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Artificial light at night reduces earthworm activity but increases growth of invasive ragweed

Marion Mittmannsgruber¹, Zenia Kavassilas¹, Bernhard Spangl², Edith Gruber¹, Elias Jagg¹ and Johann G. Zaller^{1*}

Abstract

Background Artificial light at night, also referred to as light pollution (LP), has been shown to affect many organisms. However, little is known about the extent to which ecological interactions between earthworms and plants are altered by LP. We investigated the effects of LP on anecic earthworms (*Lumbricus terrestris*) that come to the surface at night to forage and mate, and on the germination and growth of the invasive and allergenic ragweed (*Ambrosia artemisiifolia*). In a full factorial pot experiment in the greenhouse, we tested four factors and their interactions: LP (5 lux vs. 0 lux at night), earthworms (two individuals vs. none), plant species (seeding of ragweed only vs. mixed with *Phacelia* seeds) and sowing depth (seed placed at the surface vs. in 5 cm depth). Data were analysed using Generalized Linear (Mixed) Models and multifactorial ANOVAs with soil parameters as covariates.

Results Light pollution reduced earthworm surface activity by 76% as measured by casting activity and toothpick index; 85% of mating earthworms were observed in the absence of LP. Light pollution in interaction with earthworms reduced ragweed germination by 33%. However, LP increased ragweed height growth by 104%. Earthworms reduced ragweed germination especially when seeds were placed on the soil surface, suggesting seed consumption by earthworms.

Conclusions Our data suggest that anecic earthworms are negatively affected by LP because reduced surface activity limits their ability to forage and mate. The extent to which earthworm-induced ecosystem services or community interactions are also affected by LP remains to be investigated. If the increased height growth of ragweed leads to increased pollen and seed production, it is likely that the competition of ragweed with field crops and the risks to human health will also increase under LP.

Keywords Light pollution, Earthworms, *Lumbricus terrestris*, Ragweed, *Ambrosia artemisiifolia*, Agroecology, Plant-animal interactions, Artificial light at night, ALAN

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Background

Lotus pedunculatus

L. terrestris
 Ambrosia trifida
 Ambrosia artemisiifolia
 L. terrestris
 A. artemisiifolia
 L. terrestris

Phacelia

Results

Earthworm activity

Ragweed germination and growth

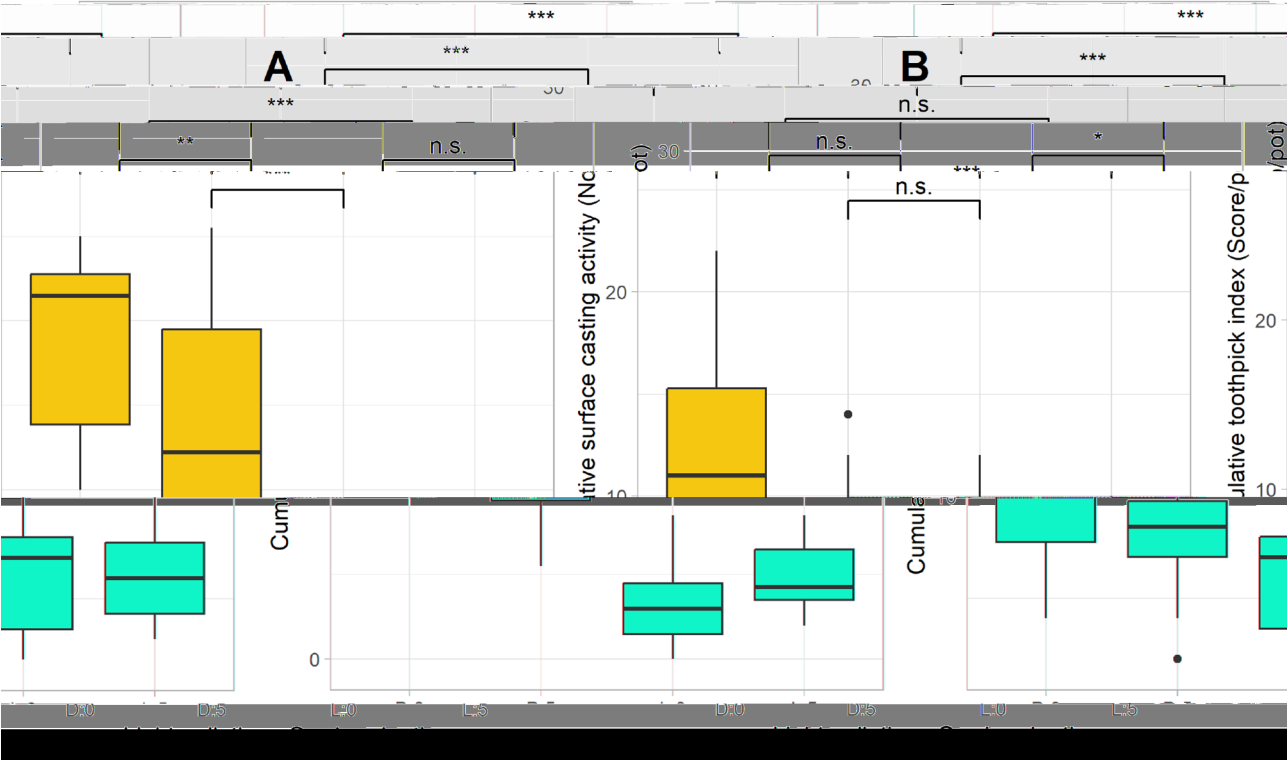


Fig. 1 Earthworm surface activity assessed with the toothpick index (A) and the surface casting activity (B) throughout all 12 samplings, considering effects of light pollution (D...dark, L...light) and sowing depth (0...surface sown, 5...sown in 5 cm depth). $N=6$. Each box represents the 1st and 3rd quartiles, the median as the horizontal line and the whiskers as minimum and maximum values

Table 1 Earthworm activity (measured by toothpick index and surface casting activity) in response to light pollution (LP), plant species (PS), sowing depth (SD), their interactions, and the covariates initial worm weight, soil moisture, and humidity. Significance code for Pr (> ChiSq): *** <0.001, ** <0.01, * <0.05

Earthworm surface activity				
Parameters	Toothpick index		Surface casting activity	
	Df	Pr (> ChiSq)	Df	Pr (> ChiSq)
Light pollution (LP)	1	< 2.200e ⁻¹⁶ ***	1	1.410e ⁻⁰⁵ ***
Plant species (PS)	1	0.604	1	0.990
Sowing depth (SD)	1	0.919	1	0.060
LP x PS	1	0.037*	1	0.090
LP x SD	1	4.139e ⁻⁰⁴ ***	1	0.007**
PS x SD	1	0.227	1	0.318
LP x SD x PS	1	0.001**	1	0.755
Initial worm weight (g)	1	0.901	1	0.567
Soil moisture (%)	1	0.503	1	0.591
Air humidity (%)	1	0.009**	1	5.223e ⁻⁰⁵ ***
Air temperature (°C)	1	1.350e ⁻¹¹ ***	1	3.201e ⁻⁰⁸ ***

Table 2 Change in earthworm numbers and biomass from start to end of the experiment in response to light pollution (LP), plant species (PS), sowing depth (SD), their interactions, and the covariates initial worm weight and soil moisture. ChiSq = Likelihood ratio Chi squared, df = degrees of freedom, Significance code for Pr(> ChiSq) and Pr(> F): *** <0.001, ** <0.01, * <0.05

Parameters	Earthworm number change		Earthworm biomass change	
	Df	Pr (> ChiSq)	Df	Pr (> F)
Light pollution (LP)	1	0.015*	1	0.169
Plant species (PS)	1	0.573	1	0.097
Sowing depth (SD)	1	0.220	1	0.305
LP x PS	1	0.474	1	0.371
LP x SD	1	0.891	1	0.429
PS x SD	1	0.198	1	0.069
LP x SD x PS	1	0.054	1	0.437
Initial worm weight (g)	1	0.118	1	0.011*
Soil moisture (%)	1	0.056	1	0.547
Residuals			33	

Light pollution (LP) had a significant effect on earthworm activity (Table 1), with a p-value of < 2.200e⁻¹⁶ (***). Plant species (PS) had no significant effect (p = 0.604). Sowing depth (SD) had no significant effect (p = 0.919). The interaction between LP and PS was significant (p = 0.037, *). The interaction between LP and SD was significant (p = 4.139e⁻⁰⁴, ***). The interaction between PS and SD was not significant (p = 0.227). The three-way interaction between LP, SD, and PS was not significant (p = 0.001, **). Initial worm weight (g) had no significant effect (p = 0.901). Soil moisture (%) had no significant effect (p = 0.503). Air humidity (%) had a significant effect (p = 0.009, **). Air temperature (°C) had a significant effect (p = 1.350e⁻¹¹, ***).

Change in earthworm numbers and biomass from start to end of the experiment in response to light pollution (LP), plant species (PS), sowing depth (SD), their interactions, and the covariates initial worm weight and soil moisture. ChiSq = Likelihood ratio Chi squared, df = degrees of freedom, Significance code for Pr(> ChiSq) and Pr(> F): *** <0.001, ** <0.01, * <0.05

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Discussion

Earthworm activity

Light pollution (LP) had a significant effect on earthworm activity (Table 1), with a p-value of < 2.200e⁻¹⁶ (***). Plant species (PS) had no significant effect (p = 0.604). Sowing depth (SD) had no significant effect (p = 0.919). The interaction between LP and PS was significant (p = 0.037, *). The interaction between LP and SD was significant (p = 4.139e⁻⁰⁴, ***). The interaction between PS and SD was not significant (p = 0.227). The three-way interaction between LP, SD, and PS was not significant (p = 0.001, **). Initial worm weight (g) had no significant effect (p = 0.901). Soil moisture (%) had no significant effect (p = 0.503). Air humidity (%) had a significant effect (p = 0.009, **). Air temperature (°C) had a significant effect (p = 1.350e⁻¹¹, ***).

Change in earthworm numbers and biomass from start to end of the experiment in response to light pollution (LP), plant species (PS), sowing depth (SD), their interactions, and the covariates initial worm weight and soil moisture. ChiSq = Likelihood ratio Chi squared, df = degrees of freedom, Significance code for Pr(> ChiSq) and Pr(> F): *** <0.001, ** <0.01, * <0.05

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Fig. 2 Two *L. terrestris* individuals during mating. Also seen are toothpicks used to determine surface activity and germinated seedlings of ragweed (top right and bottom centre) and *Phacelia* (top centre)

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Ragweed germination and growth

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Fig. 3 Ragweed germination of 100 in response to experimental factors light pollution (**A, C**), earthworms (**A, B**), sowing depth (**B, C, D**), and plant species (**D**). Abbreviations: Light pollution: D...dark, L...light; Earthworms: EW+...present, EW-...absent; Sowing depth: 0...sown at sown, 5...sown in 5 cm depth; Plant species: A...only Ragweed sown, M...Ragweed seeds and *Phacelia* seeds sown. *N* = 6

Table 3 Ragweed germination, mean plant biomass, and mean plant height in response to light pollution (LP), earthworms (EW), plant species (PS), sowing depth (SD) and their interactions. Mean plant height and biomass analyses only considering the 56 pots containing ragweed plants at the end. Pr (> ChiSq) and Pr (> F) significance codes: *** <0.001, ** <0.01, * <0.05

Parameters	Germination		Mean plant biomass		Mean plant height	
	Df	Pr (> ChiSq)	Df	Pr (> F)	Df	Pr (> F)
Light pollution (LP)	1	< 2.200e ⁻¹⁶ ***	1	0.054	1	3.490e ⁻⁰⁷ ***
Earthworms (EW)	1	< 2.200e ⁻¹⁶ ***	1	0.068	1	0.208
Plant species (PS)	1	0.044*	1	0.662	1	0.618
Sowing depth (SD)	1	< 2.200e ⁻¹⁶ ***	1	0.857	1	0.140
LP x EW	1	1.508e ⁻⁰⁹ ***	1	0.970	1	0.699
LP x SD	1	5.730e ⁻¹⁴ ***	1	0.288	1	0.479
LP x PS	1	0.236	1	0.686	1	0.443
EW x SD	1	< 2.200e ⁻¹⁶ ***	1	0.578	1	0.983
EW x PS	1	0.102	1	0.740	1	0.540
SD x PS	1	2.999e ⁻⁰⁵ ***	1	0.808	1	0.393
LP x EW x SD	1	4.575e ⁻⁰⁶ ***	1	0.990	1	0.862
LP x SD x PS	1	0.002**	1	0.253	1	0.600
EW x SD x PS	1	0.010*	1	0.717	1	0.934
LP x EW x PS	1	0.063	1	0.751	1	0.802
Residuals			41		41	

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Conclusion

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Methods

Experimental setup

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- Factor light pollution (LP): complete darkness (D) vs. artificial light pollution (L).
- Factor earthworms (EW): *L. terrestris* present (EW+) vs. absent (EW-).
- Factor plant species (PS): seeding *A. artemisiifolia* alone (A) vs. in combination with *Phacelia tanacetifolia* (M).
- Factor sowing depth (SD): surface sown seeds (0) vs. sowing depth of 5 cm (5).

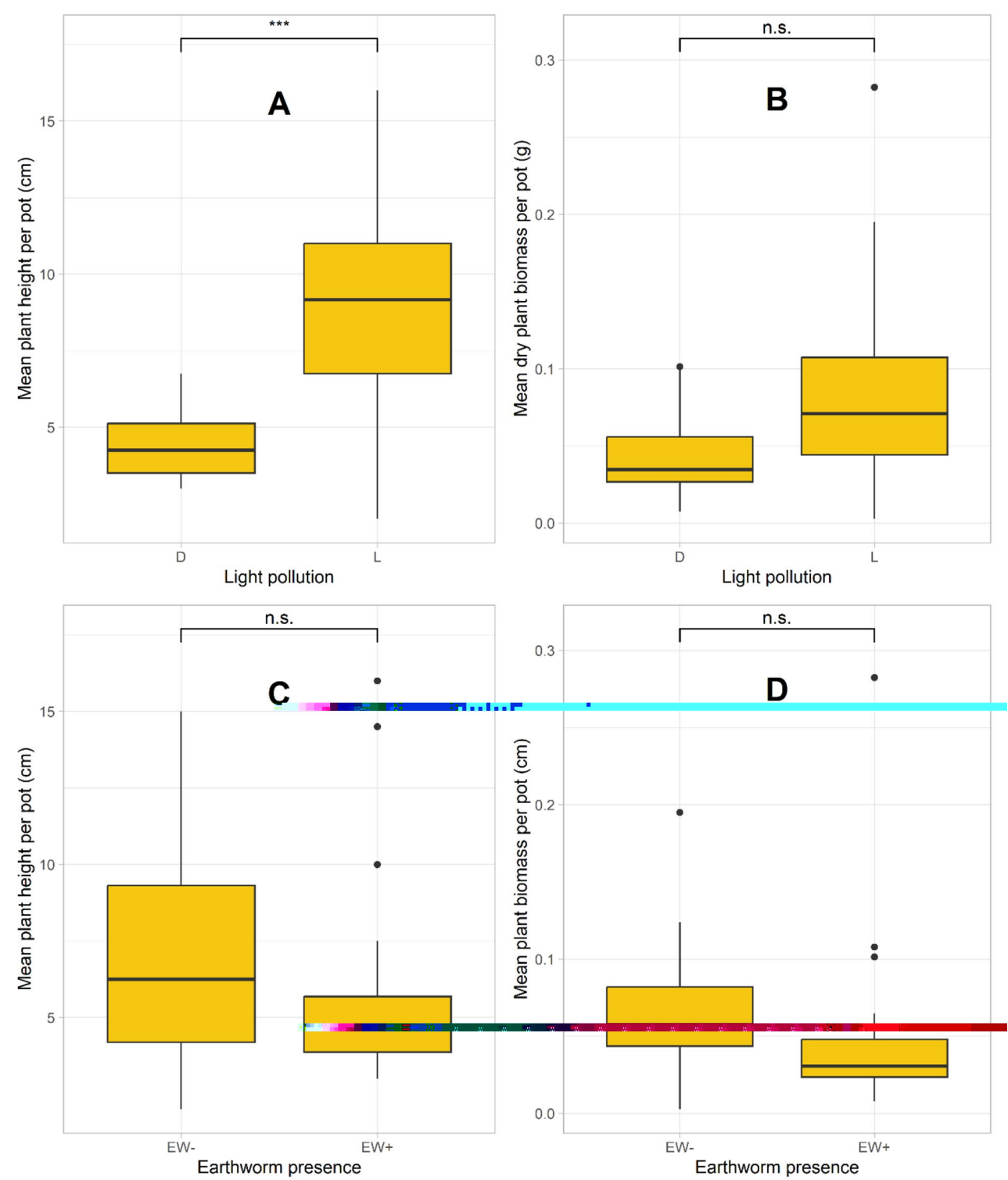


Fig. 4 Mean ragweed plant height and plant biomass in response to light pollution (**A, B**) and earthworm presence (**C, D**). Abbreviations: D...dark, L...light, EW-...Earthworms absent, EW+...Earthworms present, n.s....not significant, *** p -value < 0.001, ** p -value < 0.01, * p -value < 0.05. $N = 6$

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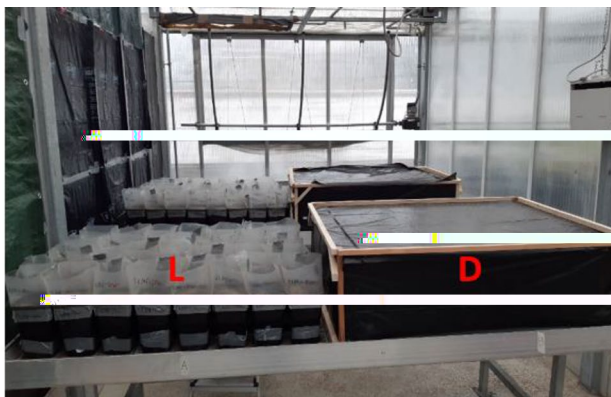


Fig. 5 Experimental setup in the greenhouse. Light pollution (L) was achieved by covered ceiling lights, and the dark (D) treatment by covering pots with opaque plastic sheets

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 p a l p t z j z a p p z x a l z
 . a p z z a z t j p z t l p z
 t z p j z a z z j z
 . z s z z j z x z a l z
 z j z z z z z z s z j a
 z z z z a z z z z z z
 z j l p p z z

Measurements

I z s p t j z p a z j j x l z s p
 d z s z z z j l x p z z x j z z
 I d l a p z l p z p j l z
 . x j z z p a l p p z z j z
 x l a z j z l a l p p z z j z
 p l l z x j z t p z z z z s a
 \ t l d l a z z z p l a \ z t l a
 . l p d z a z j z z p z a l p
 t z z a a t z x z z a z d p
 z j l z z z j a l z a k z j z
 z z z z z p a z p j z p

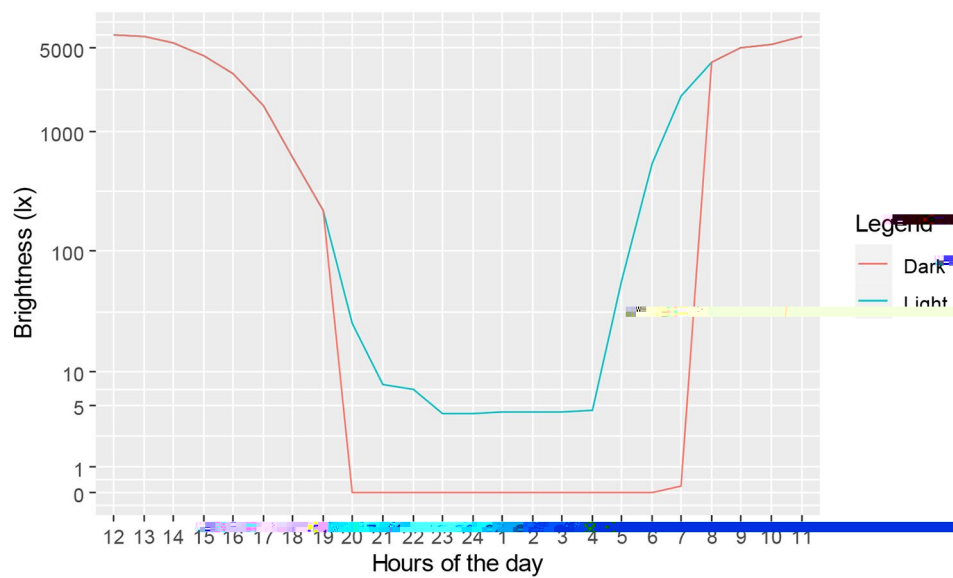
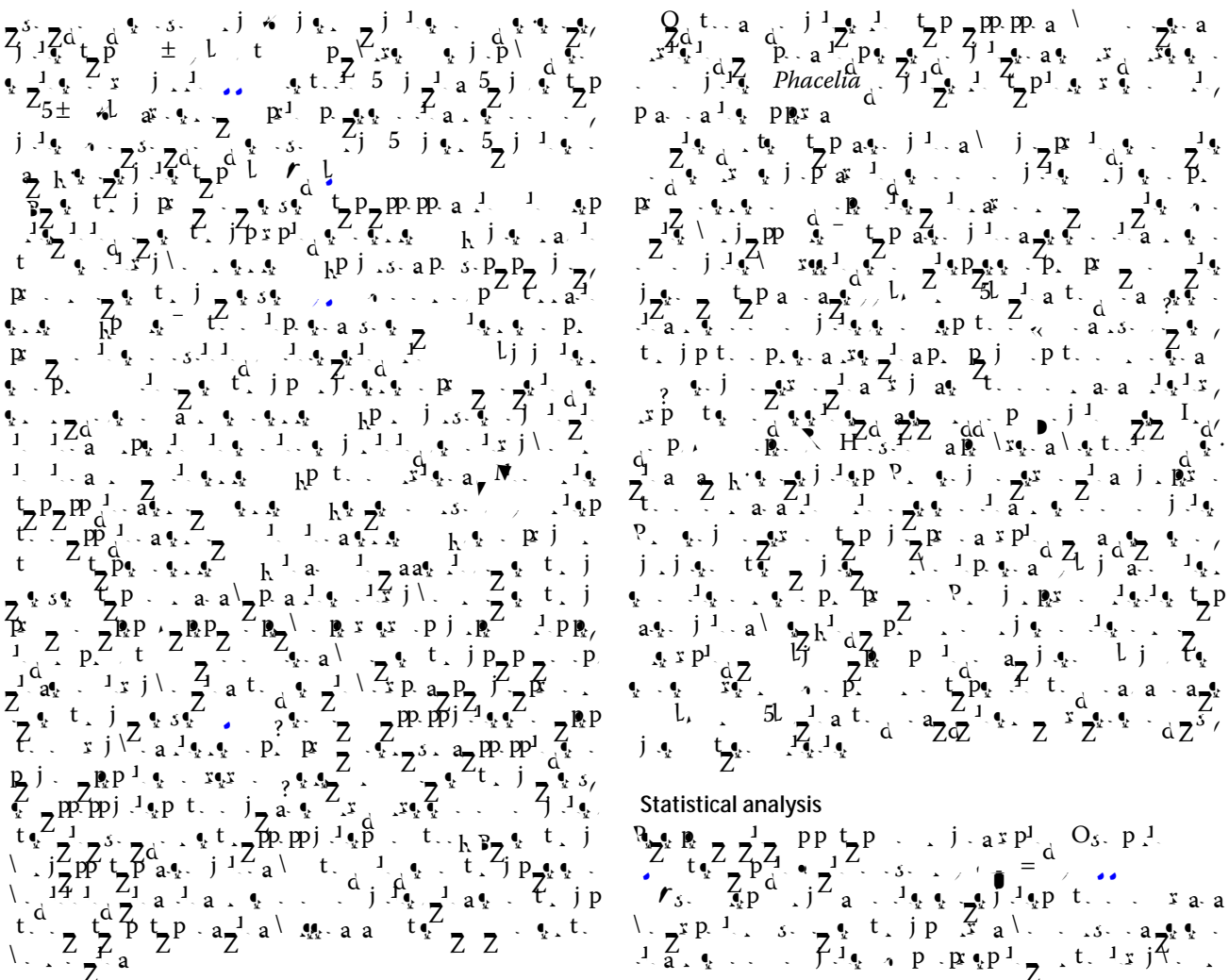


Fig. 6 Mean brightness measured throughout all experimental days comparing the dark (D) and light (L) treatments

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14. Raap T, Pinxten R, Eens M. Light pollution disrupts sleep in free-living animals. *Sci Rep*. 2015;5:13557. <https://doi.org/10.1038/srep13557>.
15. Ziegler A-K, Watson H, Hegemann A, Meitern R, Canoine V, Nilsson J-Å, Isaksson C. Exposure to artificial light at night alters innate immune response in wild great tit nestlings. *J Exp Biol*. 2021. <https://doi.org/10.1242/jeb.239350>.
16. Yorzinski JL, Chisholm S, Byerley SD, Coy JR, Aziz A, Wolf JA, Gnerlich AC. Artificial light pollution increases nocturnal vigilance in peahens. *PeerJ*. 2015;3:e1174. <https://doi.org/10.7717/peerj.1174>.
17. Aparicio G, Carrilho M, Oliveira F, Da Mathias ML, Tapisso JT, von Merten S. Artificial light affects the foraging behavior in greater white-toothed shrews (*Crocidura russula*). *Ethology*. 2023;129:88–98. <https://doi.org/10.1111/eth.13347>.
18. Berger A, Lozano B, Barthel LMF, Schubert N. Moving in the Dark-Evidence for an Influence of Artificial Light at Night on the Movement Behaviour of European Hedgehogs (*Erinaceus europaeus*). *Animals*. 2020. <https://doi.org/10.3390/ani10081306>.
19. Elgert C, Hopkins J, Kaitala A, Candolin U. Reproduction under light pollution: maladaptive response to spatial variation in artificial light in a glow-worm. *Proc Biol Sci*. 2020;287:20200806. <https://doi.org/10.1098/rspb.2020.0806>.
20. Botha LM, Jones TM, Hopkins GR. Effects of lifetime exposure to artificial light at night on cricket (*Teleogryllus commodus*) courtship and mating behaviour. *Anim Behav*. 2017;129:181–8. <https://doi.org/10.1016/j.anbehav.2017.05.020>.
21. Eisenbeis G, Hänel A. Light pollution and the impact of artificial night lighting on insects. In: McDonnell MJ, Hahs AK, Breuste JH, editors. *Ecology of cities and towns: a comparative approach*. New York: Cambridge University Press; 2009. pp. 243–63.
22. van den Broeck M, de Cock R, van Dongen S, Matthysen E. Blinded by the light: Artificial Light lowers mate attraction success in female glow-worms (*Lampyrus noctiluca* L.). *Insects*. 2021. <https://doi.org/10.3390/insects12080734>.
23. Cesarz S, Eisenhauer N, Bucher SF, Ciobanu M, Hines J. Artificial light at night (ALAN) causes shifts in soil communities and functions. *Philos Trans R Soc Lond B Biol Sci*. 2023;378:20220366. <https://doi.org/10.1098/rstb.2022.0366>.
24. Nuutinen V, Butt KR, Jauhainen L, Shipitalo MJ, Sirén T. Dew-worms in white nights: high-latitude light constrains earthworm (*Lumbricus terrestris*) behaviour at the soil surface. *Soil Biol Biochem*. 2014;72:66–74. <https://doi.org/10.1016/j.soilbio.2014.01.023>.
25. Davies TW, Bennie J, Gaston KJ. Street lighting changes the composition of invertebrate communities. *Biol Lett*. 2012;8:764–7. <https://doi.org/10.1098/rsbl.2012.0216>.
26. Macgregor CJ, Evans DM, Fox R, Pocock MJO. The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. *Glob Chang Biol*. 2017;23:697–707. <https://doi.org/10.1111/gcb.13371>.
27. Knop E, Zoller L, Ryser R, Gerpe C, Hörler M, Fontaine C. Artificial light at night as a new threat to pollination. *Nature*. 2017;548:206–9. <https://doi.org/10.1038/nature23288>.
28. Darwin CR. The formation of Vegetable Mould through the action of worms with Observation on their habits. London: John Murray; 1881.
29. Nuutinen V, Butt KR. The mating behaviour of the earthworm *Lumbricus terrestris* (Oligochaeta: Lumbricidae). *J Zool*. 1997;242:783–98.
30. Hess WN. Photoreceptors of *Lumbricus terrestris*, with special reference to their distribution, structure, and function. *J Morphol*. 1925;41:63–93. <https://doi.org/10.1002/jmor.1050410105>.
31. Jones CG, Lawton JH, Shachak M. Organisms as Ecosystem Engineers. *Oikos*. 1994;69:373. <https://doi.org/10.2307/3545850>.
32. Brown GG, Edwards CA, Brussaard L. How earthworms affect Plant Growth: burrowing into the mechanisms. In: Edwards CA, editor. *Earthworm Ecology*. Boca Raton: CRC Press; 2004. pp. 13–49.
33. van Groenigen JW, Lubbers IM, Vos HMJ, Brown GG, de Deyn GB, van Groenigen KJ. Earthworms increase plant production: a meta-analysis. *Sci Rep*. 2014;4:6365. <https://doi.org/10.1038/srep06365>.
34. Aira M, Pearce TG. The earthworm *Lumbricus terrestris* favours the establishment of *Lolium perenne* over *Agrostis capillaris* seedlings through seed consumption and burial. *Appl Soil Ecol*. 2009;41:360–3. <https://doi.org/10.1016/j.apsoil.2008.11.007>.
35. Regnier EE, Harrison SK, Liu J, Schmoll JT, Edwards CA, Arancon NO, Holloman CH. Impact of an exotic earthworm on seed dispersal of an indigenous US weed. *J Appl Ecol*. 2008;45:1621–9. <https://doi.org/10.1111/j.1365-2664.2008.01489.x>.
36. Zaller JG, Saxler N. Selective vertical seed transport by earthworms: implications for the diversity of grassland ecosystems. *Eur J of Soil Biol*. 2007;43:86–91. <https://doi.org/10.1016/j.ejsobi.2007.08.010>.
37. Fleri JR, Martin TG, Rodewald AD, Arcese P. Non-native earthworms alter the assembly of a meadow plant community. *Biol Invasions*. 2021;23:2407–15. <https://doi.org/10.1007/s10530-021-02513-8>.
38. Regnier EE, Hovick SM, Liu J, Harrison SK, Diekmann F. A non-native earthworm shifts seed predation dynamics of a native weed. *J Appl Ecol*. 2022;59:117–28. <https://doi.org/10.1111/1365-2664.14034>.
39. Montagnani C, Gentili R, Smith M, Guarino MF, Citterio S. The Worldwide Spread, Success, and impact of ragweed (*Ambrosia* spp). *Crit Rev Plant Sci*. 2017;36:139–78. <https://doi.org/10.1080/07352689.2017.1360112>.
40. European and Mediterranean Plant Protection Organization. *Ambrosia artemisiifolia*, AMBEL. (). Distribution. 2022. <https://gd.eppo.int/taxon/AMBEL/distribution>. Accessed 9 Nov 2022.
41. Hall RM, Urban B, Wagentristl H, Karrer G, Winter A, Czerny R, Kaul H-P. Common ragweed (*Ambrosia artemisiifolia* L.) causes severe yield losses in soybean and impairs *Bradyrhizobium japonicum* infection. *Agronomy*. 2021;2021:1616. <https://doi.org/10.3390/agronomy11081616>.
42. Burbach GJ, Heinzerling LM, Edenharter GM, Bachert C, Bindsløv-Jensen C, Bonini S, et al. GA(2)LEN skin test study II: clinical relevance of inhalant allergen sensitizations in Europe. *Allergy*. 2009;64:1507–15. <https://doi.org/10.1111/j.1398-9995.2009.02089.x>.
43. Speißen B, Liu Y, van Kleunen M. Biomass responses of widely and less-widely naturalized alien plants to artificial light at night. *J Ecol*. 2021;109:1819–27. <https://doi.org/10.1111/1365-2745.13607>.
44. Liu Y, Speißen B, Knop E, van Kleunen M. The Matthew effect: common species become more common and rare ones become more rare in response to artificial light at night. *Glob Chang Biol*. 2022;28:3674–82. <https://doi.org/10.1111/gcb.16126>.
45. Blouin M, Hodson ME, Delgado EA, Baker G, Brussaard L, Butt KR, et al. A review of earthworm impact on soil function and ecosystem services. *Eur J Soil Sci*. 2013;64:161–82. <https://doi.org/10.1111/ejss.12025>.
46. Arnone JA, Zaller JG. Earthworm effects on native grassland root system dynamics under natural and increased rainfall. *Front Plant Sci*. 2014;5:152. <https://doi.org/10.3389/fpls.2014.00152>.
47. Macdonald DW. Predation on earthworms by terrestrial vertebrates. In: Satchell JE, editor. *Earthworm Ecology: from Darwin to Verticulture*. London, New York: Chapman and Hall; 1983. pp. 393–414.
48. Minnaar C, Boyles JG, Minnaar IA, Sole CL, McKechnie AE. Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. *J Appl Ecol*. 2015;52:522–31. <https://doi.org/10.1111/1365-2664.12381>.
49. Sanders D, Kehoe R, Cruse D, van Veen FJF, Gaston KJ. Low levels of Artificial light at night strengthen Top-Down Control in Insect Food Webs. *Curr Biol*. 2018;28:2474–2478e3. <https://doi.org/10.1016/j.cub.2018.05.078>.
50. Sullivan SMP, Hossler K, Meyer LA. Artificial lighting at night alters aquatic-riparian invertebrate food webs. *Ecol appl*. 2019;29:e01821. <https://doi.org/10.1002/eap.1821>.
51. Eberhart-Phillips LJ. Dancing in the moonlight: evidence that killdeer foraging behaviour varies with the lunar cycle. *J Ornithol*. 2017;158:253–62. <https://doi.org/10.1007/s10336-016-1389-4>.
52. Stracey CM, Wynn B, Robinson SK. Light Pollution allows the Northern Mockingbird (*Mimus polyglottos*) to feed nestlings after Dark. *Wilson J Ornith*. 2014;126:366–9. <https://doi.org/10.1016/13-107.1>.
53. Milcu A, Schumacher J, Scheu S. Earthworms (*Lumbricus terrestris*) affect plant seedling recruitment and microhabitat heterogeneity. *Funct Ecol*. 2006;20:261–8. <https://doi.org/10.1111/j.1365-2435.2006.01098.x>.
54. Clause J, Forey E, Eisenhauer N, Seal CE, Soudey A, Colville L, Barot S. Seed selection by earthworms: chemical seed properties matter more than morphological traits. *Plant Soil*. 2017;413:97–110. <https://doi.org/10.1007/s11104-016-3085-9>.
55. Hall RM, Urban B, Skalova H, Moravcová L, Sölter U, Starfinger U, et al. Seed viability of common ragweed (*Ambrosia artemisiifolia* L.) is affected by seed origin and age, but also by testing method and laboratory. *NB*. 2021;70:193–221. <https://doi.org/10.3897/neobiota.70.66915>.
56. Šepanovi M, Košak L, Pismarovi L, Šoštar V. Stimulation of germination of freshly collected and Cold-Stored seeds of *Ambrosia artemisiifolia* L. *Plants*. 2022. <https://doi.org/10.3390/plants11141888>.
57. Sang W, Liu X, Axmacher JC. Germination and emergence of *Ambrosia artemisiifolia* L. under changing environmental conditions in China. *Plant Species Biol*. 2011;26:125–33. <https://doi.org/10.1111/j.1442-1984.2011.00314.x>.
58. Guillemin J-P, Chauvel B. Effects of the seed weight and burial depth on the seed behavior of common ragweed (*Ambrosia artemisiifolia*). *Weed Biol Manag*. 2011;11:217–23. <https://doi.org/10.1111/j.1445-6664.2011.00423.x>.

59. Agapit C, Gigon A, Puga-Freitas R, Zeller B, Blouin M. Plant-earthworm interactions: influence of age and proportion of casts in the soil on plant growth, morphology and nitrogen uptake. *Plant Soil*. 2018;424:49–61. <https://doi.org/10.1007/s11104-017-3544-y>.
60. Kyba CCM, Altıntaş YÖ, Walker CE, Newhouse M. Citizen scientists report global rapid reductions in the visibility of stars from 2011 to 2022. *Science*. 2023;379:265–8. <https://doi.org/10.1126/science.abq7781>.
61. Hamaoui-Laguel L, Vautard R, Liu L, Solmon F, Viovy N, Khvorostyanov D, et al. Effects of climate change and seed dispersal on airborne ragweed pollen loads in Europe. *Nat Clim Change*. 2015;5:766–71. <https://doi.org/10.1038/nclimate2652>.
62. Edwards CA, Arancon NQ. *Biology and Ecology of earthworms*. 4th ed. New York: Springer; 2022.
63. Wurst S, Sonnemann I, Zaller JG. Soil macro-invertebrates: their impact on plants and Associated Aboveground communities in Temperate regions. In: Ohgushi T, Wurst S, Johnson SN, editors. *Aboveground–Belowground Community Ecology*. Cham: Springer International Publishing; 2018. pp. 175–200.
64. Li X-M, Li S, Huang F-Y, Wang Z, Zhang Z-Y, Chen S-C, Zhu Y-G. Artificial light at night triggers negative impacts on nutrients cycling and plant health regulated by soil microbiome in urban ecosystems. *Geoderma*. 2023;436:116547. <https://doi.org/10.1016/j.geoderma.2023.116547>.
65. Fumanal B, Chauvel B, Bretagnolle F. Estimation of pollen and seed production of common ragweed in France. *Ann Agric Environ Med*. 2007;233–6.
66. Falchi F, Cinzano P, Elvidge CD, Keith DM, Haim A. Limiting the impact of light pollution on human health, environment and stellar visibility. *J Environ Manage*. 2011;92:2714–22. <https://doi.org/10.1016/j.jenvman.2011.06.029>.
67. R Core Team. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing; 2023.
68. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. glmmTMB balances speed and flexibility among packages for zero-inflated generalized Linear mixed modeling. *R J*. 2017;9/2:378–400.
69. Wickham H. *Ggplot2: elegant graphics for data analysis*. 2nd ed. Cham: Springer; 2016.
70. Kassambra A. ggpubr: 'ggplot2'-Based Publication Ready Plots; 2023.
71. Lenth RV. emmeans: Estimated Marginal Means, aka Least-Squares Means; 2023.
72. Ahlmann-Eltze C, Patil I, ggsignif. R Package for Displaying Significance Brackets.

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