each region, excluding Arctic regions, which have no anthropogenic light data. D) The area of GPAs exposed to each light level for each terrestrial biome classification. Marine biomes are not included as they are not listed by the IUCN database of Global Protected Areas. For A and B, numbers within open bars represent the percentage of units, and numbers within gray bars represent the percentage of area at each light level. For C and D, bars are shaded relative to light level. For D, we abbreviated the IUCN terrestrial biome categories for graphical legibility. Taiga represents taiga and boreal forests; Desert includes xeric shrublands; Savanna includes flooded grasslands; Aquatic represents inland water; Chaparral represents Mediterranean forests, woodlands and scrub; Mt. Shrub represents montane grassland and shrublands; Ice represents rock and ice; Temp Mixed includes temperate broadleaf and mixed forests; Temp Conifer represents temperate conifer forest; Temp Grass includes temperate grasslands, savannas, and shrublands; Trop Conifer includes tropical and subtropical coniferous forest; Trop Dry includes tropical and subtropical dry broadleaf forests; Trop Grass includes tropical and subtropical grasslands, savannas and shrublands; Trop Forest includes tropical and subtropical moist broadleaf forests.

Figure 4: The number of animal species affected and biological responses to different nighttime light levels consolidated from our review of published literature. A) Number of species shown to be affected by each light category. The taxonomic icons represent classes of animals for which studies have been conducted within each light level. B) Number of species found to exhibit each biological effect at each light level. The light levels range from less than 1 to 3,000 mlux, which are the natural night levels that organisms experience. The darkest levels are equivalent to new moon conditions and the brightest levels are equivalent to nautical twilight, which exceeds the brightest full moon conditions.

Extended Data Table 1: Biological consequences of light levels on taxonomic orders from our review of published literature. The mlux values indicate the range of light for each category. An order's name represents at least one study demonstrating an effect of that light level on an organism within that order, but there may be more than one species or study per order; see supplemental data 1 for species and citations. Further, we include the equivalent natural night lighting conditions.

Extended Data Figure 1: The relationship between zenith sky luminance and horizontal illuminance as measured within 279 National Park Sites. The zenith luminance is the brightness of the sky zenith under clear conditions and the horizontal illuminance is the amount of light from the hemisphere. Both values are in their respective photometric units. Zenith sky luminance is what was reported by Falchi et al. (2016) and horizontal illuminance is what we report here. The equation of best fit shows a constant of 6.66, which is close to the upper bounds of the constant reported by Kocifaj (2014) of 2π and thus we used 2π as the constant to convert the reported zenith sky brightness of the New World Atlas to horizontal illuminance.

Extended Data Figure 2. The extent and levels of anthropogenic illuminance within Key Biodiversity Areas (KBA) and Global Protected Areas (GPA) by marine and terrestrial classification. The number and area of terrestrial GPAs (A), marine GPAs (B), terrestrial KBAs (C), and marine KBAs (D) exposed to each light level. Numbers within open bars represent the percentage of units and numbers within gray bars represent the percentage of area for each light level.

Extended Data Figure 3. A) Area of Global Protected Areas (GPAs) exposed to each level of anthropogenic illuminance for each International Union for Conservation of Nature (IUCN) category (IA Strict Nature Reserves, IB Wilderness Areas, II National Parks, III Natural Monuments or Features, IV Habitat/Species Management Areas, V Protected Land and Seascapes, VI Protected Areas with

Sustainable Use of Resources). B) Area of polar, temperate and tropical GPAs exposed to each level of anthropogenic illuminance. Numbers within bars represent the percentage of area at each light level. For both A and B, marine and terrestrial units were included.

Citations

1. Davies, T. W. & Smyth, T. Why artificial light at night should be a focus for global change research in the 21st century. *Glob. Chang. Biol.* 1–11 (2017). doi:10.1111/gcb.13927
2. Gaston, K. J., Bennie, J., Davies, T. W. & Hopkins, J. The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biol. Rev.* **88**, 912–927 (2013).
3. Longcore, T. & Rich, C. *Ecological light pollution*. (Islnd Press, 2004).
4. Gaston, K. J., Visser, M. E. & Hölker, F. The biological impacts of artificial light at night: the research challenge. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **370**, 20140133- (2015).
5. Gaston, K. J., Davies, T. W., Nedelec, S. L. & Holt, L. A. Impacts of Artificial Light at Night on Biological Timings. *Annu. Rev. Ecol. Evol. Syst.* **48**, 49–68 (2017).
6. Gaston, K. J., Duffy, J. P., Gaston, S., Bennie, J. & Davies, T. W. Human alteration of natural light cycles: causes and ecological consequences. *Oecologia* **176**, 917–931 (2014).
7. Dominoni, D. The effects of light pollution on biological rhythms of birds: an integrated, mechanistic perspective. *J. Ornithol.* **156**, 409–418 (2015).
8. Land, M. F. & Nilsson, D. E. *Animal Eyes*. (Oxford University Press, 2012).
9. Gaston, K. J., Duffy, J. P. & Bennie, J. Quantifying the erosion of natural darkness in the global protected area system. *Conserv. Biol.* **29**, 1132–1141 (2015).
10. Guetté, A., Godet, L., Juigner, M. & Robin, M. Worldwide increase in Artificial Light At Night around protected areas and within biodiversity hotspots. *Biol. Conserv.* **223**, 97–103 (2018).
11. Koen, E. L., Minnaar, C., Roever, C. L. & Boyles, J. G. Emerging threat of the 21 st century lightscape to global biodiversity. *Glob. Chang. Biol.* (2018). doi:10.1111/gcb.14146
12. Garrett, J. K., Donald, P. F. & Gaston, K. J. Skyglow extends into the world ' s Key Biodiversity Areas. *Anim. Conserv.* (2019). doi:10.1111/acv.12480
13. Falchi, F. *et al.* The new world atlas of artificial night sky brightness. *Sci. Adv.* **2**, 1–26 (2016).
14. Warrant, E. & Dacke, M. Vision and visual navigation in nocturnal insects. *Annu. Rev. Entomol.* **56**, 239–254 (2011).
15. Kyba, C. C. M. *et al.* Corrigendum: Worldwide variations in artificial skyglow. *Sci. Rep.* **5**, 8409 (2015).
16. Kyba, C. C. M. *et al.* Artificially lit surface of Earth at night increasing in radiance and extent. *Sci. Adv* **3**, 1–9 (2017).
17. Kocifaj, M., Posch, T. & Solano Lamphar, H. A. On the relation between zenith sky brightness and horizontal illuminance. *Mon. Not. R. Astron. Soc.* **446**, 2895–2901 (2014).
18. Davies, T. W., Duffy, J. P., Bennie, J. & Gaston, K. J. The nature, extent, and ecological implications of marine light pollution. *Front. Ecol. Environ.* **12**, 347–355 (2014).
19. Duriscoe, D. M. Photometric indicators of visual night sky quality derived from all-sky brightness maps. *J. Quant. Spectrosc. Radiat. Transf.* 1–13 (2016). doi:10.1016/j.jqsrt.2016.02.022
20. Jenkins, C. N., Pimm, S. L. & Joppa, L. N. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci.* **110**, E2602–E2610 (2013).
21. Ceballos, G., Ehrlich, P. R. & Dirzo, R. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. 6089–6096 (2017). doi:10.1073/pnas.1704949114
22. World Database of Key Biodiversity Areas.
23. IUCN. World Database on Protected Areas. (2016).

24. Endler, J. A. The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27 (1993).
25. Atkins, J. W., Fahey, R. T., Hardiman, B. S. & Gough, C. M. Forest Canopy Structural Complexity and Light Absorption Relationships at the Subcontinental Scale. *J. Geophys. Res. Biogeosciences* **123**, 1387–1405 (2018).
26. Bennie, J., Duffy, J. P., Davies, T. W., Correa-Cano, M. E. & Gaston, K. J. Global trends in exposure to light pollution in natural terrestrial ecosystems. *Remote Sens.* **7**, 2715–2730 (2015).
27. Owens, A. C. S. & Lewis, S. M. The impact of artificial light at night on nocturnal insects : A review and synthesis. *Ecol. Evol.* 1–22 (2018). doi:10.1002/ece3.4557
28. Evans, J. A., Elliott, J. A. & Gorman, M. R. Circadian Effects of Light No Brighter Than Moonlight. *J. Biol. Rhythms* **22**, 356–367 (2007).
29. Lang, A. B., Kalko, Æ. E. K. V & Bockholdt, Æ. C. Activity levels of bats and katydids in relation to the lunar cycle. 659–666 (2006). doi:10.1007/s00442-005-0131-3
30. Wishaw, K. *The Problems of Artificial Light at Night, is a Solution at Hand?* (2017).

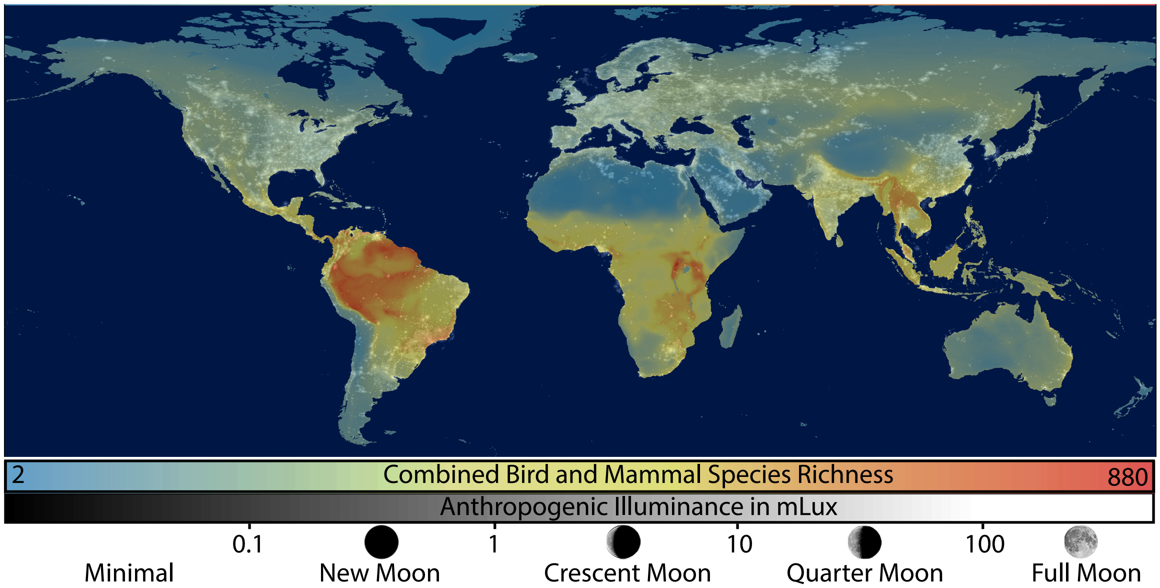

2
Combined Bird and Mammal Species Richness
880
Anthropogenic Illuminance in mLux
0.1
1
10
100
Minimal
New Moon
Crescent Moon
Quarter Moon
Full Moon

Figure 1.

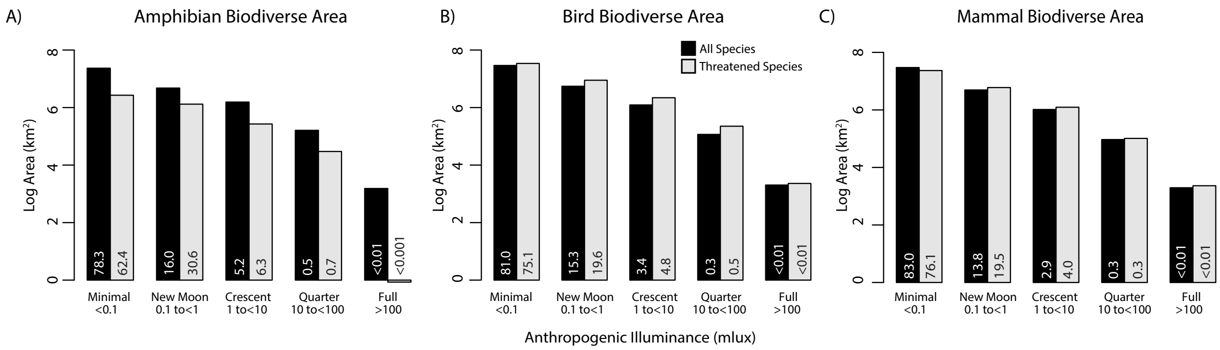

A)
Amphibian Biodiverse Area
B)
Bird Biodiverse Area
C)
Mammal Biodiverse Area
All Species
Threatened Species
Log Area (km²)
0
2
4
6
8
78.3
62.4
16.0
30.6
5.2
6.3
0.5
0.7
<0.01
<0.001
81.0
75.1
15.3
19.6
3.4
4.8
0.3
0.5
<0.01
<0.01
83.0
76.1
13.8
19.5
2.9
4.0
0.3
0.3
<0.01
<0.01
Minimal <0.1
New Moon 0.1 to<1
Crescent 1 to<10
Quarter 10 to<100
Full >100
Anthropogenic Illuminance (mlux)

Figure 2.

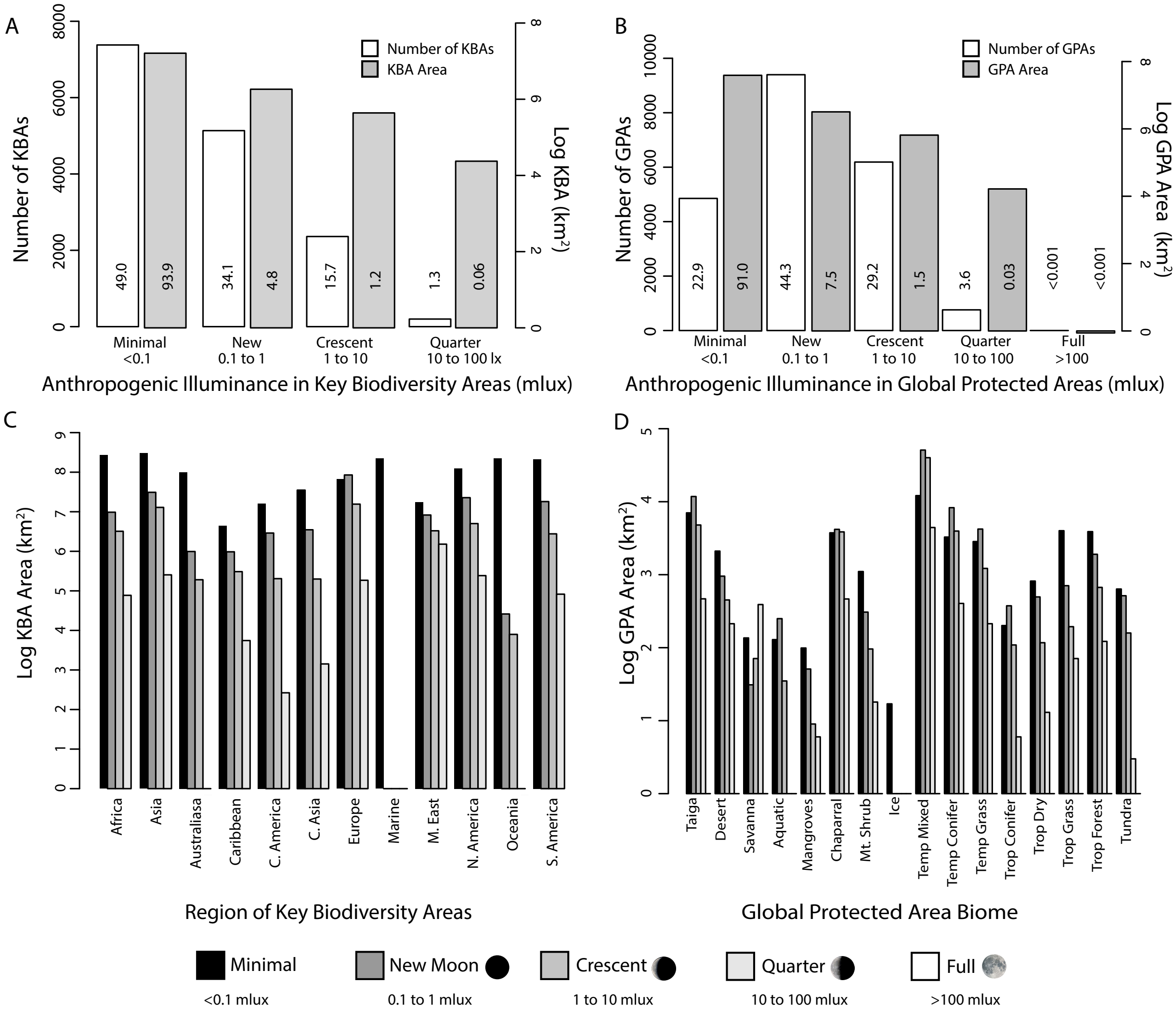

A
Number of KBAs
Log KBA (km²)
Number of KBAs
KBA Area
49.0
93.9
34.1
4.8
15.7
1.2
1.3
0.06
Minimal
<0.1
New
0.1 to 1
Crescent
1 to 10
Quarter
10 to 100 lx
Anthropogenic Illuminance in Key Biodiversity Areas (mlux)
B
Number of GPAs
Log GPA Area (km²)
Number of GPAs
GPA Area
22.9
91.0
44.3
7.5
29.2
1.5
3.6
0.03
<0.001
<0.001
Minimal
<0.1
New
0.1 to 1
Crescent
1 to 10
Quarter
10 to 100
Full
>100
Anthropogenic Illuminance in Global Protected Areas (mlux)
C
Log KBA Area (km²)
Africa
Asia
Australiasa
Caribbean
C. America
C. Asia
Europe
Marine
M. East
N. America
Oceania
S. America
Region of Key Biodiversity Areas
D
Log GPA Area (km²)
Taiga
Desert
Savanna
Aquatic
Mangroves
Chaparral
Mt. Shrub
Ice
Temp Mixed
Temp Conifer
Temp Grass
Trop Conifer
Trop Dry
Trop Grass
Trop Forest
Tundra
Global Protected Area Biome
Minimal
<0.1 mlux
New Moon
0.1 to 1 mlux
Crescent
1 to 10 mlux
Quarter
10 to 100 mlux
Full
>100 mlux

Figure 3.

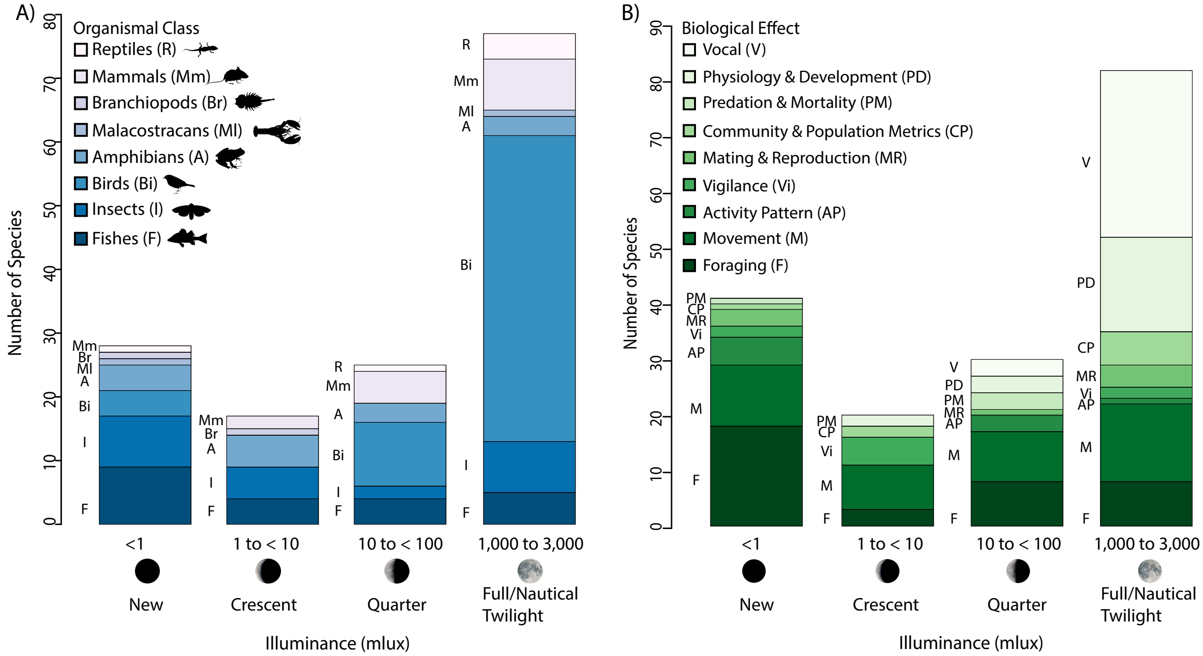
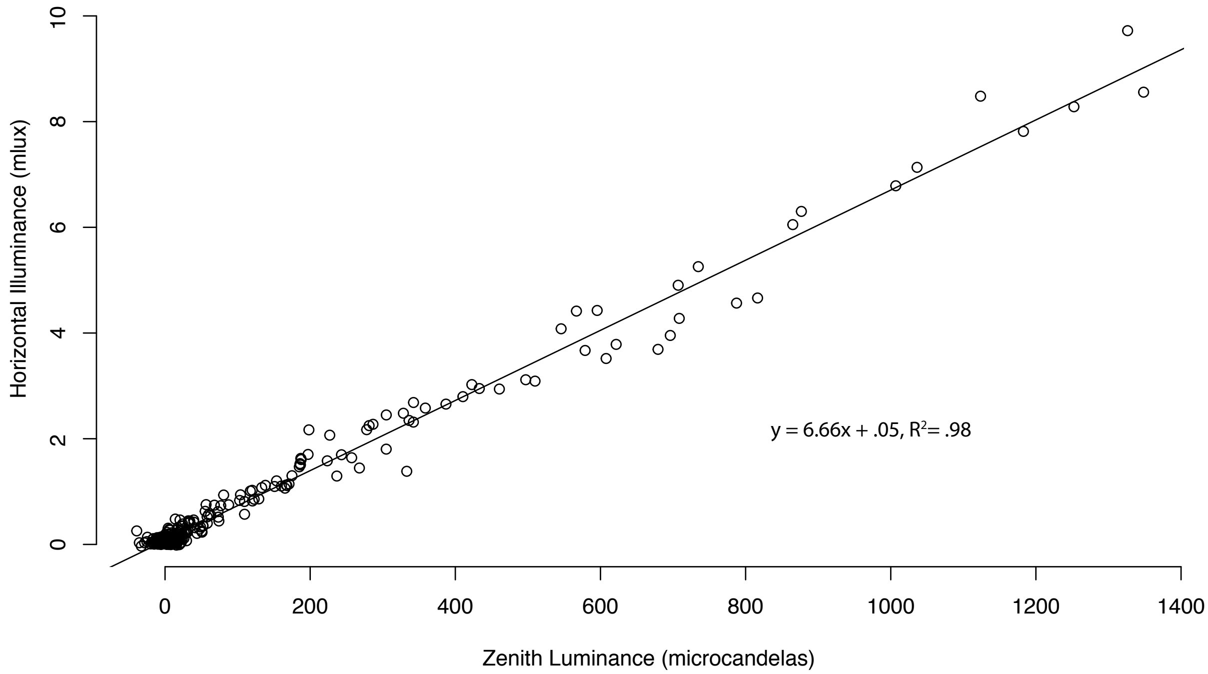

A)
Organismal Class
Reptiles (R)
Mammals (Mm)
Branchiopods (Br)
Malacostracans (Ml)
Amphibians (A)
Birds (Bi)
Insects (I)
Fishes (F)
Number of Species
0
10
20
30
40
50
60
70
80
<1
1 to < 10
10 to < 100
1,000 to 3,000
New
Crescent
Quarter
Full/Nautical Twilight
Illuminance (mlux)
B)
Biological Effect
Vocal (V)
Physiology & Development (PD)
Predation & Mortality (PM)
Community & Population Metrics (CP)
Mating & Reproduction (MR)
Vigilance (Vi)
Activity Pattern (AP)
Movement (M)
Foraging (F)
Number of Species
0
10
20
30
40
50
60
70
80
90
<1
1 to < 10
10 to < 100
1,000 to 3,000
New
Crescent
Quarter
Full/Nautical Twilight
Illuminance (mlux)

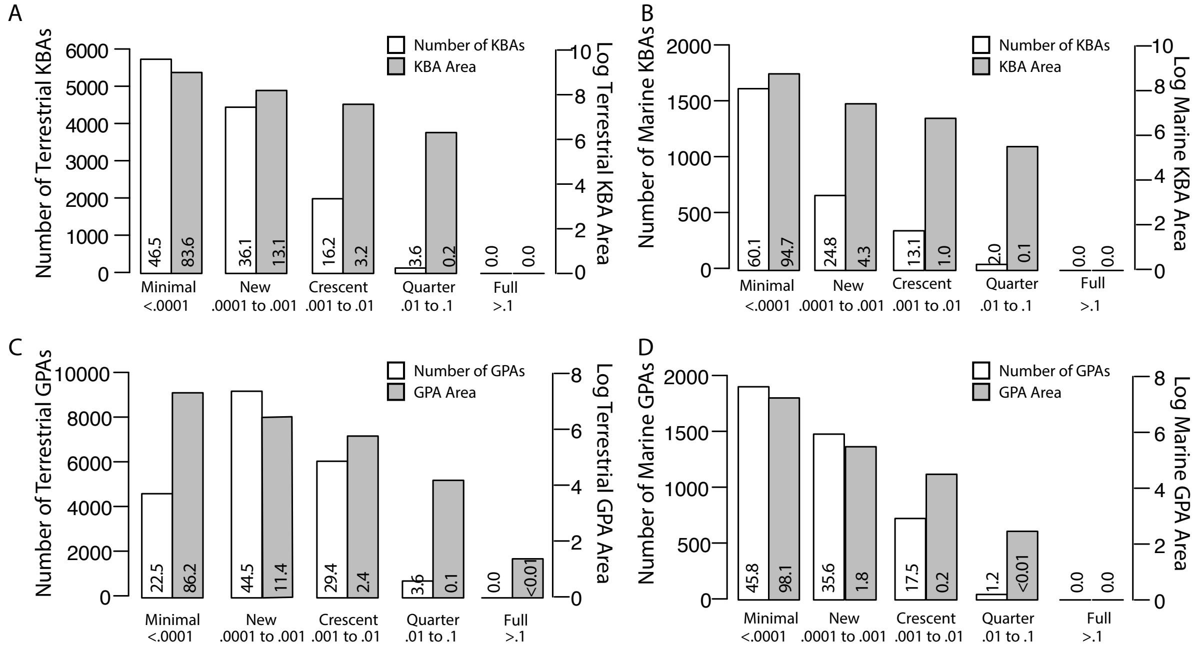
Figure 4.

mlux	Natural Lighting Conditions	Ecological Consequences							
		Activity Pattern	Foraging	Movement	Physiological	Vocal	Predation/ Vigilance	Mating/ Reproduction	Community/ Population Metrics
3,000	Nautical Twilight	Anura	Strigiformes Passeriformes Rodentia Squamata Charadiiformes	Salmoniformes Diptera Osmeriformes Passeriformes Squamata Ephemeroptera Rodentia Strigiformes Amphipoda	Perciformes Passeriformes Passeriformes Primates Galliformes Diptera	Passeriformes	Anura Galliformes	Lepidoptera Diptera	Diprotodontia Squamata Lepidoptera Anura
1,000	Full Moon	Anura Rodentia	Strigiformes Anura Salmoniformes Diptera Passeriformes Perciformes	Diptera Rodentia Anura Passeriformes Squamata	Passeriformes	Passeriformes Galliformes	Rodentia	Passeriformes Coleoptera	Ephemeroptera Trichoptera Diptera
100	Quarter Moon		Cyrpriniformes Salmoniformes	Anura Salmoniformes Clupeiformess Cladocera	Rodentia		Anura		Trichoptera Coleoptera Diptera
10	Crescent Moon	Ephemeroptera Hymenoptera Plecoptera	Strigiformes Anura Salmoniformes Hymenoptera Cyrpriniformes	Ephemeroptera Hymenoptera Plecoptera			Anostraca	Coleoptera	Anostraca
1	New Moon	Hymenoptera Ephemeroptera	Strigiformes Salmoniformes Esociformes Osmeriformes Cyrpriniformes Hymenoptera	Anura Mysida Diptera Ephemeroptera Hymenoptera			Anura		

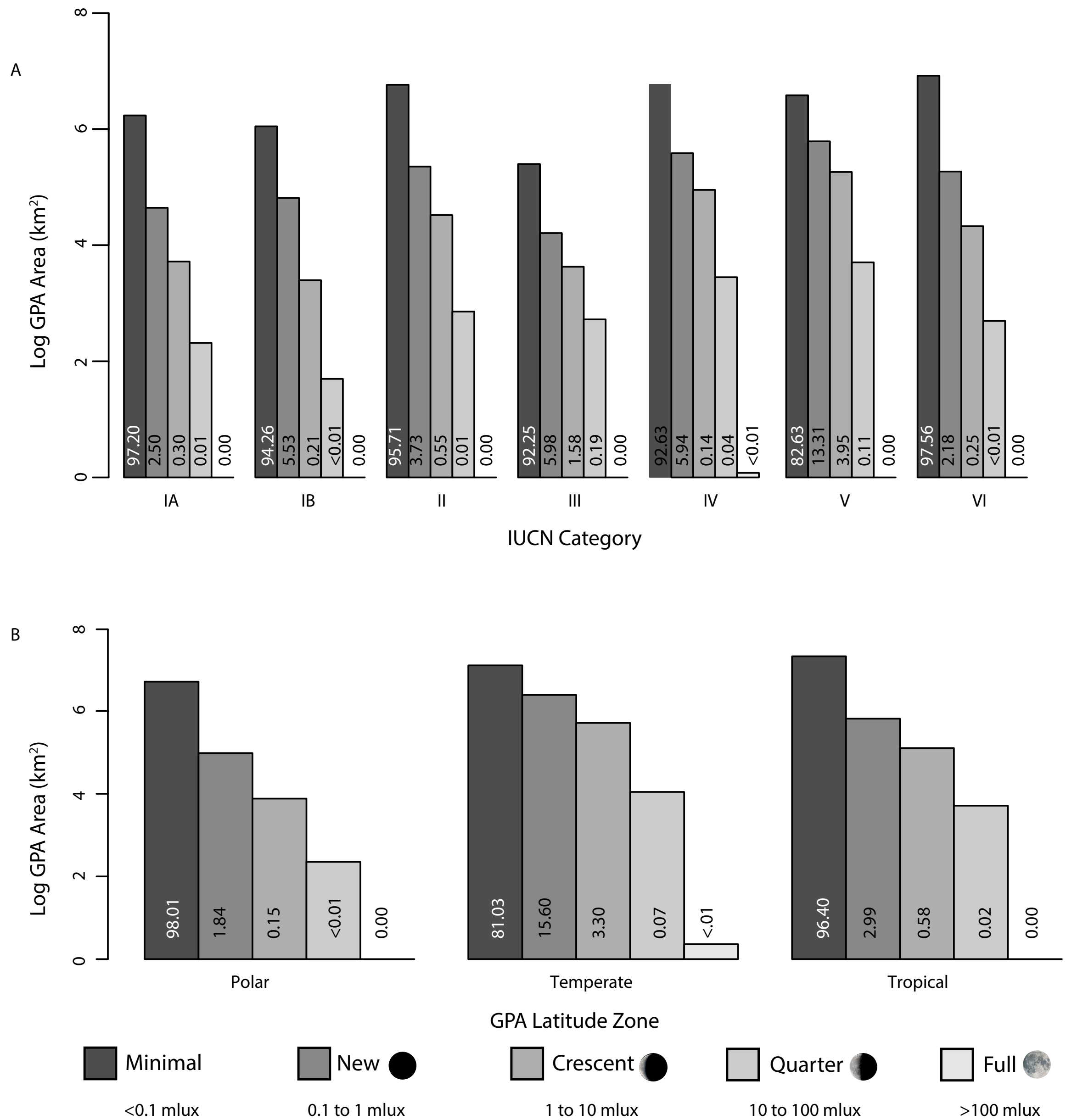
Extended Data Table 1.



Extended Data Figure 1.



Extended Data Figure 2.



321
322 **Extended Data Figure 3.**

Methods

Note: This work is currently under review at peer reviewed journals and thus the data sets are not currently publicly available. If interested in data sharing, please contact Brett Seymoure for options.

Conversion of New World Atlas to Horizontal Illuminance

This paper is distinguished from prior studies of light pollution and ecosystems[1–6] by translating higher quality satellite data into illuminance values that are relevant to organisms in their environments and with units that are compatible with natural cycles of lunar illuminance. In addition, this is the second work that accounts for the spread of light from cities in the form of skyglow and its projection into conservation areas[6]. These advances result from our use of New World Atlas of Light Pollution as our global model of light pollution[7]. The satellite data used for the atlas has nearly seven-fold greater spatial resolution and 256-fold greater dynamic range than the data used for previous studies[1–5,7,8]. In addition, the atlas incorporates radiance transfer models to account skyglow[7].

The New World Atlas described the global extent of anthropogenic luminance at zenith (i.e., directly overhead). This metric has limited function when discussing impacts to animals as many taxa perceive the illuminance of their environment rather than sky brightness[9]. Horizontal illuminance, the collective light illuminating a horizontal surface is a more informative metric as it takes into account light from all zenith angles[10]. We converted the New World Atlas of artificial night sky brightness (VIIRS data set) from luminance in candelas per square meter to illuminance in mlux, which is more appropriate for understanding lighting effects on wildlife[9–11]. By using mlux, we were able to include biologically relevant light intensities for several taxonomic groups of concern revealing natural areas that are anthropogenically illuminated.

Kocifaj et al. (2014) described methods to convert existing zenith luminance to horizontal illuminance based on three idealized atmospheric conditions: homogeneous sky brightness, an isotopically scattering atmosphere, and a stratified turbid atmosphere, with a stated goal of finding a relationship between zenith sky brightness and horizontal illuminance within an order of magnitude[12]. They concluded that a relationship based on models of a stratified turbid atmosphere was most realistic and derived an upper and lower conversion factor of: π/1.39 and 2π.

We used a simplified global conversion of artificial zenith sky luminance to artificial horizontal illuminance based on the analytical extension of an exponentially stratified atmosphere presented by Kocifaj et al. (2014). The simple formula:

$$D = 2\pi B_0$$

is used, where D is horizontal illuminance, and B is sky luminance at zenith angle 0 degrees. As further validation of this simplified conversion, we analyzed calibrated CCD measures of coincident zenith sky brightness and horizontal illuminance from the all sky monitoring dataset from the US National Park Service Night Sky Program[13,14] (Supplemental Fig. 1, accessible at https://www.nps.gov/subjects/nightskies/skymap.htm). Two hundred seventy-nine datasets were analyzed using linear regression to investigate the relationship of zenith luminance and horizontal illuminance, resulting in the formula:

$$D = 6.6 * B_0 + 0.05$$

where horizontal illumination is reported in millilux and zenith luminance is reported in microcandelas per meter^2. The corresponding R^2 value was 0.98 (Supplemental Fig. 1). These results roughly align with the upper bound of 2π found by Kocifaj et al. (2014), as well as that of Garstang (1986)[12,15].

Our analysis is subject to 4 caveats. First, we converted zenith sky luminance measurements to horizontal illuminance, thus the exact value may be subject to error especially in remote areas. Second, we measured illuminance from skyglow and not from direct sources, thus certain areas may be brighter due to electric lighting that is shielded from the sky and thus not contributing directly to skyglow. Third, the VIIRS DNB values are biased towards longer wavelengths of light (i.e. yellow and red) and underestimate short wavelengths (i.e. blue light)[7,16,17]. This is an issue for all artificial light research using satellite data, particularly as short wavelength dominant lights (LEDs) become more common[16]. Thus, the values here are likely to underestimate anthropogenic illuminance, since short wavelengths of light contribute more to skyglow[18]. Lastly, our values of horizontal illuminance predict light levels that reach the surface of the Earth (e.g. forest canopy), but may not match light levels that reach the ground, as thick canopy cover can reduce downwelling illuminance by as much as two orders of magnitude[19,20].

Natural Light Cycle Measurements and Values

The variation in illuminance due to lunar phase spans multiple orders of magnitude[10,20,21]. In addition, there is variation in reported illuminance values, with previous studies reporting a wide range of values for full moon illuminance spanning less than 100 mlux to greater than 2000 mlux[21–24]. These discrepancies are due to several factors, including the altitude of the moon, the atmospheric conditions, and latitude[20]. Greater lunar illuminance results from higher lunar altitude, murkier atmospheric conditions, and latitudes close to the equator[20,21]. However, very few reports exist on the ambient illuminance from lunar phases other than full moon (but see[20]). Thus, we collected illuminance data in a near natural location through several lunar cycles to resolve specific levels referred to here.

We measured illuminance levels with zenith sky brightness data from a naturally dark portion of Colorado's arid Piceance Basin[6], at approximately 40° N. The zenith data were collected using Unihedron SQM-L-DL units from October and November 2016, and March and April 2017. The sky brightness measurements were recorded every 5 minutes between 10:00pm and 5:00am, and we limited our analyses to clear nights. Using Suncalc in R[25], we grouped values by lunar phase (new moon, crescent, quarter, and full) and lunar altitude (greater than ten degrees above the horizon) resulting in 1,027 light values. We then converted these luminance data to horizontal illumination[8] and compared our values to published values of lunar illumination[10,26]. Further, we measured sky brightness on a clear moonless night using a calibrated CCD camera to assess all-sky conditions during the new moon. Our SQM measured values overlapped with those reported in the literature and resulted in the following averages: new moon = 1.0 mlux, quarter moon = 30 mlux, and full moon = 100 mlux. Our SQM new moon value of 1.0 mlux is likely due to air glow during our measurements as our CCD values were between 0.74 and 0.86 mlux. Thus, we assigned anthropogenic lunar levels as: new moon conditions = 0.1 to 1.0 mlux, crescent moon = 1.0 to 10 mlux, quarter moon = 10 to 100 mlux, full moon > 100 mlux. As we were concerned with understanding how anthropogenic lighting equates to natural night conditions on a global scale and not just one location, we used values that fit within the range of both our measurements and those reported in the literature[10,21,26,27].

Calculating Illuminance for Global Protected Areas and Key Biodiversity Areas

We paired our measures of artificial horizontal illuminance (mlux) with the World Database on Global Protected Areas (GPA) and World Database on Key Biodiversity Areas (KBA) to assess the extent of artificial horizontal illuminance in the world's protected areas[21,22].

The spatial extent of the New World Atlas is 80° N to -60° S[6]. Therefore, any GPAs and KBAs outside of this area were removed from the analysis resulting in a total of 211,972 GPAs and 14,856 KBAs. We included both marine and terrestrial GPAs and KBAs. For quantification of light level by the International Union for Conservation of Nature (IUCN) management category, only GPA's with defined IUCN categories were used. Those classified as "Not Applicable", "Not Recorded" or "Unavailable" (n=72,230) were removed from the analysis for a total of 139,742 GPAs. For each GPA and KBA, we extracted the median illuminance value ± standard deviation, first and third quartiles, coefficient of variation, and proportion of area below each lunar threshold (see Supplemental Data 1 and 2).

Calculating Global Species Richness

Global species richness was calculated for threatened and non-threatened terrestrial birds, mammals and amphibians[28]. Global 10 km rasters[28] were converted to polygon layers based on the distribution of species richness using rank statistics. Polygons with the top 25% of species richness for each taxon (threatened and non-threatened) were overlaid on the horizontal illuminance raster to extract light levels. Within each polygon we calculated summary statistics, including median illuminance ± standard deviation, first and third quartiles, coefficient of variation, and proportion of area below each lunar threshold.

Literature Review on the Effects of Light Levels on Animals

Much research has been conducted to understand the ecological consequences and organismal responses to light at night, both natural and anthropogenic. To compile the previous research, in April of 2018 we conducted a detailed literature search using Thompson's *ISI Web of*

Science with the following specific search terms: ["Light pollution" and "Artificial Lighting"] AND ["Effects on Animals" or "Effects on Wildlife"]. We also searched using *Google Scholar* with the search terms: “Light pollution” AND “Effects on Animals”; Light pollution’ AND “Effects on Wildlife”; “Artificial Lighting” AND “Effects on Animals”; “Artificial Lighting” AND “Effects on Wildlife”. *Web of Science* delivered 261 publications while *Google Scholar* delivered a total of 467 publications.

We reviewed all hits to locate any “effect” from light levels, with an “effect” defined as a statistically significant change in the particular biological metric as a function of light level. Furthermore, if a publication cited work that was not selected by *Web of Science* or *Google Scholar*, we added the study to our database. We included data from empirical studies showing a significant biological effect at light levels less than 3,000 mlux (which is approximately the brightest values of both full moon and nautical twilight[10,26]), resulting in a database of 87 studies. The database included the species, order, class, the experimental setting (e.g. field observation, field experiment, laboratory experiment, etc.), the effect, illuminance (in lux), and citation (Supplemental Data 3, Supplemental Data 4). We categorized biological effects in to: foraging, movement, activity patterns, vigilance, mating and reproduction, community and population biology metrics, predation and mortality, physiology and development, and vocal behavior. Population and community metrics included any effect at the population level or an interaction of more than one species. We consolidated the published literature on animal responses to both natural and artificial lighting to summarize the effects of a range of light levels that we translated to equivalent nighttime conditions, from new moon and darker (<.1 mlux) to nautical twilight (i.e. the sun is 6° to 12° below horizon, which is as bright as 3,000 mlux). We included nautical twilight in the literature review as a more comprehensive approach of understanding the lighting conditions that animals will experience when the sun is below the horizon, although we note that no GPA or KBA had anthropogenic illuminance above 1,000 mlux. Lastly, we presented the literature review by taxonomic class in Figure 4 and for greater taxonomic resolution as order in Extended Data Table 1.

Supplemental Data

KBA dataset, Supplemental Data 1

GPA dataset, Supplemental Data 2

Lit Review Data frame, Supplemental Data 3

Methods References

1. Gaston, K. J., Duffy, J. P. & Bennie, J. Quantifying the erosion of natural darkness in the global protected area system. *Conserv. Biol.* **29**, 1132–1141 (2015).
2. Davies, T. W., Duffy, J. P., Bennie, J. & Gaston, K. J. Stemming the Tide of Light Pollution Encroaching into Marine Protected Areas. *Conserv. Lett.* **9**, 164–171 (2016).
3. Bennie, J., Duffy, J. P., Davies, T. W., Correa-Cano, M. E. & Gaston, K. J. Global trends in exposure to light pollution in natural terrestrial ecosystems. *Remote Sens.* **7**, 2715–2730 (2015).
4. Guetté, A., Godet, L., Juigner, M. & Robin, M. Worldwide increase in Artificial Light At Night around protected areas and within biodiversity hotspots. *Biol. Conserv.* **223**, 97–103 (2018).
5. Koen, E. L., Minnaar, C., Roever, C. L. & Boyles, J. G. Emerging threat of the 21st century lightscape to global biodiversity. *Glob. Chang. Biol.* (2018). doi:10.1111/gcb.14146
6. Garrett, J. K., Donald, P. F. & Gaston, K. J. Skyglow extends into the world ' s Key Biodiversity Areas. *Anim. Conserv.* (2019). doi:10.1111/acv.12480
7. Falchi, F. *et al.* The new world atlas of artificial night sky brightness. *Sci. Adv.* **2**, 1–26 (2016).
8. Cinzano, P., Falchi, F. & Elvidge, C. D. The first World Atlas of the artificial night sky brightness. *Mon. Not. R. Astron. Soc.* **707**, 689–707 (2001).
9. Cronin, T. W., Johnsen, S., Marshall, N. J. & Warrant, E. J. *Visual Ecology*. (Princeton University Press, 2014).
10. Johnsen, S. *The Optics of Life*. (Princeton University Press, 2012).
11. Lythgoe, J. N. *The ecology of vision.* (Clarendon Press, 1979).
12. Kocifaj, M., Posch, T. & Solano Lamphar, H. A. On the relation between zenith sky brightness and horizontal illuminance. *Mon. Not. R. Astron. Soc.* **446**, 2895–2901 (2014).
13. Duriscoe, D. M., Luginbuhl, C. B. & Moore, C. A. Measuring night-sky brightness with a wide-field CCD camera. *Publ. Astron. Soc. Pacific* **119**, 192–213 (2007).
14. Duriscoe, D. M. Photometric indicators of visual night sky quality derived from all-sky brightness maps. *J. Quant. Spectrosc. Radiat. Transf.* 1–13 (2016). doi:10.1016/j.jqsrt.2016.02.022
15. Garstang, R. H. Model for artificial night-sky illumination. *Publ. Astron. Soc. Pacific* **98**, 364–375 (1986).
16. Kyba, C. C. M. *et al.* Artificially lit surface of Earth at night increasing in radiance and extent. *Sci. Adv* **3**, 1–9 (2017).
17. Elvidge, C. D., Oceanic, N., Zhizhin, M. N., Oceanic, N. & Hsu, F. Why VIIRS data are superior to DMSP for mapping nighttime lights. *Proc. Asia-Pacific Adv. Netw.* **35**, 62–69 (2013).
18. Aube, M. Physical behaviour of anthropogenic light propagation into the nocturnal environment. *Philos. Trans. R. Soc. B* **370**, 20140117 (2015).
19. Kelber, A. *et al.* Light intensity limits foraging activity in nocturnal and crepuscular bees. *Behav.*

Ecol. **17**, 63–72 (2005).
20. Veilleux, C. C. & Cummings, M. E. Nocturnal light environments and species ecology : implications for nocturnal color vision in forests. *J. Exp. Biol.* **215**, 4085–4096 (2012).
21. Kyba, C. How bright is moonlight ? (2017).
22. Bruce-White, C. & Shardlow, M. A review of the impact of artificial light on invertebrates. in *Buglife-The Invertebrate Conservation Trust* (2011).
23. Yorzinski, J. L. *et al.* Artificial light pollution increases nocturnal vigilance in peahens. *PeerJ* 1–19 (2015). doi:10.7717/peerj.1174
24. Todd, J. J., Barakat, B., Tavassoli, A. & Krauss, D. A. The moon's contribution to nighttime illuminance in different environments. *Proc. Hum. Factors Ergon. Soc.* **2015-Janua**, 1056–1060 (2015).
25. Team, R. C. R: A language and environment for statistical computing. (2014).
26. Bond, D. S. & Henderson, F. P. *The Conquest of Darkness*. **346297**, (1963).
27. Todd, J. J., Barakat, B., Tavassoli, A. & Krauss, D. A. The moon's contribution to nighttime illuminance in different environments. *Proc. Hum. Factors Ergon. Soc.* **59**, 1056–1060 (2015).
28. Jenkins, C. N., Pimm, S. L. & Joppa, L. N. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci.* **110**, E2602–E2610 (2013).