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Artificial Light at Night Reduces the Surface Activity of Earthworms, Increases the Growth of a Cover Crop and Reduces Water Leaching

Zenia Kavassilas [†], Marion Mittmannsgruber [*,†], Edith Gruber and Johann G. Zaller [*]

Department of Integrative Biology and Biodiversity Research, Institute of Zoology, BOKU University, 1180 Vienna, Austria; zenia.kavassilas@students.boku.ac.at (Z.K.)
[*] Correspondence: marion.mittmannsgruber@boku.ac.at (M.M.); johann.zaller@boku.ac.at (J.G.Z.)
[†] These authors contributed equally to this work.

Abstract: Artificial light at night (ALAN), also known as light pollution, is a growing environmental problem worldwide. However, only a few studies have examined whether soil organisms that search for food at the surface at night can be affected by ALAN. We investigated the effects of ALAN on the above-ground foraging activity of anecic earthworms (*Lumbricus terrestris*), on the soil water infiltration and on the germination and growth of a cover crop (*Phacelia tanacetifolia*). In a full-factorial greenhouse experiment, we tested four factors: ALAN (about 5 lx during the night vs. total darkness), earthworms (two specimens vs. none), plant species (*Phacelia* alone vs. mixed with ragweed *Ambrosia artemisiifolia*) and sowing depth (surface-sown vs. sown in 5 cm depth). Data were analysed using multifactorial ANOVAs. Earthworms removed 51% less surface litter under ALAN than under dark conditions. ALAN had no effect on *Phacelia* germination but resulted in increased height growth and biomass production when the seeds were buried. Earthworms reduced *Phacelia* germination and biomass production. ALAN reduced water leaching through the experimental units, probably due to interactions between the subsurface casts and plant roots. We conclude that ALAN, as emitted from streetlights, can lead to complex ecological effects in ecosystems that merit further investigation.

Keywords: agroecology; ALAN; artificial light at night; earthworms; light pollution; *Lumbricus terrestris*; *Phacelia tanacetifolia*; plant–animal interactions

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1. Introduction

Artificial light at night (ALAN), also referred to as light pollution, is the brightening of the night sky caused by anthropogenic light sources such as street lights, cars, buildings or advertisements [1,2]. While the night sky has always been illuminated by the natural light of the moon, stars and other celestial bodies, ALAN has changed these natural light conditions [3]. Studies have shown that artificial skyglow affects distant environments that would otherwise be dark up to hundreds of kilometres away [4], and it has become a global problem that has been steadily increasing over the past few decades [5], mainly due to increasing urbanization and industry [6]. It is estimated that about 23% of the global land area is affected by ALAN [7].

Life on earth is strongly influenced by the diurnal cycle of light and darkness, and ALAN disrupts this cycle and causes organisms to change their behaviour [8]. While the increasing use of ALAN has improved people's quality of life and is positively associated with safety, prosperity and modernity, the potential impact on the biosphere is rarely considered [9]. The effects of ALAN range from purely behavioural [10] to lethal [11]. For example, it has been found that moth species that pollinate at night carry lower pollen loads in illuminated areas than in unlit areas [12], and pollination by nocturnal insects generally decreases by more than 60% due to ALAN, which also reduces fruit production [13]. Female fireflies (*Lampyris noctiluca*) showed lower mating choice success under ALAN, which may lead to population declines [14]. Many studies have documented a change in foraging due to moonlight or ALAN, leading to better visual detection of food, including prey, but also increasing predation risk [15]. ALAN can also affect plants' physiology, phenology, morphology and resource allocation [16]. In addition, studies report earlier or later phenology, increased [17] or suppressed growth, reduced flower production [13] and altered leaf toughness as direct plant responses to ALAN [18].

While it has been demonstrated that ALAN alters the composition of soil communities [19], the effects on soil organisms have rarely been investigated [20,21]. This is understandable, since most soil organisms spend their lives in the soil and usually do not come into contact with light. However, some soil organisms, such as some vertically burrowing, anecic earthworm species, come to the soil surface at night to feed on plant litter and to mate [21]. At the soil surface, they are also exposed to nocturnal predators [15,22]. Thus, anecic earthworms can be expected to respond to ALAN, and this has indeed been shown in recent studies [17,21].

The effects of ALAN on earthworms may be of importance for ecosystems, as earthworms are among the most important soil organisms in temperate regions [23,24]. Earthworms can interact with plants both directly and indirectly. Direct effects include root feeding and transport of plant seeds, as earthworms are increasingly recognized as important dispersers and predators of seeds [25]. Seeds can be ingested during foraging and transported vertically in the soil profile [26,27]. Indirect effects of earthworms may arise from creating, altering and maintaining suitable habitats for plants and other soil organisms [23] that can even increase crop yields [24]. Earthworms also influence decomposition, nutrient cycling, soil porosity, aggregate formation and water infiltration [28].

Overall, arable fields are generally not very attractive to earthworms due to frequent disturbances from tillage and/or pesticide application [29,30]. However, cover cropping to increase soil organic carbon [31] and reduce soil erosion generally improves the soil quality [32], which has been shown to benefit earthworms [33,34]. Overall, cover crops are crop species grown in an agricultural rotation between cash crops [35]. One species that is frequently used as a cover crop in arable rotations is *Phacelia tanacetifolia* (Fam. *Boraginaceae*) [36], a plant that originated in the USA and Mexico but is now increasingly cultivated in Central Europe. Due to its abundant flowering and high-quality nectar and pollen, *Phacelia* is very attractive to honeybees, bumblebees and hoverflies, as well as other beneficial insects [37]. It is also grown as a fodder crop in mixtures for direct feeding or silage [38]. Often, *Phacelia* fields are infested by the invasive common ragweed, *Ambrosia artemisiifolia* [39].

The current study investigated the effects of ALAN on the activity of the anecic earthworm species *Lumbricus terrestris* and its interaction with the cover crop species *Phacelia tanacetifolia*. Based on previous research, we expected that ALAN would result in a reduction in the surface activity of anecic earthworms [21,40]. Although the effects of ALAN on *Phacelia* were less clear, we expected that the seeds would not germinate well under ALAN, because they normally germinate well when buried in the soil [37]. Since earthworms feed on plant seeds, we also assumed that the effects of ALAN on earthworms would have a cascading effect on *Phacelia* germination and growth. If ALAN alters the behaviour of earthworms, it would also affect their burrowing activity and, consequently, the water infiltration in the soil.

2. Materials and Methods

2.1. Experimental Setup

A full factorial pot experiment was conducted at BOKU University, Vienna, over a period of 45 days in April and May 2022, alongside a previously published study on ALAN [17].

Four factors with two levels and six replicates were considered:

- ALAN: complete darkness (D) vs. artificial light pollution (L);
- Earthworms (EW): *L. terrestris* present (EW+) vs. absent (EW−);

- Plant species: sowing *Phacelia tanacetifolia* alone (P) vs. in combination with *Artemisia artemisiifolia* (M);
- Sowing depth: surface-sown (0) vs. 5 cm deep (5).

This resulted in 96 experimental units (2 × 2 × 2 × 2 factors × 6 replicates). Each unit was a 3 L plastic pot filled with sieved topsoil (0–15 cm depth) from the BOKU Experimental Farm, with a bulk density of 1 g cm^{-3}. The filled pots were weighed to confirm similar bulk density conditions. The pots were randomized once at the start and randomized again after 20 days. To prevent earthworms from escaping, the pots were fitted with mesh and plastic barriers; all pots had the same setup to ensure uniformity.

The soil characteristics taken at the site included a pH ($CaCl_2$) of 7.6, 73 mg kg^{-1} phosphorus, 167 mg kg^{-1} potassium and 3.9% soil organic matter.

For the factor of ALAN, the pots under the “L” level were exposed to artificial light from 20:00 to 8:00 every night using covered greenhouse ceiling lights (fluorescent tubes, 36 W, 4000 K), while the pots under the “D” level were kept in complete darkness, covered by a wooden frame lined with black plastic foil.

For the earthworm factor, “EW+” pots received two adult *Lumbricus terrestris* (average biomass 8.9 ± 1.0 g per pot, equivalent to 395 g m^{-2}), while “EW−” pots had no earthworms. The earthworms were purchased from a fishing supply shop and stored in a climate chamber before being added to the experiment.

For the plant species factor, “P” pots were sown with six *Phacelia tanacetifolia* seeds (equivalent to 266 seeds m^{-2}), while “M” pots were sown with three *Phacelia* seeds and three *Ambrosia artemisiifolia* seeds to simulate ragweed infestation of *Phacelia* stands. For the factor sowing depth, seeds were placed on the soil surface (Factor level “0”) or buried at a 5 cm depth (Factor level “5”). Seeds of *Phacelia* were obtained from the BOKU Experimental Farm, while *Ambrosia* seeds were obtained from the Institute of Botany of BOKU University.

All pots were irrigated with 250 mL of water and watered evenly throughout the experiment. One gram of hay was added weekly as food for the earthworms, even to pots without earthworms to maintain similar conditions. From week three onwards, hay was only added to EW+ pots to prevent plant litter buildup. Unwanted weeds and deceased earthworms were removed regularly.

The mean air temperature for the duration of the experiment was 21.2 ± 1.5 °C, at a relative humidity of 61.7 ± 13.6% for the L and 72.7 ± 10.8% for the D treatment.

2.2. Measurements

Light conditions were monitored throughout the experiment using a handheld luxmeter (Voltcraft LX-2000, Conrad Electronics SE, Hirschau, Germany). Nighttime light levels were recorded at 30 min intervals for 29 nights. In the “L” treatment, the average light level from 20:00 to 08:00 was 218 ± 129 lx, influenced by increasing day length and earlier sunrises. During the core nighttime hours (21:00 to 04:00), the light level averaged 5.1 ± 1.5 lx. In the “D” treatment, the light level remained consistently at 0 lx throughout the night (Figure 1).

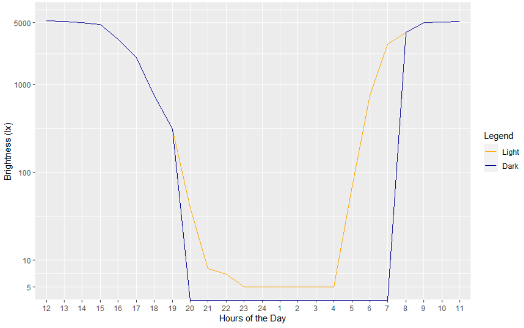

Figure 1. Mean brightness in lx measured throughout all experimental days comparing the light and dark treatments.

Earthworm activity was approximated by visually estimating the percentage of bare soil, indicating how much plant litter (chopped hay) had been removed from the surface. Active earthworms interact with the litter by pulling it into their burrows or piling it around their middens, thereby increasing the amount of bare soil. Litter was added to all pots, including those without earthworms. These estimations were made three days after litter was added, repeated three times and estimated by two people independently, with the results averaged.

The germination of *Phacelia* was determined by counting the number of germinated seedlings throughout the experiment and expressed as a percentage of total seeds. *Phacelia* growth was determined by measuring the final plant height from the soil surface to the highest central nodule of each plant and expressed as the mean plant height per pot. Dry plant biomass was determined at the end of the experiment by cutting the plants at the soil surface and drying the above-ground plant material at 55 °C for 48 h and weighing it. This was expressed as mean plant biomass per pot. In pots with mixed *Phacelia* and *Ambrosia* plants, only *Phacelia* was assessed.

Soil water infiltration was assessed once before harvest by adding 500 mL of tap water to each pot and measuring the time until all water had completely drained into the soil (=infiltration time). Additionally, the volume of water that leached through the soil was collected in the saucers of the plant pots under each pot.

The air temperature and air relative humidity were measured continuously using eight Tinytag data loggers (Gemini Data Loggers, Chichester, UK). Four data loggers were placed in the L treatment and the other four in the D treatment.

The soil temperature and soil moisture were measured only once at the end of the experiment. The soil temperature was measured with a digital thermometer at a depth of 15 cm, with the mean soil temperature being 19.9 °C. To determine the soil moisture, a soil core (⌀ 2 cm, 7 cm long) was taken from each pot, weighed, dried at 100 °C for 48 h and weighed again to determine the water content of each sample. The mean soil water content was 28.5%.

2.3. Statistical Analysis

Data were analysed using the statistics programme R version 4.3.2 with a significance level set to $\alpha = 0.05$ [41]. Graphs were created using the package ggplot2 [42].

In total, there were 96 experimental units, distributed across four fully crossed experimental factors: ALAN, sowing depth, plant species and earthworm presence.

Six EW+ experimental units were excluded from the final statistical analyses, because earthworms could not be found at the end of the experiment and their activity cannot be guaranteed, resulting in a sample size of 90 experimental units.

Multifactorial ANOVAs were conducted to analyse the data, based on log-transformed response variables when necessary and considering all main effects and two-way interactions. In all ANOVAs, the covariates soil moisture and soil temperature measured at the end of the experiment were also included. Further, the ANOVA for litter cover included the covariate of assessment iteration. Assumptions for normal distribution and homogeneity of variance for residuals were confirmed for all analyses.

All raw data used for the statistical are provided in Supplementary Table S1.

3. Results

3.1. Effects on Earthworm Surface Foraging Activity

Litter removal was significantly affected by ALAN, earthworm presence, the interaction between ALAN and earthworms, and plant species (Figure 2, Table 1). Litter removal was significantly lower under ALAN. The iteration of visual assessments did not significantly affect litter removal, indicating a consistent effect over time.

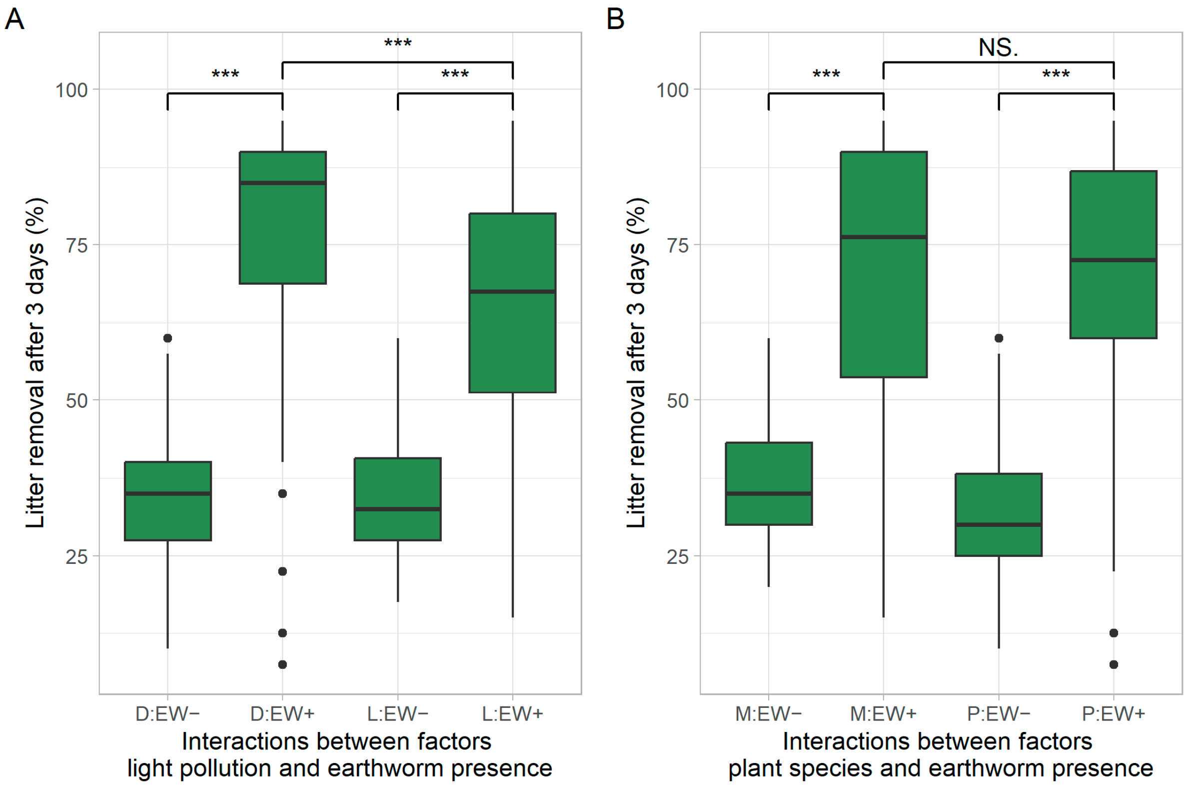

Figure 2. Litter removal from the soil surface in response to (**A**) complete darkness at night (D) or ALAN (L) when earthworms were absent (EW−) or present (EW+) or (**B**) when two plant species where present (M) or only *Phacelia* was present (P) when earthworms were absent (EW−) or present (EW+). Each box represents the 1st and 3rd quartiles, the median as the horizontal line and the whiskers as minimum and maximum values. N = 6. Asterisks denote statistical significances: *** <0.001; NS—not significant.

Table 1. Statistical analysis of the effects of ALAN, sowing depth, plant species and earthworms on litter removal. *p*-values from ANOVAs; soil moisture and temperature were included covariates. Bold text and asterisks denote statistical significances: *** <0.001, ** <0.01, * <0.05.

		Ground Litter Removal		
Parameter	**Df**	**Sum Sq**	**F Value**	**Pr (>F)**
ALAN	1	1770	7.828	**0.006** **
Sowing depth	1	41	0.181	0.671
Plant species	1	155	0.684	0.409
Earthworms	1	84,875	375.418	**<0.001** ***
Iteration	2	537	1.188	0.307
Soil moisture	1	92	0.407	0.524
Soil temperature	1	747	3.305	0.070
ALAN × sowing depth	1	402	1.776	0.184
ALAN × plant species	1	4114	18.196	**<0.001** ***
ALAN × earthworms	1	4067	17.988	**<0.001** ***
Sowing depth × plant species	1	123	0.544	0.461
Sowing depth × earthworms	1	3	0.014	0.905
Plant species × earthworms	1	1012	4.476	**0.035** *
Residuals	255	57,651		

3.2. Phacelia Germination and Growth

Overall, 24.8% of the sown *Phacelia* seeds germinated. *Phacelia* germination was significantly reduced by earthworm presence but was not affected by ALAN (Figure 3A, Table 2). The mean final height of the *Phacelia* was significantly affected by ALAN but not by earthworms (Figure 3B, Table 2). The interaction between the factors light pollution and sowing depth was also significant. The dry weight of *Phacelia* at harvest time was significantly affected by earthworms and sowing depth, but not by ALAN; however, there was a significant interaction between ALAN and sowing depth (Figure 3C,D, Table 2). Soil moisture had a significant effect on *Phacelia* biomass (Table 2).

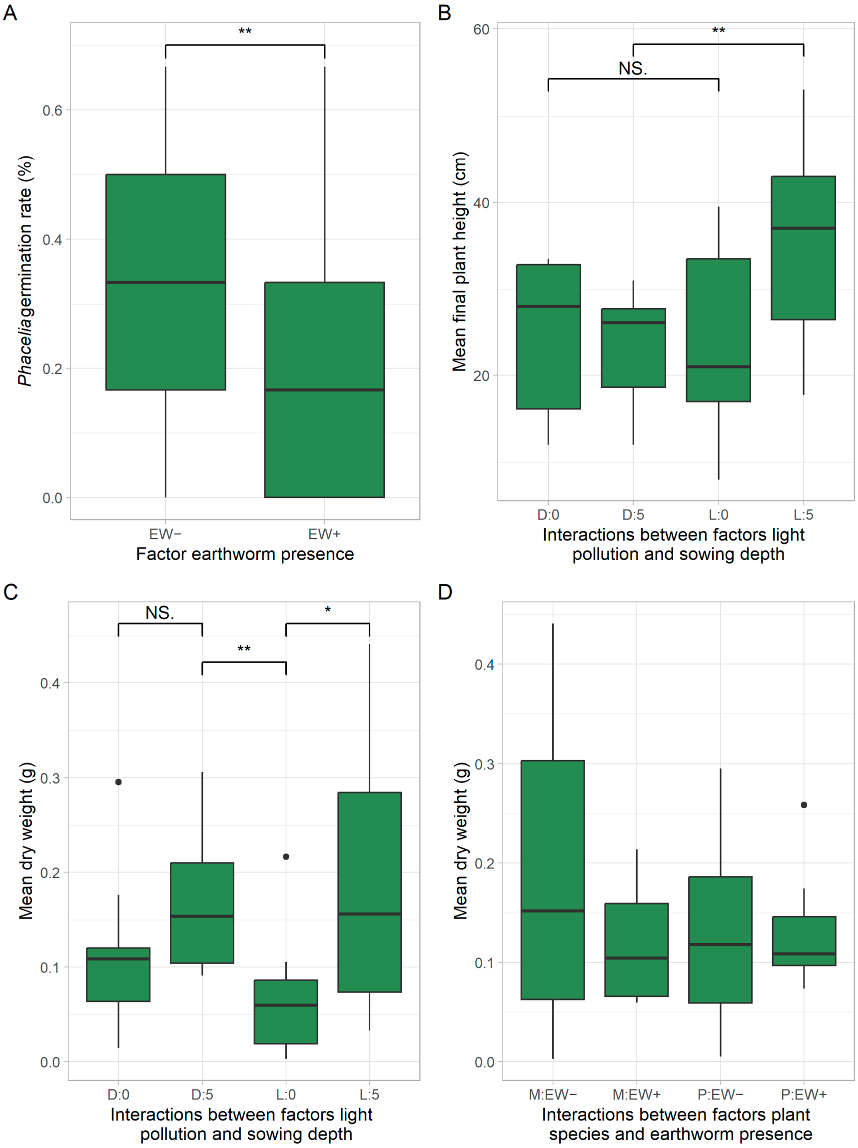

Figure 3. *Phacelia* germination (**A**), height growth (**B**) and biomass production (**C**,**D**) in response to complete darkness at night (D) or ALAN (L) when earthworms were absent (EW−) or present (EW+) (**A**) or when two plant species where present (M) or only *Phacelia* was present (P). Each box represents the 1st and 3rd quartiles, the median as the horizontal line and the whiskers as minimum and maximum values. N = 6. Asterisks denote statistical significances: ** <0.01, * <0.05; NS—not significant.

Table 2. Statistical analysis of the effects of ALAN, sowing depth, plant species and earthworms on *Phacelia* germination, height growth and biomass production. Statistical analysis *p*-values were obtained with ANOVAs. For analysis of *Phacelia* plant height and biomass, pots without any germinated plants were excluded. Bold text and asterisks denote statistical significances: *** <0.001, ** <0.01, * <0.05.

	Germination (%)				Height (Mean cm pot^{-1})				Biomass (Mean g pot^{-1})			
Parameter	**Df**	**Sum Sq**	**F Value**	**Pr (>F)**	**Df**	**Sum Sq**	**F Value**	**Pr (>F)**	**Df**	**Sum Sq**	**F Value**	**Pr (>F)**
ALAN	1	0.079	1.656	0.202	1	666.7	7.064	**0.012** *	1	0.001	0.117	0.735
Sowing depth	1	0.090	1.892	0.173	1	217.0	2.299	0.140	1	0.082	15.752	**<0.001** ***
Plant spp.	1	0.040	0.846	0.361	1	7.1	0.075	0.786	1	0.021	3.952	0.056
Earthworms (EW)	1	0.485	10.154	**0.002** **	1	209.3	2.217	0.147	1	0.026	5.076	**0.031** *
Soil moisture	1	0.094	1.980	0.163	1	387.6	4.107	0.051	1	0.112	21.607	**<0.001** ***
Soil temperature	1	0.056	1.163	0.284	1	0.4	0.004	0.950	1	0.000	0.001	0.978
ALAN × depth	1	0.017	0.361	0.550	1	522.8	5.540	**0.025** *	1	0.022	4.194	**0.049** *
ALAN × plant spp.	1	0.014	0.301	0.585	1	32.5	0.345	0.561	1	0.004	0.836	0.368
ALAN × EW	1	0.007	0.145	0.704	1	1.3	0.014	0.907	1	0.006	1.074	0.308
Depth × plant spp.	1	0.041	0.864	0.355	1	27.2	0.288	0.595	1	0.040	7.715	**0.009** **
Depth × EW	1	0.117	2.456	0.121	1	30.9	0.327	0.572	1	0.004	0.792	0.380
Plant spp. × EW	1	0.131	2.737	0.102	1	59.0	0.626	0.435	1	0.032	6.084	**0.019** *
Residuals	77	3.675			33	2925.5			31	0.161		

3.3. *Effects on Water Infiltration and Leaching*

The water infiltration in l min^{-1} was significantly lower in the presence of earthworms but was not affected by ALAN or any other treatment factor (Figure 4, Table 3). There were no significant interaction effects either. Only the covariate soil moisture also showed a significant effect. The leachate amount was significantly lower under ALAN but was not influenced by other treatment factors (Figure 4, Table 3). In addition, the interaction between the factors light pollution and plant species was significant.

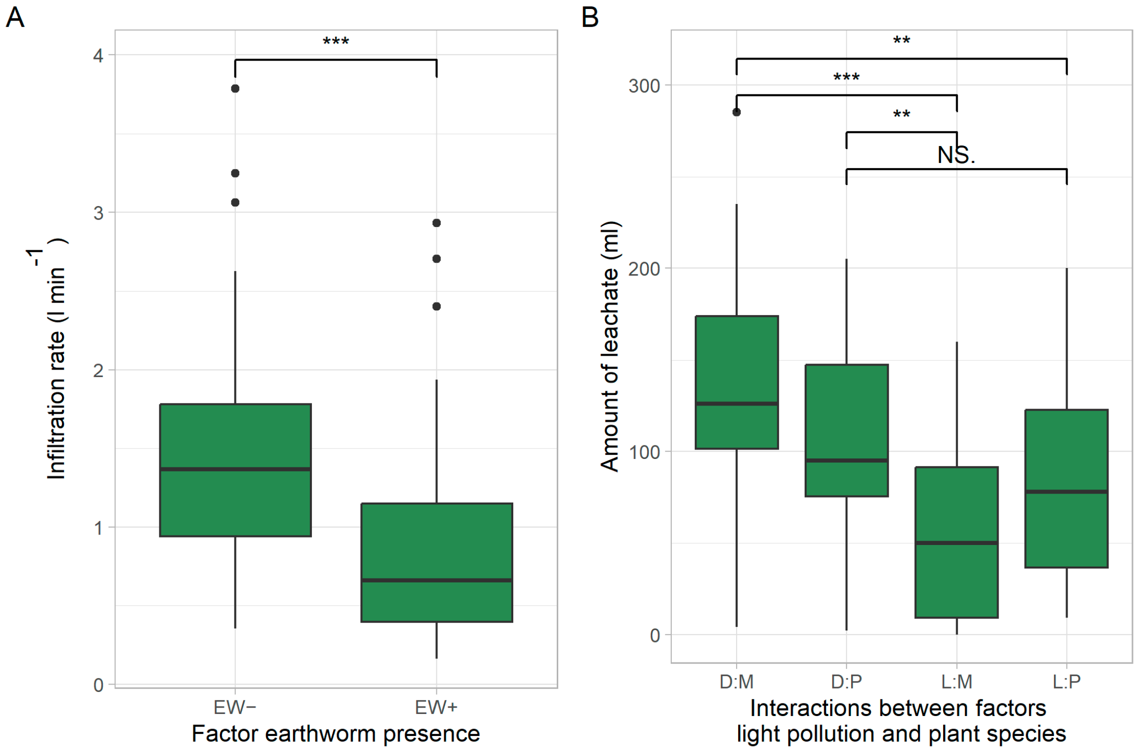

Figure 4. Water infiltration (**A**) and leachate amount (**B**) in response to complete darkness at night (D) or ALAN (L) when earthworms were absent (EW−) or present (EW+) (**A**) or when two plant species were present (M) or only *Phacelia* was present (P). Each box represents the 1st and 3rd quartiles, the median as the horizontal line and the whiskers as minimum and maximum values. N = 6. Asterisks denote statistical significances: *** <0.001, ** <0.01, NS—not significant.

Table 3. Statistical analysis of the effects of ALAN, sowing depth, plant species and earthworms on water infiltration. *p*-values from ANOVAs; soil moisture and temperature were included covariates. Bold text and asterisks denote statistical significances: *** <0.001, * <0.05.

		Water Infiltration (L min^{-1})			**Leachate Amount (mL)**		
Parameter	**Df**	**Sum Sq**	**F Value**	**Pr (>F)**	**Sum Sq**	**F Value**	**Pr (>F)**
ALAN	1	0.479	1.307	0.257	53,047	16.253	**<0.001 *** **
Sowing depth	1	1.297	3.541	0.064	27	0.008	0.927
Plant spp.	1	0.001	0.003	0.954	230	0.070	0.792
Earthworms	1	9.452	25.813	**<0.001 *** **	6644	2.036	0.158
Soil moisture	1	2.190	5.981	**0.017 * **	1720	0.527	0.470
Soil temperature	1	0.577	1.575	0.213	3870	1.186	0.280
ALAN × sowing depth	1	0.156	0.425	0.517	10,695	3.277	0.074
ALAN × plant spp.	1	0.346	0.946	0.334	15,946	4.886	**0.030 * **
ALAN × earthworms	1	0.015	0.040	0.842	1836	0.563	0.456
Sowing depth × plant spp.	1	0.412	1.126	0.292	2150	0.659	0.420
Sowing depth × earthworms	1	0.721	1.968	0.165	1780	0.545	0.463
Plant spp. × earthworms	1	0.814	2.223	0.140	7495	2.296	0.134
Residuals	77	28.197					

4. Discussion

We found that ALAN (i) reduced the surface foraging activity of an anecic earthworm species, (ii) did not affect *Phacelia* germination but increased the height growth and biomass production of surface-sown but not deep-sown *Phacelia* plants, and (iii) reduced water leaching through experimental pots but did not affect water infiltration.

The reduced activity of the anecic *L. terrestris* under ALAN confirmed earlier results [17,21] and suggests that photoreceptor cells in the epidermis of earthworms [43] can detect even the relatively low light levels (about 5 lx) of our experimental treatments. The current study was rather short-term, so we cannot assess the long-term effects of reduced surface foraging by earthworms. However, because the foraging and mating of this species mainly occur at the soil surface, this could lead to less well-fed earthworms and smaller populations. Indeed, lower mating activity of *L. terrestris* under ALAN was observed in a previous study [17]. Smaller populations could impact the ecosystem services provided by earthworms, such as soil fertility and soil health [44], plant growth and plant biomass production [24], plant uptake of beneficial elements [45], and even the establishment of soil-borne plant diseases [46]. However, if earthworms are less active at the soil surface during nights under ALAN, they are also less exposed to predators such as birds, amphibians, reptiles or wild mammals [15]. In addition, species that are normally day-active can extend their activity periods due to ALAN and prey on organisms that are attracted to ALAN [47]. The influence of ALAN on the surface activity of earthworms was also influenced by the plant species, suggesting that ALAN may be mitigated by plant species. Previous studies have shown that earthworms interact closely with plant species [48,49], but further research is needed to determine how ALAN alters these interactions.

The germination of *Phacelia* was rather low at 25% and was not affected by ALAN, but the germination was reduced by earthworms. This contrasts with a previous study that found a 33% decline in ragweed germination due to ALAN and earthworm activity [17]. These contrasting effects suggest that plant species respond differently to ALAN [16,50]. The height growth of *Phacelia* was similar under dark conditions, regardless of whether the seeds were placed on the soil surface or buried in the soil; however, the height growth was increased under ALAN when the seeds were buried. This suggests that ALAN may, indeed, have some effect on *Phacelia* germination by interacting with the sowing depth, although the main effect was not statistically significant. Previous studies have found interactions between the sowing depth of ragweed, ALAN and earthworms [17]; however, this was not the case with *Phacelia*. Regarding the factor sowing depth, the germination rates were higher and plants grew taller and had more biomass when seeds were buried five centimetres deep, which again is not surprising, since *Phacelia* prefers darkness to germinate well [37]. The biomass production of *Phacelia* was only lower under ALAN when the seeds were placed on the soil surface, again suggesting some light influence during the night. Since no interaction between earthworms and sowing depth was detected, earthworms do not appear to feed on *Phacelia* seeds, possibly due to the relatively large seeds. Other studies have reported on the selective sowing of plant seeds by earthworms [27] and the effects of seed germination after passing through the earthworm guts [25].

ALAN showed significant effects on the height growth of *Phacelia,* suggesting that the plants benefitted from the few additional hours of light each day during sunrise [16]. Thus, the average brightness of 5.1 ± 1.5 lx between 21:00 and 04:00 each night did, indeed, stimulate additional photosynthesis and growth. However, beyond the scope of the current study, ALAN has also been shown to influence plant physiology and phenology [18]. It has also been shown that ALAN disrupts nocturnal pollination networks and has negative effects on the reproductive success of plants [13]. Since *Phacelia* is an important nectar source for honeybees and wild bees [37,38], further studies on the effects of ALAN on the interaction between insect pollinators and *Phacelia* would be interesting.

Earthworm activity reduced the germination of *Phacelia*, which had been found in previous studies regardless of the plant species [51]. Earthworms had little effect on the plant biomass production, which was unexpected, as earthworms usually increase plant biomass [24]. However, this could be due to the short duration of the experiment, since the effects of earthworms on plant growth and biomass production occur slowly [52] and also depend on earthworm densities [53] and on the age and proportion of casts [54].

Surprisingly, ALAN significantly reduced water leaching through the experimental units, both in those planted with *Phacelia* alone and especially in those where *Phacelia* was mixed with ragweed. Although we did not test for three-way interactions, we hypothesize that these effects may be the result of interactions between ALAN, plants and earthworms. We were able to show that earthworms under ALAN spent less time on the soil surface, possibly resulting in higher casting and tunnelling activity below ground. It is known that casts have a high water holding capacity and retain water in the soil column [55,56]. In addition, the better height growth of *Phacelia* under ALAN could also mean a larger root system with higher water uptake by the plants [57], and subsurface casts also influence root growth [58]. Moreover, earthworms increase the aggregate stability, especially in the presence of plant roots [59]. Unfortunately, we did not analyse the root system in our study. In any case, these interpretations require further research to be validated. It can be concluded that the change in the soil pore structure caused by anecic earthworms has an influence on the water retention and mineralization processes in the soil [60].

Water infiltration was not affected by ALAN. However, the finding that water infiltration was lower in pots with earthworms contradicts the general knowledge about the role of earthworms in soil hydrology [57,61,62]. We explain this contradictory result by the different soil structure of the experimental units with and without earthworms. The pots were filled with soil with a rather low bulk density of 1 g cm^{-3} and were able to absorb the water relatively quickly, as a large pore volume was present. In the pots with earthworms, these pores were filled with subsurface casts and hindered the infiltration of water. Since ALAN reduced the surface activity of the earthworms, we assume that their casting activity shifted belowground. The reduced leaching under ALAN may also indicate that there is no preferential flow of water through vertical earthworm tunnels with exits at the soil surface [63,64]. Of course, the effects of ALAN on earthworm activity may also influence other ecosystem services provided by earthworms, such as improving nutrient cycling, soil aeration or soil health [44,65], but this was beyond the scope of the current study.

While this study provided many interesting results, it was limited by several constraints, as it was still a pot experiment under artificial controlled conditions. Therefore, the results cannot be perfectly transferred to natural conditions. Specifically, the density of adult *L. terrestris* individuals is probably unnaturally high, and their burrowing was also likely limited by the depth of the pots (20 cm). Otherwise, they would have burrowed much deeper [66], which could affect the results in terms of water infiltration and leaching. Additionally, the light conditions did not fully correspond to natural light conditions, as this was not practically possible. Overall, it would be ideal to repeat such an experiment under field conditions to confirm our results.

Taken collectively, it was remarkable to observe these effects of ALAN on earthworm activity and *Phacelia* growth, as the light levels used in this experiment corresponded to residential street lighting (5.1 ± 1.5 lx) [67]. We showed that soil organisms such as anecic earthworms can be affected by ALAN, foraging less on the soil surface on illuminated nights compared to dark nights. The long-term consequences of this effect are difficult to assess based on our short-term experiment. However, since the removal of litter from the soil surface impairs the germination of plant seeds [68], it could even affect the diversity of plant communities [69]. In any case, studying interactions in natural environments is complex, because many other organisms could be affected by light pollution at the same time.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/land13101698/s1: Table S1. Raw data on ALAN, earthworms and Phacelia.xlsx.

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