Grubisic, M., van Grunsven, R. H. A., Kyba, C., Manfrin, A., Hölker, F. (2018): Insect declines and agroecosystems: does light pollution matter? - *Annals of Applied Biology*, *173*, 2, pp. 180—189.

DOI: http://doi.org/10.1111/aab.12440

Insect declines and agroecosystems: does light pollution matter?

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Summary

Drastic declines in insect populations, “Ecological Armageddon”, have recently gained increased attention in the scientific community, and are commonly considered to be the consequence of large-scale factors such as land-use changes, use of pesticides, climate change and habitat fragmentation. Artificial light at night (ALAN), a pervasive global change that strongly impacts insects, remains however infrequently recognized as a potential contributor to the observed declines. Here, we provide a summary of recent evidence of impacts of ALAN on insects, and discuss how these impacts can drive declines in insect populations in light-polluted areas. ALAN can increase overall environmental pressure on insect populations, and this is particularly important in agroecosystems, where insect communities provide important ecosystem services, e.g. natural pest control, pollination, conservation of soil structure and fertility and nutrient cycling, and are already under considerable environmental pressure. We discuss how changes in insect populations driven by ALAN and ALAN itself may hinder these services to influence crop production and biodiversity in agricultural landscapes. Understanding the contribution of ALAN and other factors to the declines of insects is an important step towards mitigation and the recovery of the insect fauna in our landscapes. In future studies, the role of increased nocturnal illumination also needs to be examined as a possible causal factor of insect declines in the ongoing “Ecological Armageddon”, along with the more commonly examined factors. Given the large scale of agricultural land use and the potential of ALAN to indirectly and directly impact crop production and biodiversity, a better understanding of effects of ALAN in agroecosystems is urgently needed.

Keywords: agroecosystems, ALAN, artificial light at night, drivers of environmental change, “Ecological Armageddon”, insect declines

Introduction

Declines in insect populations have been reported for several insect groups in Germany and the UK (see Leather, 2018), and land-use changes, use of pesticides, climate change and habitat fragmentation are commonly considered as drivers of these declines. This topic recently received considerable attention in the media and the scientific community, following the latest report of drastic declines of flying insects in protected areas in Germany (Hallmann *et al.*, 2017), popularly named “Ecological Armageddon”. The authors used Malaise traps to collect data from 63 sites located within protected areas that are embedded in an agricultural landscape in two regions in Germany, and found that biomass of flying insects decreased more than 75% over 27 years. This trend could not be explained by the changes in habitat, climate, or land use (Hallmann *et al.*, 2017), suggesting that another large-scale factor must therefore be involved. We suggest that artificial lighting could be an overlooked driver of insect declines. Artificial light at night (ALAN) is known to have strong impacts on insects, it is widespread and has been increasing at an annual rate of 2-6% over the last decades worldwide (Hölker *et al.*, 2010a; Kyba *et al.*, 2017), imposing an unprecedented alteration of natural light regimes and threatening biodiversity (Hölker *et al.*, 2010b). Despite its ubiquity, the importance of ALAN as an agent of global change is often overlooked when analysing insect population declines. For example, the vast majority of study locations analysed by Hallmann *et al.* (2017) are situated near densely populated areas in one of the most brightly illuminated regions in Germany (Fig 1, Table S1). The presence of ALAN is substantial in these areas, therefore ALAN may be an influential factor for insect populations, but this has not been tested or discussed. We suggest that in light-polluted areas, increased nocturnal illumination has to be considered when analysing insect population trends.

Artificial lighting has become an integral part of many nightscapes. It is not only relevant for directly illuminated areas close to the light sources, but also for more remote areas that are affected by light pollution through skyglow, light scattered in the atmosphere that extends tens to hundreds of kilometres from its source (Fig 1). Protected areas are intended to buffer biodiversity from anthropogenic stressors, but many are not sheltered from ALAN: up to 42% of protected territory in several regions of Europe, Asia, South and Central America have experienced recent significant increases in nocturnal lighting (Gaston *et al.*, 2015). Protected areas, such as those analysed by Hallmann *et al.* (2017) are often embedded in agricultural landscapes where insect populations are pressured by multiple stressors. Therefore, declines observed in protected areas may be a reflection of population declines acting at a larger landscape scale. In agroecosystems, insects perform many functions and provide important supporting and regulating ecosystem services such as decomposition of organic material, regulation of nutrient and energy flows, seed and pathogen dispersal, pollination, pest control and biodiversity maintenance (see Schowalter *et al.* 2018). Therefore, insect declines may substantially affect maintenance of these functions and services, with consequences for food production and biodiversity.

In this paper, we emphasize the importance of ALAN for insects. We summarize current evidence of impacts of ALAN on insects at different levels of biological organization and discuss how these effects can contribute to insect population declines in light-polluted areas. Insects provide important ecosystem services to agriculture, but effects of ALAN in agroecosystems have rarely been discussed. Therefore, we provide an overview of impacts of ALAN in agroecosystems and discuss how direct effects of ALAN on crops and indirect effects on invertebrates, e.g. pests, their natural enemies and pollinator species may influence crop production and biodiversity in light-polluted areas.

Importance of light for insects

Light as a visual and non-visual cue

Even at very low intensities, light is an important visual and non-visual cue for insects (see Tierney *et al.*, 2017). More than 60% of all invertebrates are nocturnal (Hölker *et al.*, 2010b) and they utilize nocturnal light for orientation, navigation, avoidance of predators, location of food and reproductive behaviour (Warrant 2017). Many nocturnal and crepuscular insects use celestial light sources such as stars and the moon as visual cues for dispersal across landscapes (see Foster *et al.* 2018). For example, dung beetles are known to use the diffuse light of the Milky Way as an orientation marker (Dacke *et al.*, 2013) while moths are long known to use light from both stars and the moon for orientation (Sotthibandhu and Baker, 1979). As a non-visual cue, light is critical for the regulation of biological clocks: gradual changes in light intensity and spectral composition during dusk and dawn as well as throughout the seasons provide crucial information for entrainment of circadian, circalunar and circannual rhythms that regulate many physiological processes, the timing of life-history events and nocturnal activities (Kronfeld-Schror *et al.* 2013, Seymore 2018). Lunar rhythms are reported for foraging activities of nocturnal, crepuscular and some diurnal bees (Kerfoot, 1967, Oehmke 1973), and mayflies synchronize their life history to emerge and reproduce during bright moon (Corbet *et al.* 1974).

Nocturnal and crepuscular insects are considered especially sensitive to, and often negatively affected by ALAN, because of their exceptional visual abilities in low-light conditions. By increasing background illumination at night ALAN may interfere with visual perception (Frank, 2006), while by masking natural cues and light cycles, ALAN may alter the perception of the photoperiod and thereby affect regulated processes (Seymore 2018). This may have important, yet unknown consequences for insect communities in illuminated landscapes (Kyba and Hölker, 2013).

Sensitivity of insects to ALAN

Insect typically possess multiple photoreceptor systems, most commonly three, with maximum sensitivity in UV, blue, and green parts of the spectrum (Briscoe & Chittka, 2001). Therefore, ALAN can have different effects depending on the overlap of its spectrum with the sensitivity of insect's visual systems. For example, lights with strong emission of UV and short wavelengths such as mercury vapour (MV) and fluorescent lamps have long been known to attract the highest numbers and diversity of insects (e.g. Eisenbeis, 2006; van Langevelde *et al.*, 2011). MV and high-pressure sodium (HPS) lamps were historically the most common street lights in Europe (van Tichelen *et al.*, 2007) and are recently being replaced by broad-spectrum white light-emitting diodes (LED). White LED lamps can vary greatly in their spectral composition (Aubé *et al.*, 2013) and their attractiveness to insects is controversial and still not well understood. White LEDs usually have a pronounced peak of short-wavelength blue light. This peak is pronounced in "cool-white" LEDs, and Pawson and Bader (2014) found that such lamps caught 48% more insects than HPS. In the study by Wakefield *et al.* (2018) "neutral-white" LED (with a lower blue component) and HPS lamps caught the same amount of insects, although LEDs caught more diverse communities. Reducing harmful short wavelengths is a promising approach to reduce attractiveness of light to insects (Longcore *et al.*, 2015; van Langevelde *et al.*, 2011; Davies *et al.*, 2017), although contradictory results exist (Wakefield *et al.*, 2016; Pawson and Bader, 2014). Attractiveness can also be taxon-specific, for example, compared to HPS lamps, LED lamps attract more flies, moths and butterflies (Pawson and Bader, 2014), but less beetles (Wakefield *et al.*, 2018). Furthermore, attractiveness to light can vary with developmental stages for a given species, as the visual systems undergo profound changes during development, but this has been relatively unexplored.

LEDs are used in outdoor lighting because of their high luminous efficacy that can allow for reduction in energy consumption. However, the use of LEDs may also result in higher light levels due to the so-called rebound effect (Kyba *et al.*, 2017). The ongoing increase in nocturnal light levels and current technological shift towards broad-spectrum lights that affect a wider range of narrow-tuned photoreceptors are expected to have negative effects on biodiversity and even stronger impacts on insects in the future (Gaston *et al.*, 2012).

Evidence for disruptive impacts of artificial light at night on insects

Effects of ALAN at the organism level

Most experimental studies on ALAN have focused on individual organisms and provide mechanistic understanding of effects of artificial lighting in nature. Numerous lethal and sublethal effects of ALAN on insects have been demonstrated at the organism level, and could contribute to population declines. The most obvious and well-documented effect of ALAN on insects is attraction of nocturnal insects to artificial light sources, even though the underlying causes are still not clear. Flight-to-light behaviour directly increases insect mortality as some insects are killed immediately in contact with the lamp, while many die of exhaustion or predation, as they often stay trapped flying around the lamps, unable to disperse and migrate elsewhere (Eisenbeis, 2006). This can create local population sinks. The radius of attraction reported in the literature varies from 3 and 130 m depending on the species, light type (i.e. spectral composition) and environmental illumination (see Degen *et al.*, 2016; van Grunsven *et al.*, 2014 and references therein). However, lower light levels imposed by sky glow at greater distances from direct illumination may disorient nocturnal insects by increasing background illumination levels and increase the chances they will enter the attraction zone when moving across the landscape (Frank, 2006). In some moths, attraction was demonstrated to be size-dependent, indicating higher mortality for larger species with potential consequences for population dynamics (van Langevelde *et al.*, 2011). By acting as a barrier for movement of nocturnal insects, ALAN can cause fragmentation of the night habitat and limit their dispersal (Degen *et al.*, 2016). Depending on dispersal activities and sensitivity of individual taxa, this may reduce landscape connectivity for local populations in fragmented landscapes. In agricultural landscapes, where semi-natural habitats are limited to small, isolated areas between the cropping fields, ALAN may disrupt recolonization of habitat patches, decreasing population resilience to habitat fragmentation by disrupting insect mobility (Thomas, 2000), and contributing to insect population declines.

Apart from acting as an ecological trap (Eisenbeis, 2006; Frank, 2006; Macgregor *et al.*, 2015), light pollution harms insects by impeding communication, changing their physiology, life-history traits and night habits, e.g. migration, feeding and reproductive behaviour. ALAN was found to inhibit initiation of pupal diapause (van Geffen *et al.*, 2014), reduce sex pheromone production (van Geffen *et al.*, 2015a), reduce mating (van Geffen *et al.*, 2015b) and interrupt feeding in moths (van Langevelde *et al.*, 2017), reduce courtship behaviour and mating success in fireflies (Firebaugh and Haynes, 2016), decrease fecundity and adult survival, prolong courtship and alter oviposition patterns in *Drosophila melanogaster* (McLay *et al.*, 2017, 2018). By decreasing fitness, survival and reproduction, ALAN can increase mortality and decrease reproduction rates and population growth. ALAN thus has the potential to decrease insect populations.

Effects of ALAN at the community and population levels

Increasing evidence shows that ALAN affects higher levels of biological organization such as communities and ecosystems, often with species- and seasonally-specific impacts. ALAN was shown to alter composition and structure of flying and ground-dwelling arthropods in grasslands and riparian areas, with taxon-specific changes in abundances and diversity of scavenger and predatory species such as spiders, beetles, harvestmen, ants, woodlice and amphipods (Davies *et al.*, 2017; Davies *et al.*, 2012; Manfrin *et al.*, 2017; Meyer and Sullivan, 2013). Meyer and Sullivan (2013) observed a decrease of 44% in abundance of tetragnathid spiders under ALAN conditions, and Manfrin *et al.* (2017) found a decrease in beetles. In aquatic systems, ALAN increases emergence and abundance of aquatic insects while decreasing their diversity and body size (Manfrin *et al.*, 2017; Meyer and Sullivan, 2013). Such alterations in aquatic-terrestrial fluxes of organisms were linked to species- and season-specific dietary changes of consumers (predators and scavengers) in a surrounding riparian area (Manfrin *et al.*, 2018). These studies provide evidence that ALAN can alter fluxes across ecosystem boundaries, with yet unknown consequences for species interactions and ecosystem functions. That ALAN induces population changes with cascading effects through food webs was also demonstrated for several species of herbivores and parasitoids of leguminous plants. In the bean plant *Vicia faba,* ALAN decreased densities of aphid populations by 20% over 5 generations, with negative direct and indirect effects on their specialist parasitoid wasps that declined by 40% over 4 generations (Sanders *et al.*, 2015). ALAN affected predator-prey interactions by providing benefits to a nocturnal visual predator ladybeetle *(Coccinella septempunctata)* that strongly suppressed abundance of its pea aphid prey (*Acyrthosiphon pisum*), although this was observed only as an interactive effect with increased nocturnal temperature (Miller *et al.*, 2017). Negative effects of ALAN are not limited to nocturnal insects, but are also found for diurnal arthropod communities (Manfrin *et al.*, 2017; Knop *et al.*, 2017).

Implications for insect population declines and missing evidence

In summary, there is a large body of evidence of negative impacts of ALAN on insects, and these can increase overall environmental pressure on insect populations in light polluted areas. Most of the studies conducted to date have investigated ALAN impacts on the organism level in the laboratory and in the field, and they point to various underlying mechanisms for how ALAN may drive insect population declines. Studies on communities and higher levels of biological organizations are increasing, but experimental studies on long-term effects on populations are still lacking. Recent correlative studies established direct links between ALAN and population declines in moths. Analysing moth declines over 30 years in the Netherlands, van Langevelde *et al.* (2018) found that species that are nocturnally active and attracted to light have stronger population declines compared to species that are diurnal or not attracted to lights. This indicates that light pollution plays an important role in the observed declines in moths. Other supporting evidence was found in the UK and Ireland, where light pollution accounted for 20% of variation in long-term changes of moth abundance (Wilson *et al.*, 2018). ALAN is also considered as a conservation threat for firefly populations worldwide (Firebaugh and Haynes, 2016).

Direct experimental evidence linking ALAN to insect population declines and the loss of ecosystem services is still missing. Tracking movements of individuals across larger areas would provide a better understanding of demographic processes between local populations and population dynamics. For mobile species, quantifying the exposure to light at night, especially in spatially and spectrally heterogeneous environments is challenging. A better understanding of sensitivities of different taxa and life stages and to different light spectra is necessary to assess sublethal, cumulative effects of ALAN. As artificial lighting often co-occurs with other anthropogenic pressures, it is often hard to disentangle its effects and determine its importance relative to other stressors. A combination of laboratory experiments across taxa, well-replicated field studies where impacts of ALAN are isolated from other anthropogenic factors, and long-term studies, is necessary to better understand the complex and interactive effects of ALAN in real-world settings, and its impacts on ecosystem dynamics. Studies that investigate effects of ALAN in agroecosystems are particularly lacking.

Does ALAN affect agroecosystems?

Agricultural areas cover 11% of Earth's land surface and 36% of total arable land area (FAOSTAT), and are extremely important for humanity for their provisioning services such as food, fibre, and timber production. Agriculture is, however, still largely dependent on natural processes provided by wild organisms, including insects. In agroecosystems, insects provide a variety of regulating and supporting services such as dung burial, nutrient cycling, conservation of soil structure and fertility, natural pest control, and pollination (Schowalter *et al.* 2018). Insects are facing multiple pressures in agricultural areas, and their populations are in decline (see Leather 2018). As a relatively novel anthropogenic pressure, ALAN can act as additional stressor, but effects of light pollution on agroecosystems have still not been systematically studied. ALAN may affect crop production by directly influencing crops in illuminated areas (Fig. 2;1), but also indirectly by changing populations of pest species and their natural enemies (predators and parasitoids) (Fig. 2;2, a-c), or by changing the abundance and behaviour of pollinators (Fig. 2;3). Effects on individual species and species interactions are likely to be complex, depending on light intensity and spectrum, season, and species, and are therefore hard to predict.

Direct effects of ALAN on crops

Very few studies have investigated direct effects of light pollution from street illumination on crops, while more information exists for wild plants and urban trees. Proximity to street lights was found to promote vegetative growth, delay development and flowering and decrease yield in soybean (Palmer *et al.*, 2017), maize, and young cassava plants (Sinnadurai, 1981). By contrast, ALAN suppressed growth in a bean plant *V. faba* (Sanders *et al.*, 2015) and decreased biomass and leaf numbers in several grasses (*Bothriochloa bladhii, B. ischaemum, Panicum virgatum, Sorghastrum nutans*), with species-specific height reduction (Flowers and Gibson, 2018). Other grass species *(Agrostis tenuis* and *Holcus lanatus)* were found to alter flowering phenology and vegetation cover under ALAN (Bennie *et al.*, 2017). By mimicking high level street light illumination in the laboratory, ALAN was found to interfere with circadian regulation in yellow poplar *Liriodendron tulipifera* (Kwak *et al.*, 2018), and to act as a repressor of photosynthesis and growth by inducing oxidative damage in chloroplasts (Kwak *et al.*, 2017). In urban areas, street lights affected phenology of several species of deciduous trees (e.g. *Acer pseudoplatanus, Quercus robur, Fagus silvatica, Fraxinus excelsior, Rhus typhina*) by promoting growth, causing earlier budburst, changing the timing of flowering, delaying onset of leaf colouring and prolonging leaf fall (ffrench-Constant *et al.*, 2016; Skvareninova *et al.*, 2017; Cathey and Campbell, 1975). Earlier flowering and prolonged leaf fall may increase the risk of frost damage in orchards and directly affect yield. Such changes may have consequences for plant health and survival of over-wintering crops, disrupt temporal matching with pollinators and alter resource allocation, with negative consequences for yield.

Effects of ALAN on pests and their natural enemies

ALAN has been demonstrated to have indirect, bottom-up effects on herbivore (Fig. 2;a) and parasitoids (Fig. 2;c) on leguminous plants in grassland ecosystems. Resource limitation through a lower plant biomass (observed in *V. faba*) or flower head density (observed in *Lotus pedunculatus)* induced seasonal suppression of aphids (Sanders *et al.*, 2015; Bennie *et al.*, 2015, respectively) and their parasitoids (Sanders *et al.*, 2015) under ALAN. ALAN may alter these interactions in agroecosystems as well, and predator-prey interactions may also be affected (Miller *et al.*, 2017). Furthermore, attraction to lights can increase abundance of pests (e.g. slugs, van Grunsven *et al.* 2018), potentially increasing damage to crops in illuminated fields. ALAN can also alter community composition of ground-dwelling invertebrates (Fig. 2;4), including abundance of predatory species (e.g. spiders, beetles) (Davies *et al.*, 2012; Davies *et al.*, 2017, Meyer and Sullivan, 2013; Manfrin *et al.*, 2017), with potential consequences for natural pest control. Some nocturnal predators (e.g. *Pachygnatha clercki*, Trohosa sp., Silpha sp.) can increase their nocturnal activities under ALAN, or extend their activities into the day (Manfrin *et al.*, 2017), but diel predators may also extend their activities into artificially-lit nights (see Johansen *et al.*, 2011 for a review on greenhouse lighting and pest control). Predatory invertebrates are important agents of biological control in agroecosystems. However, a dietary shift, as observed for tetragnathid spiders (*P. clercki* and *P. prativaga*) under ALAN, may release some pest species from predatory control (Manfrin *et al.*, 2018). The consequences of altered interaction networks for pest suppression and crop production remain to be determined.

Effects of ALAN on nocturnal pollinators

Insects provide key pollination services to agricultural crops and wild plants, but relatively little is known about the importance of nocturnal pollination. Moths are important nocturnal pollinators for diverse plant species across different ecosystems including agroecosystems (Macgregor *et al.*, 2015; Hahn and Bruhl, 2016), but no study has yet quantified benefits from nocturnal pollination to any economically valuable crop. ALAN was found to disrupt nocturnal pollination in a temperate agroecosystem: light from street lights decreased the probability of nocturnal pollen transport by moths by changing their behaviour and nocturnal patterns, attracting moths to fly higher above the field margins (Macgregor *et al.*, 2017). ALAN reduced flower visitation by nocturnal pollinators by 62% in an alpine meadow, resulting in 13% reduction of fruit set in thistle *(Cirsium oleraceum)* compared to the control (skylit) conditins (Knop *et al.*, 2017), despite numerous flower visits by diurnal pollinators. This indicates that both nocturnal and diurnal pollinator communities play important and complementary roles in plant reproduction. Disruption of nocturnal pollination may propagate to the diurnal pollinator community through plant-mediated interactions (Fig. 2;d) (Knop *et al.*, 2017), further exacerbating ongoing declines in pollinators, pollination services and plants that rely upon them, driven mainly by agricultural intensification (Hahn and Bruhl, 2016).

Importance of insect diversity in agroecosystems

In agroecosystems, bees have been long considered to be the main pollinators; however, a recent synthesis revealed that non-bee insects including moths, butterflies, beetles, flies and wasps provide similar pollination services and therefore play a significant, although underestimated role in global crop production (Rader *et al.*, 2016). High diversity of pollinators can be beneficial to crops, as it can buffer impacts of environmental changes on pollination services (Brittain *et al.*, 2013). In temperate agroecosystems, moths seem to have a limited role in pollination of crops, however they contribute to pollination of diverse non-crop species in semi-natural elements between the crop fields such as field margins, road verges, hedgerows, meadows, and vegetated margins of agricultural drainage ditches, thereby playing an important role in maintenance of biodiversity in agricultural landscapes (Hahn and Bruhl, 2016). These diverse semi-natural habitats are increasingly recognized as important refuges and dispersal corridors that support diverse networks of both aquatic and terrestrial taxa, and provide enhancement of pollination and biological control in agroecosystems as well as functional connectivity within landscapes (Hanley and Wilkins, 2015; Marshall and Moonen, 2002; Herzon and Helenius, 2008). Such valuable habitats are often located near road networks and illuminated by street lights. By altering the composition of invertebrate communities (including pest species and their natural enemies) and interfering with nocturnal pollination (Fig. 2), ALAN may affect biodiversity in agricultural landscapes. How these direct and indirect effects of artificial lighting interplay to affect crop production, biodiversity and ultimately, food security in illuminated areas is, however, unclear, and further research in this direction is sorely needed.

Conclusions

The use of artificial lighting has been increasing over several decades, increasing natural nocturnal light levels, introducing barriers, and simultaneously changing the spectral composition in the nightscape. We urge that the role of increased nocturnal illumination be considered as a causal factor of insect declines, the ongoing “Ecological Armageddon”, along with land-use changes, use of pesticides, habitat fragmentation and climate change. Numerous disruptive and fitness-relevant impacts of ALAN have been demonstrated for both diurnal and nocturnal insects, which can increase overall environmental pressure on insect populations in light-polluted landscapes. This is especially important in agricultural landscapes, where insect communities on which many ecosystem services depend, are under considerable environmental pressure. Given the large scale of agricultural land use and the potential of ALAN to impact crop production and biodiversity in agricultural landscapes, a better understanding of effects of ALAN in agroecosystems is urgently needed. Agricultural management may need to develop nocturnal strategies to mitigate adverse effects of ALAN on insects and help maintenance of ecosystem services they provide.

Acknowledgements

MG was supported by Freie Universität Berlin - Dahlem Research School HONORS fellowship and IGB Equal opportunity fund for young female scientists. FH acknowledges the support by the Federal Agency for Nature Conservation, Germany (FKZ 3514821700). CCMK acknowledges the funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 689443 via project GEOEssential. We thank the editor and the two anonymous reviewers for their valuable input during the review process.

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Figures

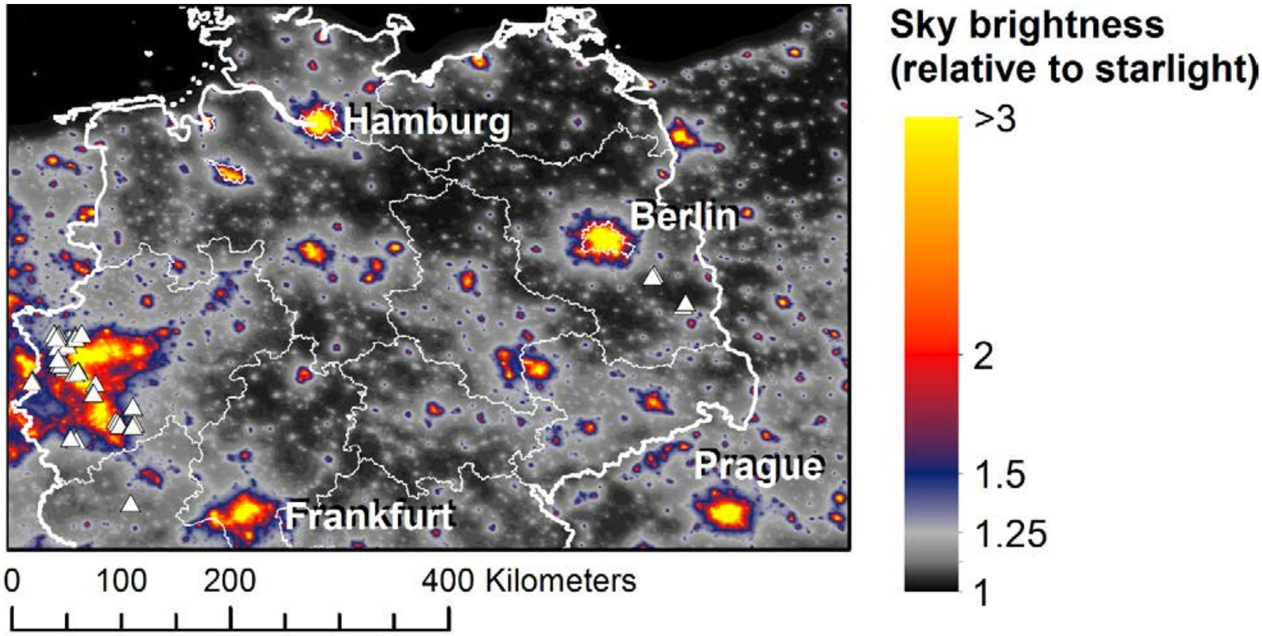

Fig. 1. Map of clear night sky brightness at zenith (relative to starlight, 0.25 cd $m^{-2} \equiv 1$) showing the position of study sites analysed by (Hallmann *et al.*, 2017) (white triangles) in the nightscape. Sky brightness data from the model of Falchi *et al.* (2016), see S1 Table.

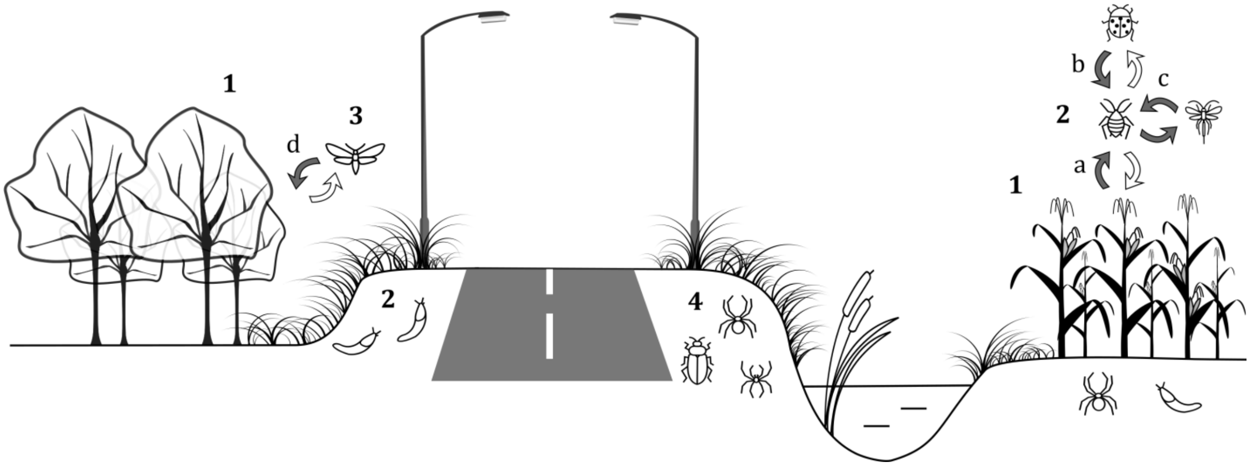

Fig. 2. Pathways through which artificial light at night (ALAN) may impact road-side habitats and agroecosystems. Direct effects of ALAN on (1) crops and trees, (2) pest species and their natural enemies, (3) nocturnal pollinators and (4) ground-dwelling arthropod communities have been described, as well as ALAN-mediated indirect trophic and behavioral effects (indicated by grey arrows), such as (a) bottom-up effects driven by plant growth and phenology, (b) top-down effects driven by predation, (c) host-parasite interactions and (d) plant-pollinator interactions. White arrows indicate potential effects of ALAN.

Supporting Information

S1 Table. Night sky brightness at zenith (relative to starlight, 0.25 cd $m^{-2} \equiv 1$) of the sites analyzed in Hallmann *et al.* (2017)**.** Sky brightness data from the model of Falchi *et al.* (2016).

Sampling site	Relative sky brightness
WAN2	7.46
SPE1	7.08
LAT2	6.93
SPE2	6.73
URD2	6.26
WAN1	6.24
LAT3	5.93
LAT1	5.93
URD1	5.88
PIM1	5.35
GEO1	4.94
NIE1	4.84
WAN3	4.43
WAN4	4.43
BOO1	4.06
HUK1	4.01
CAR1	3.96
SLL1	3.93
ORS1	3.80
KAN2	3.72
KAN1	3.72
ORB1	3.66
ORB2	3.66
RAH2	3.48
RAH1	3.43
BRA2	3.34
PLI1	3.32
PLI2	3.25
BRA1	3.18
BRA3	3.11
BRA4	3.08
SCH1	3.07
LEU1	2.64
LEU2	2.56
XAN1	2.53

LOO1	2.52
XAN2	2.46
SOL1	2.45
BIS6	2.36
WAH1	2.34
BIS7	2.31
BIS2	2.31
BIS5	2.30
WAH2	2.30
WAH3	2.30
WAH6	2.28
BIR1	2.27
BIS3	2.27
BIS8	2.27
BIS9	2.27
BIS10	2.27
BIS1	2.27
LIN2	2.25
SOL2	2.23
LIN1	2.16
WAH4	2.10
WAH5	2.10
POM1	1.50
GRI1	1.35
LAN1	1.30
BKL1	1.22
LIE1	1.20
LIE3	1.20