1   **Insect communities under skyglow: diffuse nighttime illuminance induces**
2   **spatiotemporal shifts in movement and predation**

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4   Alexander Dyer,[1,2,*] Remo Ryser,[1,2] Ulrich Brose,[1,2] Angelos Amyntas,[1,2] Nora Bodnar,[1,2] Thomas

5   Boy,[1,2] Solveig Franziska Bucher,[1,3] Simone Cesarz,[1,4] Nico Eisenhauer,[1,4] Alban Gebler,[1,4] Jes Hines,[1,4]

6   Christopher C. M. Kyba,[5,6] Myles H. M. Menz,[7] Karl Rackwitz,[1,2] Tom Shatwell,[8] Jördis F. Terlau,[1,2]

7   Myriam R. Hirt[1,2]

8   [1] *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany*

9   [2] *Institute of Biodiversity, Friedrich-Schiller-University Jena, Jena, Germany*

10 [3] *Institute of Ecology and Evolution with Herbarium Haussknecht and Botanical Garden, Professorship*

11 *of Plant Biodiversity, Friedrich-Schiller-University, Jena, Germany*

12 [4] *Institute of Biology, Leipzig University, Leipzig, Germany*

13 [5] *Remote Sensing and Geoinformatics, Deutsches GeoForschungsZentrum Potsdam, 14473 Potsdam,*

14 *Germany*

15 [6] *Geographisches Institut, Ruhr-Universität Bochum, 44780 Bochum, Germany*

16 [7] *College of Science and Engineering, James Cook University, Australia*

17 [8] *Department of Lake Research, Helmholtz Centre for Environmental Research (UFZ), Magdeburg,*

18 *Germany*

19 *Corresponding author: alexander.dyer@idiv.de*

20

21   Abstract

22

23   Artificial light at night (ALAN) is predicted to have far-reaching consequences for natural ecosystems

24   given its influence on organismal physiology and behaviour, species interactions, and community

25   composition. Movement and predation are fundamental ecological processes that are of critical

26   importance to ecosystem functioning. The natural movements and foraging behaviours of nocturnal

27 invertebrates may be particularly sensitive to the presence of ALAN. However, we still lack evidence
28 of how these processes respond to ALAN within a community context. We assembled insect
29 communities to quantify their movement activity and predation rates during simulated moon cycles
30 across a gradient of diffuse nighttime illuminance including the full range of observed skyglow
31 intensities. Using radio frequency identification, we tracked the movements of insects within a
32 fragmented grassland Ecotron experiment. We additionally quantified predation rates using prey
33 dummies. Our results reveal that even low-intensity skyglow causes a temporal shift in movement
34 activity from day to night, and a spatial shift towards open habitats at night. Changes in movement
35 activity are associated with indirect shifts in predation rates. Spatiotemporal shifts in movement and
36 predation have important implications for ecological networks and ecosystem functioning,
37 highlighting the disruptive potential of ALAN for global biodiversity and the provision of ecosystem
38 services.

39

40 **Keywords**: light pollution, ALAN, fragmented landscapes, activity pattern, foraging, nocturnal,
41 crepuscular

42

Introduction

44

45 Artificial light at night (ALAN) is a rapidly increasing global phenomenon impacting the physiology
46 and behaviour of organisms [1], their interactions [2,3] and space use [4,5] as well as the
47 composition of species within and across communities [6–8]. It, therefore, has the potential to
48 drastically alter natural ecosystems, and has been proposed as a major driver of insect decline
49 [9,10].

50 To date, studies of the ecological impacts of ALAN have focussed almost exclusively on the responses
51 of animals near to individual bright sources of light (such as streetlights). However, ALAN also affects
52 ecosystems much further from areas of human activity via the phenomenon known as "skyglow",
53 the diffuse and low-intensity artificial light that is reflected back to Earth by clouds and aerosols in
54 the atmosphere [11–13]. The illuminance of skyglow is often far larger than starlight [14], and can
55 approach the brightness of the full moon [15]. Furthermore, in areas affected by skyglow, overcast
56 nights are no longer dark [16], so the overall range of nighttime illuminance experienced by the

57 ecosystem is reduced by several orders of magnitude compared to natural conditions. For instance,

58 it has been shown that even low levels of artificial light intensities have the capacity to modify

59 foraging efficiency and the strength of interspecific interactions, which lead to corresponding

60 changes in community structure [2], highlighting the need to study the community- and ecosystem-

61 level effects of comparatively low-intensity skyglow [17,18]

62 To better address the effects of ALAN in general and skyglow in particular on biodiversity and

63 ecosystem functioning, we require a holistic understanding of the underlying ecological processes

64 that drive species' distributions and abundances, such as animal space use and biotic interactions.

65 Movement is a key mediator of these processes as it enables animals to explore their environment

66 for food, potential mates and suitable habitats. Unfortunately, the sensitivity of animal movement to

67 the presence of diffuse nighttime illuminance such as skyglow remains unclear.

68 Light pollution has been shown to have widespread effects on movement behaviours across several

69 spatial scales, such as migration [19–21], dispersal [22,23], as well as local movements within and

70 between habitats [24–27]. These effects can be diverse [8]; for instance, at local scales, there is

71 evidence of reduced [28–31] as well as increased movement activity [32] in response to ALAN, which

72 may be induced by the elevated risk or facilitation of predation, respectively. Moreover, animals may

73 shift their activity temporally with or without affecting their overall activity time budget [33–35].

74 Generally, the onset and duration of movement activity among visual predators depend on

75 illumination levels that facilitate successful foraging activity [36]. This implies that ALAN acts on the

76 temporal as well as spatial dimension of movement, with diverse knock-on effects for encounter

77 rates and interactions among hetero- and conspecifics.

78 Predation is a key ecological interaction that determines the structure and functioning of

79 ecosystems. ALAN can drive predation rates (i) by affecting spatiotemporal movement activity (i.e.

80 where and when they move) and local densities, and thus encounters between predator and prey, or

81 (ii) by affecting detection ability [37] (Figure 1). Among animals that rely on visual cues to orient

82 themselves or detect and capture their prey, visual acuity facilitates the processing of spatial

83 information and increases the minimum distances at which potential prey becomes visible. Visual

84 predators, particularly those that possess adaptations which increase visual acuity under the

85 ambient light conditions of their temporal niche [38], are expected to be particularly sensitive to

86 ALAN [2,39]. Habitat structure can modify the effects of ALAN on animal movement and foraging

87 behaviour by altering the trade-off between foraging success and predation risk [25,34,40], for

88 instance, by impeding predators' movements and their visual detection of prey or through the

89 provision of prey refuges [41]. Moreover, ALAN can change species' preferences for certain habitats

90 and thus influence space-use, habitat connectivity [4,5,26], and (co-)occurrence, with profound
91 effects on encounter probabilities. This demonstrates that ALAN has the potential to fundamentally
92 disrupt trophic interactions with implications for food webs, species distributions, biodiversity, and
93 ecosystem functioning (Figure 1).

94 We designed an Ecotron experiment with simulated diel light and moon cycles to elucidate the
95 interactive effects of skyglow and habitat structure on movement and predation. We continuously
96 tracked the movements of individual insects (792 individuals across seven beetle and one bug
97 species) within experimental grassland-patch landscapes using RFID tracking and measured
98 predation rates on artificial caterpillar prey dummies. We quantified how temporal- (Q1) and spatial
99 movement activity (Q2) respond to nighttime illuminance across a gradient from 0.001 lux (starlight)
100 to 30 lux (under a streetlight). Furthermore, we measured the effect of light on predation rates and
101 discuss their dependence on detection probabilities and encounter rates (Q3 & Q4) (Figure 1).

102

Methods

103

104

105 *General setup and experimental design*

106 We conducted our experiment at the iDiv Ecotron experimental facility, which is an indoor
107 mesocosm facility consisting of independent, experimental chambers called "EcoUnits" [42]. The
108 Ecotron is located in Bad Lauchstädt, Saxony-Anhalt, Germany, at the Experimental Research Station
109 of the Helmholtz Centre for Environmental Research (UFZ, 51.3917° N, 11.8762° E). Multiple
110 environmental conditions in the EcoUnits can be fully controlled (e.g., nutrient supply and irrigation).
111 Each EcoUnit has internal dimensions of 1.46 m × 1.46 m × 1.50 m (L × W × H, aboveground) and
112 1.24 m × 1.24 m × 0.80 m (L × W × H, belowground) with the soil surface area measuring 1.54 m²
113 [42]. We conducted the experiment in 12 EcoUnits from July to October 2020.

114 To assess the interactive effects of diffuse nighttime illuminance and landscape structure on animal
115 movement patterns, we established a patch-grassland system which consisted of four meadow
116 patches within each of the corners of an EcoUnit, separated by an area of bare ground (Figure 2a, b).
117 The EcoUnits were filled with 1.23 m³ of unsterilised and homogenised soil from the vicinity of the
118 iDiv Ecotron, and plant communities of 16 plant species were sown on February 4th 2020 (Table S1).
119 We allowed for a settlement phase of roughly 5 months before starting our measurements.

120   *Light treatment*

121   Across the 12 EcoUnits, we simulated diel light and moon cycles and added a treatment of diffuse

122   nighttime illuminance including the full range of observed skyglow intensities [44,45,16].

123   *Daylight*

124   The daytime lighting (manufactured by Roschwege GmbH, Germany) within all EcoUnits was set to

125   the same daylight settings. Photoperiods were adjusted every four weeks to approximate local

126   sunrise and sunset times throughout the duration of the experimental period. Daylight was gradually

127   (i.e. linearly) brightened or dimmed over the course of two hours before sunrise and sunset,

128   respectively. The maximum brightness of the daytime lighting was approximately 35,000 lux, which

129   corresponds roughly to a sunny day in Germany, and a light spectrum that approximates sunlight.

130   *Moonlight*

131   At night, moonlight within each EcoUnit was simulated by a single sunlike LED (SunLike3030 by Seoul

132   Semiconductor Co. Ltd., Korea) with a light spectrum that approximates sunlight (Figure S1). We

133   simulated moonlight because complete darkness is not a meaningful control [46,47], and organisms

134   have adapted to moon cycles over the course of evolutionary history. Moonlight intensities for clear-

135   sky conditions were modelled for the real time and location of the experiment using an astronomical

136   model of solar and lunar illuminance. The illuminance model calculates direct and diffuse

137   illuminance and was based on the model of Janiczek and DeYoung [48], with several enhancements

138   to increase accuracy. Illuminance of the moonlight LED was adjusted automatically every minute

139   using a Python script running on a raspberry pi, and could be adjusted to 57 illuminance levels

140   spanning from 0 lux (off) to the maximal modelled moonlight brightness of approximately 0.274 lux.

141   *Nighttime illuminance*

142   We established a skyglow treatment with a gradient of diffuse nighttime illuminance that spanned

143   from 0.0014 lux (slightly brighter than starlight) to 30 lux on a log10 scale. The very upper end of our

144   gradient is brighter than the skyglow that is observed in nature today but might cover future

145   scenarios of diffuse nighttime illuminance. The levels of nighttime illuminance at both ends of the

146   gradient were replicated once. We used LED lights (type 2835 by HuiYuan Opto-Electronic Co. Ltd.,

147   China) with a typical blue light peak within their spectrum (Figure S2). This resulted in illuminance of

148   0.0014 (no pollution control), 0.0087, 0.028, 0.081, 0.1, 0.3, 0.94, 3.03, 9.88, and 30.31 lux (in the

149 absence of moonlight). Note that half of the gradient lies below the maximum brightness of the full

150 moon during the experimental phase (0.274 lux). We chose to cover these low light intensities for

151 two major reasons: (1) they represent light levels organisms naturally experience and have adapted

152 to for millions of years, and (2) reflect typical intensities of far-reaching skyglow [14]. To avoid

153 stunning animals by sudden changes in brightness, the treatment lights were always switched on

154 and off at sunrise and sunset, respectively (when daylight was at 50%). To avoid point sources of

155 light and simulate diffuse nighttime illuminance such as skyglow, the light was scattered using

156 diffusion foil.

157 All units were covered with black theatre curtains to block light from outside (see Fig. 2c). The

158 illuminance in the units was calibrated via a sky brightness measurement approach using a fisheye-

159 lens camera [16].

160 *Study animals*

161 We collected the insects for the experimental communities in the surrounding area of Leipzig,

162 Saxony, Germany (51.3213° N, 12.3964° E and 51.2799° N, 12.4119° E) from June to August 2020

163 using pitfall traps. Our species selection (Table S2) depended on seasonal densities and occurrences,

164 and consisted of seven species of carabid ground beetle (Coleoptera: Carabidae) which are primarily

165 crepuscular or nocturnal (Table S2, [49]): *Abax parallelus* (Duftschmid), *Calathus fuscipes* (Goeze),

166 *Carabus granulatus* (Linnaeus), *Carabus nemoralis* (Müller), *Harpalus rufipes* (De Geer), *Nebria*

167 *brevicollis* (Fabricius), and *Pterostichus melanarius* (Illiger) (Table S2). All species were housed in

168 separate containers which were bedded with moistened soil and foliage, and fed ad libitum with

169 beetle jelly from a commercial supplier (The Pet Factory, Germany) prior to the experiment. In total,

170 our Ecotron communities constituted a total of 792 RFID-tagged individuals from seven species

171 across two orders with body masses ranging from 47 mg (*Calathus fuscipes*) to 707 mg (*Carabus*

172 *nemoralis,* Table S2). We distributed them equally across the EcoUnits at densities that reflect a

173 natural abundance-mass relationship (Table S2).

174 *Movement tracking via RFID*

175 We used a Radio Frequency Identification (RFID) tracking system consisting of passive RFID-tags,

176 RFID-readers (transceivers), and a host system (controller) to track the movements of our study

177 animals (see [43] for details). We distributed 36 RFID sensors equally across patch and matrix areas

178 in the EcoUnits (4 sensors in each patch and 20 sensors in the matrix, Fig. 2b). Before adding the

179 study animals to the EcoUnits, we weighed and tagged the individuals with a unique RFID-tag. We

180   kept the insects at 4°C for 15 min before gluing the tag to the elytra of the beetles. We used

181   medium-sized (size: 8.3 x 8.3 x l 0.7 mm, reading range: 25 mm, mass: 35 mg, Murata LXMSAPHA17-

182   176) and small RFID-tags (size: 3.2 x 3.2 x 0.75 mm, reading range: 12 mm, mass: 20 mg, Murata

183   LXMS33HCNK-171), for large- (body mass > 200 mg) and small-bodied (body mass < 200 mg) species,

184   respectively. We recorded the tag-ID together with the identity and body mass of the individual.

185   Movement tracking inside the EcoUnits was performed across two temporal experimental blocks,

186   each corresponding to a period of approximately one lunar cycle (i.e., 28 days: experimental block I:

187   21.07.2020 - 18.08.2020, experimental block II: 15.09.2020 - 13.10.2020). Newly tagged individuals

188   were added a few days prior to the start of the respective experimental block for acclimatisation.

189   During the tracking periods, individuals were identified with a unique timestamp when crossing a

190   sensor and disturbances were minimised by only opening the EcoUnits once for the exchange of prey

191   dummies. Together with the exact position of the RFID sensor in the EcoUnit, this provides unique

192   spatiotemporal information for each tagged individual. We defined detections as distinct and only

193   counted them when they (1) occurred on different sensors or when (2) at least 10 seconds had

194   elapsed (without detection on the same sensor) between two consecutive detections on the same

195   sensor. This prevented the repeated detection of resting or dead animals. We used the number of

196   RFID detections as a measure of the movement activity of the community, which is the product of

197   local densities and individual movement.

198   *Predation rates*

199   Predation rates were estimated across the skyglow gradient by recording bite marks on prey

200   dummies [50–52]. We moulded artificial prey dummies from odourless, non-toxic green plasticine

201   (Noris 8421 by Staedler, Germany) to resemble model caterpillars of a standardised appearance (Fig

202   2d). We mounted 16 prey dummies on pins that were equally spaced within the four habitat patches

203   of each EcoUnit (Figure 2b) for two successive 14-day exposures within each 4-week temporal

204   experimental block. Two independent observers scored the prey dummies by identifying and

205   counting the bite marks left by carabid predators. Although there are limits to the precision of

206   identification [53], we were able to identify and group the parallel marks left by the mandibles of

207   carabid beetles in order to identify the number of successful attacks on individual prey dummies,

208   thereby quantifying predation rates during each 14-day exposure. This approach is likely only able to

209   elucidate predation rates of visual predators, rather than predators that search via olfaction.

210   Notably, visual hunters are the predators that are also likely to be affected by light.

Statistical analysis

212   We fitted generalised linear mixed effects models (GLMM) using the 'glmmTMB' package [54] in R

213   4.2.2 [55] to investigate the effects of ALAN as diffuse nighttime illuminance on the total movement

214   activity, space use, and predation rates in the insect communities. To test our first hypothesis, that

215   ALAN alters animal movement activity (Q1), we modelled the interactive effects of diffuse nighttime

216   illuminance and diel light cycle (day vs night) on species' movement activity. Movement activity was

217   estimated from the number of detections per day/night and analysed both on the community- and

218   species-level. To assess the effects of ALAN on animal space use during each phase of the diel light

219   cycle (Q2), we modelled the interactive effects of diffuse nighttime illuminance and habitat (patch vs

220   matrix) on species' movement activity (sum of detections per day/night). We used a negative

221   binomial distribution to account for overdispersion in the movement activity data and included the

222   temporal experimental block as a random intercept to account for temporal replication of the 4-

223   week experimental tracking within the same EcoUnit. To test whether the effect of nighttime

224   illuminance on total movement activity of the community is more driven by individual movement or

225   by local densities, we leveraged the individual-level information provided by the RFID tags to correct

226   the sum of detections for differences in local densities. Therefore, we included the number of

227   unique RFID tag detections, aggregated at the corresponding spatial and temporal scale (see Table

228   S3 for detailed information), as an offset term to the GLMM models reported in our supplementary

229   analyses. To evaluate if ALAN mediates the predation rates of visual predators by increasing the

230   detection of prey dummies (Q3), we modelled the effect of diffuse nighttime illuminance on

231   predation rates (bite counts per 14 days). Predation rates during each of the two 4-week

232   experimental blocks were estimated by counting and summing the number of bite marks left by

233   carabid beetles during two successive 14-day exposures. We modelled predation rates using a quasi-

234   Poisson distribution to account for overdispersion, and included the temporal experimental block as

235   a random intercept. To test our final hypothesis, that skyglow affects predation rates via an

236   increased encounter rate with prey (H4), we first aggregated the data on movement activity and

237   predation rates to comparable spatial scales (Fig 2b, Table S3): We modelled the effect of patch-level

238   movement activity (sum of detections per 14 days within each patch, Fig. 2b) on patch-level

239   predation rates (bite counts per 14 days within each patch) using a quasi-Poisson distribution. We

240   included the number of prey dummies recovered from each patch as an offset term, with the

241   temporal experimental block as a random intercept. The patch-level movement activity used in the

242   analyses of predation rates excluded detections of species that are not expected to leave bite marks,

243   i.e., species that are too small to reach mounted prey dummies (body size < 200 mg). Figures were

244   created using the R packages 'ggplot2' [56] and 'ggeffects' [57].

245

Results

247

248 We recorded a total of 25,378 RFID-detections across all experimental insect communities. With

249 regard to our first research question (Q1) on how movement activity (measured as the number of

250 detections per day/night, see Methods) is altered by skyglow, we found no significant effect of

251 nighttime illuminance on overall movement activity (Fig. 3a, slope = 0.014, p = 0.530, Table S4a).

252 However, with increased nighttime illuminance and despite some variability across species (see

253 Table S5), we found a significant decrease in movement activity at the community level during the

254 day (Fig. 3b, slope = -0.099, p = 0.008, Table S6a) and a significant increase in movement activity

255 during the night (Fig. 3b, slope = 0.069, p = 0.014, Table S6a). Together, these results imply a

256 temporal shift in activity from day to night without effects on the overall activity time budget.

257 Furthermore, we observed a spatial shift in movement activity of the insect community in response

258 to nighttime illuminance (Q2). During daytime, the movement activity within the matrix decreased

259 with nighttime illuminance (Fig. 4a, slope = -0.183, p = 0.001, Table S7a), while the movement

260 activity increased in the habitat patches (Fig. 4a, slope = 0.114, p = 0.048, Table S7a). This suggests a

261 shift in space use towards denser habitats during daytime. In contrast, we found that nighttime

262 movement activity increased within the matrix in response to the effect of nighttime illuminance

263 (Fig. 4b, slope = 0.072, p = 0.028, Table S8a), while no significant effect was observed within habitat

264 patches (Fig. 4b, slope = 0.018, p = 0.653, Table S7). This suggests that the increased nocturnal

265 movement activity of the insect community as well as the corresponding decreased movement

266 activity during day predominantly took place within the matrix.

267 To elucidate whether the effects of nighttime illuminance on movement activity are driven by

268 changes in individual movement or local densities, we performed all analyses (Q1 & Q2) with the

269 local densities as an offset. All results remained virtually identical (see Figures S3 & S4 and Tables

270 S4b, S6b, S7b & S8b). Furthermore, the number of detected individuals per EcoUnit during the

271 second half of each experimental block was not significantly affected by the diffuse nighttime

272 illumination (see Table S9), suggesting that abundances were unaffected by the light treatment.

273 Together, this indicates that nighttime illuminance drives the community-level movement activity

274 mainly through changes in individual movement.

275   Contrary to our expectations, there was no significant effect of nighttime illuminance on the overall

276   predation rate (estimated by the number of bite marks on individual prey dummies) by the

277   experimental insect community (Fig. 5a, slope = 0.029, p = 0.127, Table S10) (Q3). This reflects the

278   neutral effect of nighttime illuminance on the overall movement activity (Fig. 3a). In contrast to

279   movement activity (Fig. 3b), bite marks could not be associated with night or day, as they were only

280   collected every two weeks. However, we did find a strong correlation between patch-level predation

281   rate and movement activity (Fig. 5b, slope = 0.131, p = 0.002, Table S11), i.e., we counted

282   significantly more bite marks on prey dummies from patches that reported a higher movement

283   activity. Together with our results showing no effect of nighttime illuminance on local densities, this

284   supports our expectation that higher movement activity, which enables more frequent encounters

285   between predators and artificial caterpillar prey dummies, is the primary driver of predation rates

286   (Q4).

287

288   Discussion

289

290   We experimentally exposed artificial grassland communities to a gradient of diffuse nighttime

291   illuminance, and demonstrated that nighttime illuminance elicits spatiotemporal shifts in movement

292   and predation of insects. We found shifts in community-level movement activity from daytime to

293   nighttime (Q1) as well as shifts in habitat use from vegetated habitat patches to open habitat at

294   night (Q2). While we did not detect an overall response of predation rates to nighttime illuminance,

295   we deduce spatiotemporal shifts in predation rates via their strong correlation with patch-level

296   movement activity (Q3 & Q4).

297   We tracked the movements of individual animals within experimental insect communities using an

298   RFID sensor array in order to investigate their response to diffuse nighttime illuminance such as

299   skyglow (Q1). The lightweight, passive RFID tags [58] are well-suited to the tracking of small animals

300   such as insects [59]. Moreover, this approach enabled us to track the movement of the insects in

301   darkness as well as complex physical habitats, which is limited with other methods such as image-

302   based tracking [60]. Despite finding no effect of nighttime illuminance on the overall activity time

303   budget (Figure 3a), we did detect a temporal shift in movement activity from day to night (Figure

304   3b). Our community is composed primarily of crepuscular and nocturnal species that are likely to be

305   able to extend their temporal niche into the night when artificial light maintains their ability to see

306   and thus forage. As nocturnal foraging probably evolved to reduce competition and predation

307   pressure, crepuscular species may benefit from opportunities that reduce their interactions with

308   diurnal species, which explains the simultaneous reduction in movement activity during the day.

309   Furthermore, by keeping the total time budget constant, these species avoid an overall increase in

310   their total energy expenditure.

311   In addition to this temporal shift, we observed a change in the insect communities' space use in

312   response to skyglow (Q2), marked by a concomitant increase in nocturnal- and decrease in diurnal

313   movement activity within the bare-soil matrix. The dense vegetation within the habitat patches in

314   our experimental landscapes (Figure 2a) reduces light intrusion and visibility, in contrast to the open

315   ground of the interstitial matrix area. This can have important implications for animal movement

316   and foraging behaviour, for instance, by facilitating foraging or increasing predation risk [25,40,61].

317   The observed increase in movement activity in the matrix at night (Figure 4b) fits our interpretation

318   that crepuscular species shift their activity towards nocturnality due to increased foraging and

319   exploration opportunities. During daytime, not only does the overall movement activity decrease,

320   but there is an additional shift in activity from the matrix to the habitat patches in response to

321   increasing nighttime illuminance (Figure 4a). A shift towards nocturnal exploration activity could

322   result in a preference for habitat patches that provide protection from potential predators during

323   the day.

324   Predation rates can be driven by detection success as well as by the probability of encounters

325   between predators and their prey. Higher detection ability facilitated by increased visibility under

326   ALAN should generally lead to higher predation rates. However, as we did not find a significant effect

327   of nighttime illuminance on the total number of attacks (bite counts per 14 days) on prey dummies

328   (Q3, Figure 5a), we can deduce that there is likely also no significant effect on predation rates via

329   detection probability within our experimental grassland communities. In addition to the predators'

330   movement activity, local densities, and detection success, predation rates could also be influenced

331   by the predators' decision to forage or the behaviour of the prey. In contrast to studies that employ

332   immobile prey dummies, future studies that simultaneously track the movement of prey could

333   elucidate the role of prey responses to ALAN in determining the outcomes of predator-prey

334   interactions (e.g. [61]). Moreover, our use of prey dummies does not allow us to differentiate

335   daytime and nighttime predation rates; nevertheless, we found a strong spatiotemporal association

336   between patch-level predation rate and movement activity (Q4). Therefore, based on the absence of

337   an effect of nighttime illuminance on movement activity (Figure 3a), we expect a corresponding

338   absence of an effect on predation rates when measured across day and night, which is supported by

339   our analysis (Figure 5a). This highlights that nighttime illuminance drives predation through the rate

340   of encounters between predators and their prey rather than via the predators' visual detection of

341   prey. Together with the observed temporal and spatial shift in movement activity (Figure 3b and

342   Figure 4b, respectively), our results suggest that diffuse nighttime illuminance leads to a congruent

343   spatiotemporal shift in predation rates.

344   Organisms show diverse and context-dependent responses to ALAN [8,62], which was also reflected

345   by some variability in how the species in our experimental community responded. This might

346   translate to distinct community-level responses depending on, for example, the species composition

347   of the community and the ecosystem it is integrated within (e.g. [63]). Here, we could show that in

348   grasslands, diffuse nighttime illuminance such as skyglow can influence movement and by extension

349   prey encounters of seven predominantly crepuscular species. Our focus on diffuse nighttime

350   illuminance and the range of our experimental gradient covers most of the real-world light

351   conditions from natural starlight to cities [14], suggesting that our results are relevant for light

352   pollution experienced by invertebrates in open habitats such as grasslands and agricultural fields

353   throughout the world. We were able to show that even low levels of nighttime illuminance can

354   cause substantial changes in animal movement and consequently predation rates. For instance,

355   more than 50% of the observed change in movement activity (Fig. 3b) across the whole gradient of

356   nighttime illuminance occurred at illuminance levels that were below that of an average full moon

357   (approx. 0.3 lux). This strong response to low illuminance levels is to be expected among organisms

358   that have adapted to respond to subtle changes in illuminance such as the moon cycle [61,64] and to

359   life under starlight [65].

360   Our evidence for skyglow affecting fundamental ecological processes such as the movement of

361   invertebrates and predation suggests cascading and far-reaching repercussions for landscape

362   connectivity, biodiversity and ecosystem functioning. For instance, the shift of predator activity to

363   open habitats, as shown here, could increase the predation risk of dispersing nocturnal prey and

364   diminish landscape connectivity. This is particularly relevant for animals which rely on behavioural

365   shifts towards nocturnal activity to buffer against thermal and water stress [66–68]. Spatiotemporal

366   shifts in predation rates can also have strong implications for species interactions, either by rewiring

367   food webs or by modifying the strengths of interactions. This can fundamentally change the

368   structure of food webs and their stability [69]: A temporal shift in the activity of crepuscular species

369   into the night as found in our study could lead to new interactions with nocturnal species, and in

370   turn, cause interactions with diurnal species to be lost or weakened. Furthermore, changes to

371   encounter probabilities and, consequently, interaction strengths can alter energy fluxes in food

372   webs. For instance, an increase in predation rates at night could lead to higher energy fluxes, with

373 knock-on effects on the stability of nocturnal as well as diurnal food webs [70–72]. Such

374 spatiotemporal changes in movement activity have also been shown to affect other types of

375 ecological networks such as plant-pollinator and host-parasitoid networks [2,7,73]. This suggests

376 that skyglow, as a recent and intensifying anthropogenic disturbance [13], has far-reaching

377 consequences, and the potential to fundamentally disrupt natural communities and the services

378 they provide.

379

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381

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581

Figure captions

583

584 **Figure 1.** Concept illustrating how ALAN may cascade from physiological and behavioural processes

585 (A), to interactions and functions (B), and ultimately to community and ecosystem responses (C).

586 Orange circles and black arrows indicate our research questions: How does ALAN affect temporal-

587 (Q1) and spatial movement activity (Q2) in a patchy habitat? Does ALAN predominantly affect

588 predation rates through detection probabilities (Q3), or are predation rates rather driven by the

589 effects of spatiotemporal movement activity on encounter rates between predator and prey (Q4)?

590

Figure 2. Experimental design (a) Interior view of the grassland habitat patches established in an EcoUnit, (b) schematic representation of the patch design highlighting the distribution of RFID sensors and prey dummies across the EcoUnit. (c) EcoUnits covered with black theatre curtains to prevent cross-contamination with light. (d) Pictures of a beetle with medium-sized RFID tag (taken from an experiment using the same tracking approach and setting, [43]) and an artificial caterpillar prey dummy with bite marks.

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Figure 3. Movement activity (sum of detections per day/night) in response to nighttime illuminance. EcoUnit-level daily movement activity (per 24 hours) (a) and daytime (light blue) and nighttime movement activity (dark blue) (b). Dashed lines represent non-significant relationships ($p > 0.05$). Shaded regions represent 95% confidence intervals.

602

Figure 4. Movement activity (sum of detections per day/night) in habitat patches (green) and matrix (orange) in response to nighttime illuminance during the day (a) and during night (b). Dashed lines represent non-significant relationships ($p > 0.05$). Shaded regions represent 95% confidence intervals.

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Figure 5. (a) EcoUnit-level predation rate (bite counts per 14 days) in response to nighttime illuminance. (b) Patch-level predation rate (bite counts per 14 days per patch) in response to patch-level movement activity (sum of detections per 14 days per patch, Fig. 2). Dashed lines represent non-significant relationships ($p > 0.05$). Shaded regions represent 95% confidence intervals.

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Data accessibility

The underlying data are available in an open access repository at

https://doi.org/10.5281/zenodo.8017438 [74]

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Supplementary information

Insect communities under skyglow: diffuse nighttime illuminance induces spatiotemporal shifts in movement and predation

Alexander Dyer,[1,2,*] Remo Ryser,[1,2] Ulrich Brose,[1,2] Angelos Amyntas,[1,2] Nora Bodnar,[1,2] Thomas Boy,[1,2] Solveig Franziska Bucher,[1,3] Simone Cesarz,[1,4] Nico Eisenhauer,[1,4] Alban Gebler,[1,4] Jes Hines,[1,4] Christopher C. M. Kyba,[5,6] Myles H. M. Menz,[7] Karl Rackwitz,[1,2] Tom Shatwell,[8] Jördis F. Terlau,[1,2] Myriam R. Hirt[1,2]

[1] *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany*

[2] *Institute of Biodiversity, Friedrich-Schiller-University Jena, Jena, Germany*

[3] *Institute of Ecology and Evolution with Herbarium Haussknecht and Botanical Garden, Professorship of Plant Biodiversity, Friedrich-Schiller-University, Jena, Germany*

[4] *Institute of Biology, Leipzig University, Leipzig, Germany*

[5] *Remote Sensing and Geoinformatics, Deutsches GeoForschungsZentrum Potsdam, 14473 Potsdam, Germany*

[6] *Geographisches Institut, Ruhr-Universität Bochum, 44780 Bochum, Germany*

[7] *College of Science and Engineering, James Cook University, Australia*

[8] *Department of Lake Research, Helmholtz Centre for Environmental Research (UFZ), Magdeburg, Germany*

*Corresponding author: alexander.dyer@idiv.de

Tables S1-S11

Figures S1-S4

Table S1. Sown plant species in each EcoUnit. For every species 1000 seeds m^{-2} were sown.

Species	Sown (mg/1000 seeds)
Bromus hordeaceus	3443.0
Campanula patula	65.0
Cynosurus cristatus	556.7
Festuca pratensis	2467.3
Festuca rubra	869.3
Lathyrus pratensis	10889.5
Leucanthemum vulgare	1004.0
Lotus corniculatus	1244.3
Luzula campestris	681.3
Medicago lupulina	2079.2
Plantago media	384.9
Prunella vulgaris	796.3
Ranunculus repens	1804.8
Trifolium repens	692.1
Veronica chamaedrys	205.4
Vicia sepium	12995.5

Table S2. Body masses and abundances of animals used for RFID movement tracking.

Species	Experimental block I (21.07. - 18.08.2020)		Experimental block II (15.09. - 13.10.2020)	
	Mean body mass [mg]	Abundance per unit	Mean body mass [mg]	Abundance per unit
Abax parallelus	302	2	269	5
Calathus fuscipes	67	6	75	6
Carabus granulatus	NA	NA	273	1
Carabus nemoralis	538	5	550	3
Harpalus rufipes	112	2	128	6
Nebria brevicollis	69	6	NA	NA
Pterostichus melanarius	151	4	NA	NA

Table S3. Overview of the response and predictor variables used to answer our four research questions (Q1-Q4) including units as well as spatial and temporal aggregation level. Aggregation on patch level means aggregation across the four individual patches in an EcoUnit contrary to aggregation on individual patch-level as in Q4.

Question	Response	Unit - response	Aggregation level - response		Predictor	Unit - predictor	Aggregation level - predictor	
			Spatial	Temporal			Spatial	Temporal
Q1	activity	number of detections	EcoUnit	day/night	ALAN	lux	NA	NA
Q2	activity	number of detections	matrix/ patch	day/night	ALAN	lux	NA	NA
Q3	predation	number of bites	none	14 days	ALAN	lux	NA	NA
Q4	predation	number of bites	individual patch	14 days	activity	number of detections	individual patch	14 days

Table S4a. Generalised linear mixed effects model results of the influence of nighttime illuminance on EcoUnit-level daily movement activity (sum of detections per day/night) (Q1). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept	2.743	0.347	< 0.001
Slope: log10 nighttime illuminance	0.014	0.022	0.530

Table S4b. Generalised linear mixed effects model results of the influence of nighttime illuminance on EcoUnit-level individual daily movement (sum of detections per day/night, corrected for individual densities) (Q1). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept	2.793	0.253	< 0.001
Slope: log10 nighttime illuminance	0.025	0.022	0.247

Table S5. Estimates for species-level responses of daytime and nighttime movement activity to nighttime illuminance. Insufficient data corresponds to species with fewer than 10 data points. Estimates are given on ln-scale, intercept is given at 1 lux.

		Intercept			Slope: log10 nighttime illuminance		
		Estimate	**Std. Error**	**p-value**	**Estimate**	**Std. Error**	**p-value**
Abax parallelus	Day	2.833	0.152	<0.001	-0.036	0.045	0.414
	Night	2.890	0.144	<0.001	0.065	0.034	0.053
Calathus fuscipes	Day	0.907	0.188	<0.001	-0.075	0.055	0.169
	Night	1.247	0.140	<0.001	-0.115	0.041	0.005
Carabus nemoralis	Day	2.969	0.187	<0.001	0.270	0.121	0.024
	Night	3.158	0.119	<0.001	0.293	0.059	<0.001
Carabus granulatus	Day	3.624	0.122	<0.001	-0.483	0.098	<0.001
	Night	4.016	0.107	<0.001	-0.120	0.081	0.143
Nebria brevicollis	Day	0.404	0.523	0.440	insufficient data		
	Night	0.770	0.118	<0.001	0.044	0.088	0.612
Pterostichus melanarius	Day	0.522	0.196	0.007	0.238	0.150	0.113
	Night	1.006	0.125	<0.001	-0.314	0.089	<0.001
Harpalus rufipes	Day	-0.366	1.118	0.743	insufficient data		
	Night	1.004	0.147	<0.001	-0.071	0.092	0.442

Table S6a. Generalised linear mixed effects model results of the interaction between nighttime illuminance and diel light cycle (day vs night) on movement activity (number of sensor crossing events per day/night) (Q1). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept [day]	2.527	0.362	< 0.001
Intercept [night]	2.840	0.360	< 0.001
Slope: log10 nighttime illuminance [day]	- 0.099	0.038	0.008
Slope: log10 nighttime illuminance [night]	0.069	0.028	0.014

Table S6b. Generalised linear mixed effects model results of the interaction between nighttime illuminance and diel light cycle (day vs night) on individual movement (number of sensor crossing events per day/night, corrected for individual densities) (Q1). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept [day]	2.736	0.264	< 0.001
Intercept [night]	2.809	0.260	< 0.001
Slope: log10 nighttime illuminance [day]	- 0.103	0.038	0.007
Slope: log10 nighttime illuminance [night]	0.090	0.026	< 0.001

Table S7a. Generalised linear mixed effects model results of the interaction between nighttime illuminance and habitat (patch vs matrix) on daytime movement activity (sum of detections per day/night) (Q2). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept [matrix]	2.649	0.336	< 0.001
Intercept [patch]	2.157	0.341	< 0.001
Slope: log10 nighttime illuminance [matrix]	-0.183	0.054	< 0.001
Slope: log10 nighttime illuminance [patch]	0.114	0.058	0.048

Table S7b. Generalised linear mixed effects model results of the interaction between nighttime illuminance and habitat (patch vs matrix) on individual daytime movement (sum of detections per day/night, corrected for individual densities) (Q2). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept [matrix]	2.774	0.245	< 0.001
Intercept [patch]	2.510	0.254	< 0.001
Slope: log10 nighttime illuminance [matrix]	-0.202	0.050	< 0.001
Slope: log10 nighttime illuminance [patch]	0.127	0.058	0.030

Table S8a. Generalised linear mixed effects model results of the interaction between nighttime illuminance and habitat (patch vs matrix) on nighttime movement activity (sum of detections per day/night) (Q2). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept [matrix]	3.089	0.278	< 0.001
Intercept [patch]	2.178	0.282	< 0.001
Slope: log10 nighttime illuminance [matrix]	0.072	0.033	0.028
Slope: log10 nighttime illuminance [patch]	0.018	0.041	0.653

Table S8b. Generalised linear mixed effects model results of the interaction between nighttime illuminance and habitat (patch vs matrix) on individual nighttime movement (sum of detections per day/night, corrected for individual densities) (Q2). Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept [matrix]	3.012	0.199	< 0.001
Intercept [patch]	2.253	0.206	< 0.001
Slope: log10 nighttime illuminance [matrix]	0.087	0.032	0.008
Slope: log10 nighttime illuminance [patch]	0.072	0.041	0.077

Table S9. Linear model results of the effect of nighttime illuminance [lux] on the number of detected individuals for the second half of each temporal experimental block. Estimates are given on ln-scale, intercept is given at 1 lux.

Predictor	Estimate	Std. Error	p-value
Intercept	6.157	1.926	0.048
Slope: log10 nighttime illuminance	-0.278	0.213	0.198

Table S10. Generalised linear mixed effects model results of the influence of nighttime illuminance on EcoUnit-level predation rate (bite counts per 14 days) (Q3).

Predictor	Estimate	Std. Error	p-value
Intercept	1.421	0.037	< 0.001
Slope: log10 nighttime illuminance	0.029	0.019	0.127

Table S11. Generalised linear mixed effects model results of the influence of individual-patch-level movement activity (sum of detections) on individual-patch-level predation rate (bite counts per 14 days per individual patch) (Q4).

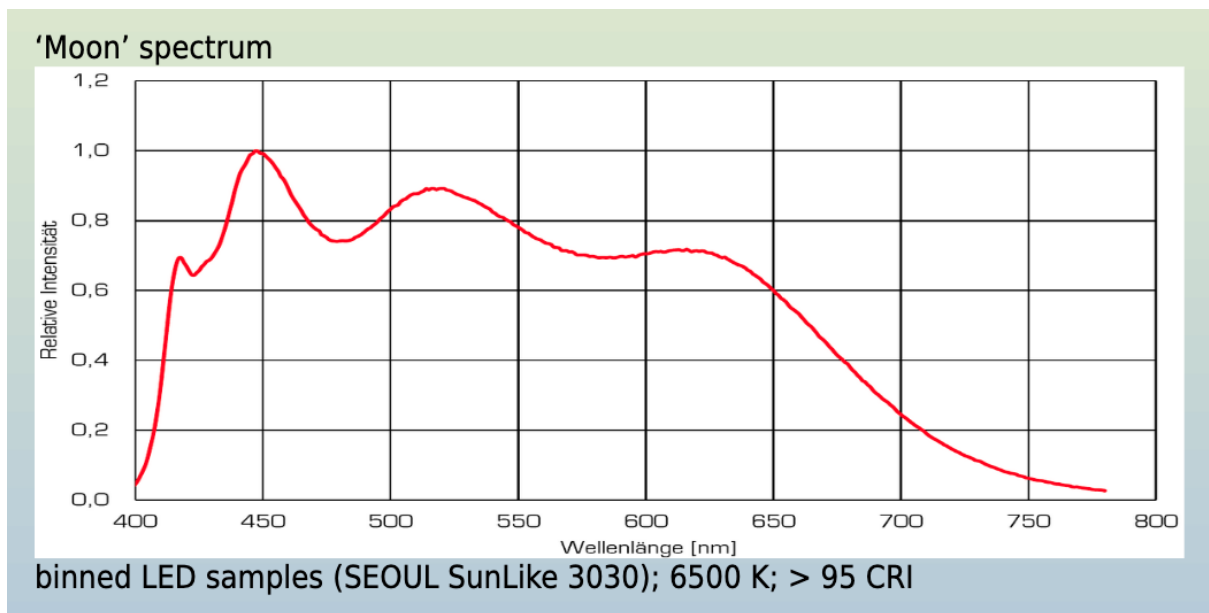| Predictor	Estimate	Std. Error	p-value
Intercept	1.308	0.048	< 0.001
Slope: log10 movement activity	0.131	0.042	0.002

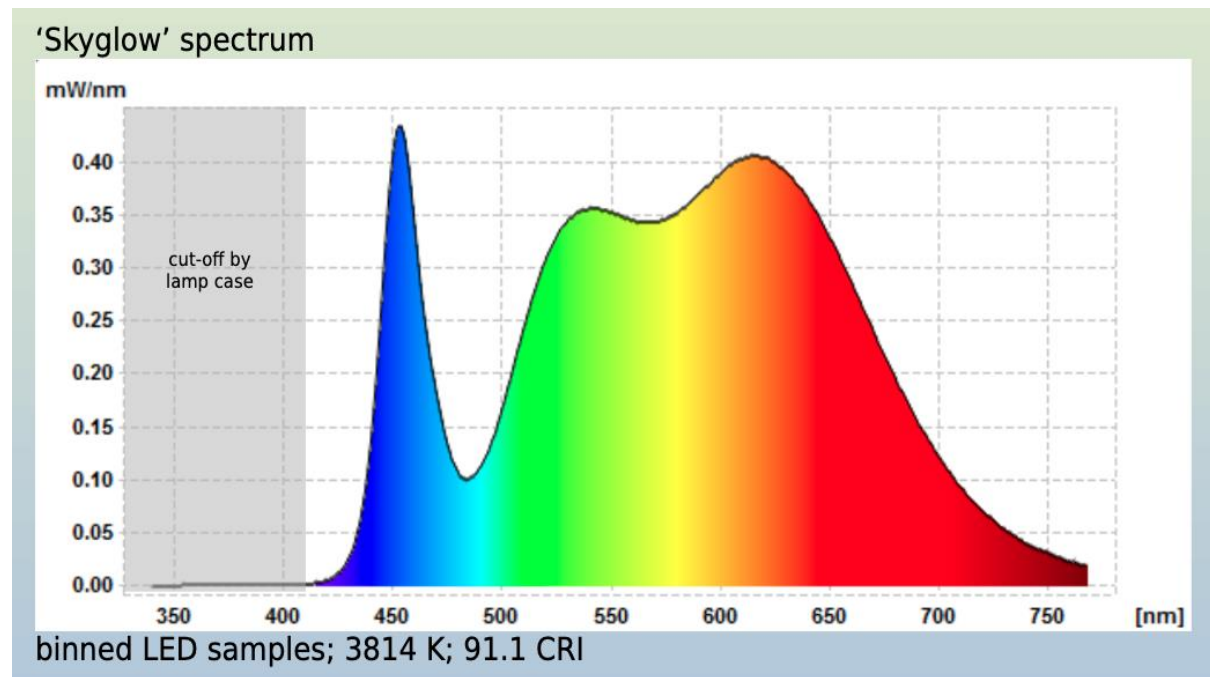**Figure S1.** Spectrum of the LED used to simulate moonlight in the EcoUnits.

'Moon' spectrum

binned LED samples (SEOUL SunLike 3030); 6500 K; > 95 CRI

Figure S2. Spectrum of the LED used to simulate skyglow in the EcoUnits.

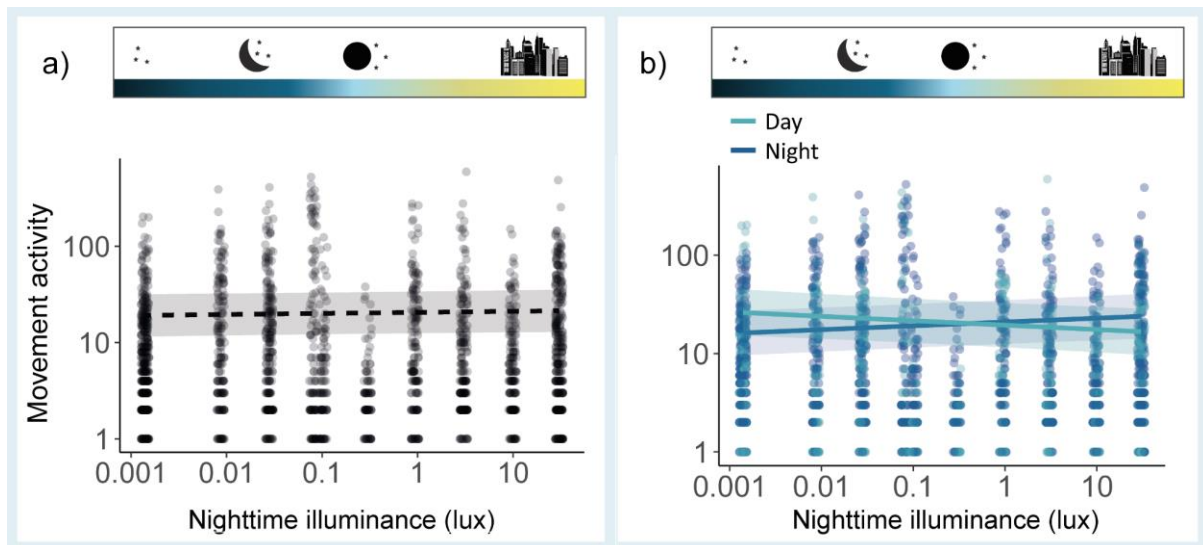'Skyglow' spectrum

binned LED samples; 3814 K; 91.1 CRI

Figure S3. Individual movement (sum of detections per day/night, corrected for individual densities) in response to nighttime illuminance. EcoUnit-level daily movement (per 24 hours) **(a)** and daytime (light blue) and nighttime movement (dark blue) **(b)**. Dashed lines represent non-significant relationships (p > 0.05). Shaded regions represent 95% confidence intervals.
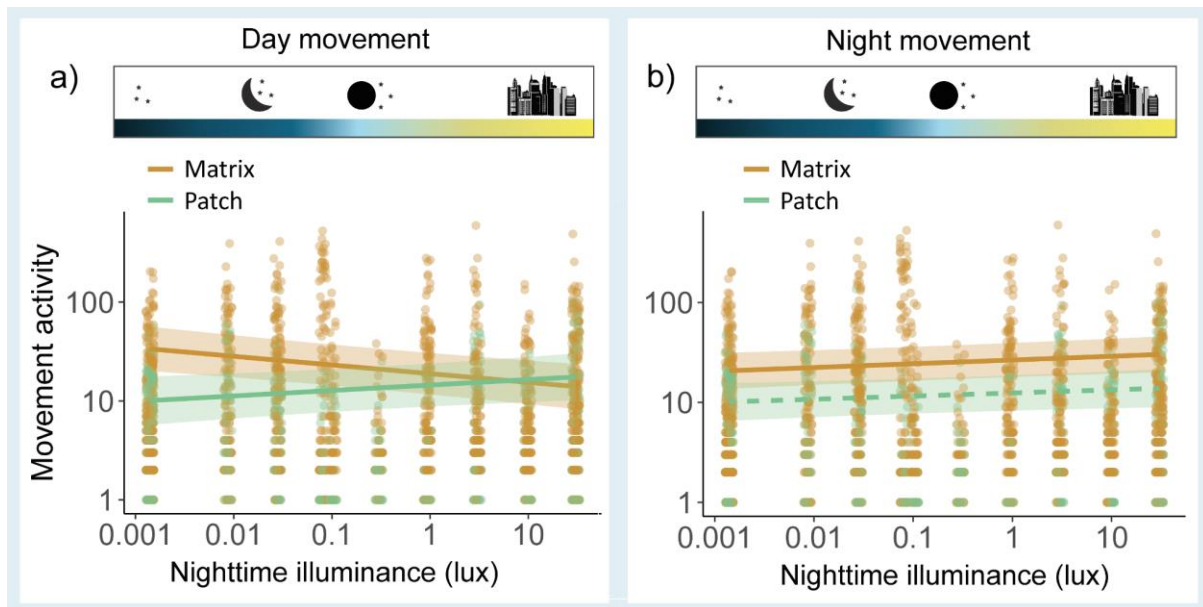
Figure S4. Individual movement (sum of detections per day/night, corrected for individual densities) in habitat patches (green) and matrix (orange) in response to nighttime illuminance during the day (a) and during night (b)**.** Dashed lines represent non-significant relationships ($p > 0.05$). Shaded regions represent 95% confidence intervals.