DIETARY CHANGES IN PREDATORS AND SCAVENGERS IN A NOCTURNALLY ILLUMINATED RIPARIAN ECOSYSTEM

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Abstract

Aquatic and terrestrial ecosystems are linked by fluxes of carbon and nutrients in riparian areas. Processes that alter these fluxes may therefore change the diet and composition of consumer communities. We used stable carbon isotope ($\delta^{13}C$) analyses to test whether the increased abundance of aquatic prey observed in a previous study led to a dietary shift in riparian consumers in areas illuminated by artificial light at night (ALAN). We measured the contribution of aquatic-derived carbon to diets in riparian arthropods in experimentally lit and unlit sites along an agricultural drainage ditch in northern Germany. The $\delta^{13}C$ signature of the spider *Pachygnatha clercki* (Tetragnathidae) was 0.7‰ lower in the ALAN-illuminated site in summer, indicating a greater assimilation of aquatic prey. Bayesian mixing models also supported higher intake of aquatic prey under ALAN in summer (34% vs. 21%). In contrast, isotopic signatures for *P. clercki* (0.3 ‰) and *Pardosa prativaga* (0.7‰) indicated a preference for terrestrial prey in the illuminated site in summer. Terrestrial prey intake increased in spring for *P. clercki* under ALAN (from 70% to 74%) and in spring and autumn for *P. prativaga* (from 68% to 77% and from 67% to 72%) and Opiliones (from 68% to 72%; 68% to 75%). This was despite most of the available prey (up to 80%) being aquatic in origin. We conclude that ALAN changed the diet of riparian secondary consumers by increasing the density of both aquatic and terrestrial prey. Dietary changes were species- and season-specific, indicating that the effects of ALAN may interact with phenology and feeding strategy. Because streetlights can occur in high density near freshwaters, ALAN may have widespread effects on aquatic-terrestrial ecosystem linkages.

Keywords: spiders, food web, ALAN, predator-prey, stable isotopes, SIAR, feeding strategies

Introduction

Complex trophic connections among organisms can extend across ecosystem boundaries (Polis et al. 1997). This is particularly evident in riparian zones where fluxes of nutrients and organic matter link adjacent aquatic and terrestrial ecosystems (Baxter et al. 2005). Such fluxes can cause a strong bottom-up effect for consumers in receiving habitats as resource subsidies (Polis et al. 1997, Nakano and Murakami 2001, Richardson et al. 2010). Quantifying these resource exchanges and measuring their effects on consumers is crucial for understanding the strength and the direction of the interaction of such coupled ecosystems (Marczak et al. 2007, Hoekman et al. 2011).

Abiotic and biotic factors both can influence spatial and temporal variation in the availability and use of aquatic subsidies in riparian zones (Sabo and Power 2002, Paetzold et al. 2005). The importance of aquatic subsidies generally decreases with distance from the stream edge. A recent review found the density of aquatic insects to be reduced by 50% after only 1.5 m from the water's edge, with a small portion of this subsidy (10%) moving much farther away (>500 m) (Muehlbauer et al. 2014). Seasonal variation in aquatic insect emergence results in varying contributions of aquatic subsidies to riparian spiders (Nakano and Murakami 2001, Kato et al. 2004, Paetzold et al. 2005). The natural dynamic of subsidy exchange between aquatic and terrestrial ecosystems is also influenced by anthropogenic environmental changes (reviewed in Schulz et al. 2015, Larsen et al. 2016). Increased water temperature can cause earlier reproduction and emergence in aquatic insects with faster larval development (Harper and Peckarsky 2006), thereby affecting the timing of aquatic subsidy availability in riparian areas. Faster larval development and smaller adult body size was observed in drying streams (Shama and Robinson 2006, Jannot et al. 2008, Mikolajewski et al. 2015). Removal of the natural riparian vegetation can decrease inland dispersal and flight activity of aquatic insects (Petersen et al. 1999). Gergs et al. (2014) also found that the introduction of the invasive amphipod *Dikerogammarus villosus* reduced emergence of chironomids.

Artificial light at night (ALAN) is a globally pervasive alteration of the landscape (Hölker et al. 2010, Kyba et al. 2017) that is particularly widespread near freshwaters (e.g., streams, lakes), where human populations are often concentrated (Kummu et al. 2011). The effect of ALAN on these ecosystems can be substantial, in particular on aquatic insects that live as larvae in the water and then emerge as flying adults (Manfrin et al. 2017). ALAN has been found to decrease mean body size and taxonomic richness (family-level) in emerging aquatic insects (Meyer and Sullivan 2013). ALAN also attracts post-emerging aquatic insects into adjacent riparian ecosystems, thereby disrupting their natural dispersal patterns (Horvath et al. 2009, Meyer and Sullivan 2013, Perkin et al. 2014). In some cases, ALAN has been found to increase aquatic insect mortality by exhaustion or increased predation (Eisenbeis 2006, Szaz et al. 2015). All of these ALAN-induced alterations have the potential to significantly alter the energy flows between aquatic and terrestrial ecosystems.

A recent study (Manfrin et al. 2017) compared experimentally lit traps with control (dark) traps and reported a 3-fold increase in aquatic insect emergence and an increased abundance of both aquatic (70- to 918-fold) and terrestrial flying insects

(34- to 81-fold) in an ALAN-illuminated area. There were significant changes in the abundance of thick-jawed spiders *P. clercki* (Tetragnathidae) and harvestmen (Opiliones) in ALAN-exposed areas (see also Davies et al. 2012). We hypothesise that the change in taxonomic composition observed in the community of riparian invertebrate consumers exposed to artificial light was due to ALAN-induced bottom-up effects, namely an increase in aquatic-derived resources available. We therefore expect higher relative consumption of aquatic insects by riparian invertebrate consumers in the illuminated field. To test this hypothesis, we used stable carbon isotope analyses to assess whether there was a shift in consumer stable isotope signature towards aquatic food sources. We tested whether there were dietary shifts in these two consumers, as well as in *P. prativaga* (Lycosidae) which was an abundant consumer in both sites. Bayesian mixing models of $\delta^{13}C$ values were used to quantitatively infer the relative contribution of aquatic (e.g. non-biting midges, mayflies) and terrestrial prey (e.g. aphids, leaf hoppers) to the consumer diet under natural (control) and altered (treatment) light regimes across three seasons in 2013.

Methods

Study area and experimental design

The field experiment was carried out using a large-scale experimental infrastructure fully described by Holzhauer et al. (2015). It is located in the Westhavelland Nature Park in northeastern Germany and within a 750-km² International Dark-Sky Reserve that is one of the least illuminated areas in Germany (International Dark Sky Association, IDA 2015) (Fig. 1b). In April 2012, two managed grassland areas of 2400 m^2 each with no prior exposure to ALAN were selected for an experiment to study the impact of artificial light on aquatic and terrestrial ecosystems (Fig. 1a, c). To our knowledge this is among the largest field experiment studying the ecological impact of ALAN (Holzhauer et al. 2015, Manfrin et al. 2017). The two sites were environmentally very similar in characteristics other than artificial light (Holzhauer et al. 2015, Manfrin et al. 2017). Monitoring started at the beginning of May 2012, prior to any illumination. Both sites were equipped with 3 parallel rows (3 m, 23 m, and 43 m away from the water) of 4 conventional 4.75 m high streetlights located 20 m apart (Fig. 1c) and with one 70-W high-pressure sodium lamp each (OSRAM VIALOX NAV-T Super 4Y). Maximum illuminance of the lit field was around 50 lux, minimum illuminance between two rows of street lamps was around 1 lux and minimum illuminance between two adjacent street lamps of the same row was around 10 lux (see Holzhauer et al. 2015 for further details about light distribution and spectral composition). Ecological monitoring started at the beginning of May 2012, prior to any illumination. From July 25 onward, one site (the treatment) was illuminated at night, i.e., one set of streetlights was switched on between civil twilight at dusk and dawn. The control (dark) site remained dark yet provided identical physical structure (see Holzhauer et al. 2015 for further details).

Study species

We studied four consumer species that exhibited significant differences in abundance between lit and dark traps (Manfrin et al.2017): the spider *P. clercki* (Tetragnathidae) and three long-legged harvestmen species (Opiliones). Opiliones species composition varied seasonally, thus we studied *Rilaena triangularis* in spring, *Nelima sempronii* and *Phalangium opilio* in summer and *N. sempronii* in autumn. For statistical analyses (see below), data from these three species of

Opiliones were combined. Adults of *P. clercki* are night-active visual hunters and do not use webs (Keer et al. 1989). This is an atypical feeding strategy for Tetragnathidae as most species build webs and are sit-and-wait predators. *P. prativaga* (Lycosidae) did not exhibit any difference in abundance due to ALAN (Manfrin et al. 2017), but was included in the present study because it is a dominant species at the study sites. *P. prativaga* is a day-active spider that catches prey without using a web (Kuusk and Ekbom 2010). Opiliones are mainly active at night (Williams 1962) and were almost exclusively caught at night in our experiment (Manfrin et al. 2017). Opiliones either ambush live prey or feed on dead animals. They do not employ webs (Pinto-da-Rocha et al. 2007).

Sample collection

Emerging adult aquatic insects (predominantly Ephemeroptera, Trichoptera and Chironomidae) were collected using four emergence traps per site, one placed on the water surface in front of each street light (Fig.1c, d). Sampling of emerging insects occurred monthly from May to October 2013 except in July when sampling occurred weekly because emergence rates were very high. At each time, sampling was continuous for 128 - 192 hours. Aquatic and terrestrial flying insects (predominantly Ephemeroptera, Lepidoptera and Coleoptera) were collected using 12 air eclector traps per site consisting of two transparent plexiglas panels. Traps were placed 0.5 m below each streetlight (Fig.1c, d). Ground-dwelling arthropods were collected using 24 pitfall traps per site, positioned between and under the streetlamps at different distances from the ditch (Fig.1c, d). Air eclector and pitfall trap sampling occurred bi-weekly from May to October 2013. Sampling always occurred on rainless nights within one night of each half-moon phase (first and third quarter, s. a. Holzhauer et al. 2015). All samples were stored in 70% not denaturated ethanol for a period no longer than 6 months (Sarakinos et al. 2002). All animals were sorted, counted and identified to the lowest taxonomic level possible under a binocular microscope and using taxonomical literature (Roberts 1995, Schaefer 2010, Stresemann 2011).

Stable isotope analysis

Stable isotopes have been widely used to quantify carbon fluxes within and between ecosystems and to better understand riparian food web interactions. A difference in the uptake of CO_2 in water and air (Rounick and Winterbourn 1986, Peterson and Fry 1987) makes the stable carbon isotope signal differ between aquatic and terrestrial primary producers. Organisms that consume different proportions of aquatic- and terrestrial-derived sources can therefore exhibit different $\delta^{13}C$ values, as the carbon isotopes change (fractionate) little between prey and predator (e.g. Kato et al. 2004). Akamatsu et al. (2004), Baxter et al. (2005) and Paetzold et al. (2005) all provide examples of how stable isotope data indicate that many riparian consumers rely on aquatic subsidies in the form of emergent insects. In fact, isotopes have indicated that aquatic-derived sources can constitute up to 50% of the carbon in the diet of Tetragnathidae orb-weaver spiders inhabiting riparian canopies (Kelly et al. 2015) and temperate forests (Krell et al. 2015), while potentially approaching 100% for individuals inhabiting meadows along riparian areas in temperate regions (Krell et al. 2015) and along desert streams (Sanzone et al. 2003).

We analysed a total of 294 consumer individuals (*P. clercki,* n = 116*; P. prativaga,* n = 120*;* and Opiliones, n = 57) and 544 prey individuals (aquatic, n = 165;

terrestrial, n = 379) for $\delta^{13}C$. We inspected at least 9 individuals of each consumer and 4 individuals of each potential prey taxon (10 taxa were considered potential prey; Supplementary material Appendix 1 Table A1) for each site (control, treatment) and season (spring, summer, autumn). Potential prey was selected based on direct field observations and literature (Nyffeler and Benz 1988, Pinto-da-Rocha et al. 2007). Selected samples were washed with distilled water in the laboratory, oven-dried at 70°C for 4 days, and ground to a fine powder using a milling machine (Pulveristette 23; Fritsch GmbH, Germany). An aliquot of each sample (0.5 - 2 mg) was weighed on a microbalance (Sartorius, Germany) and loaded into tin capsules (Costech Analytical Technologies, Valencia, CA) for stable isotope analysis. Lipids were not extracted from the samples. A preliminary comparison performed on five different taxa (Supplementary material Appendix 1 Fig. A1) found no difference between $\delta^{13}C$ values of fat- extracted and control samples (t-test, $p > 0.05$) (Supplementary material Appendix 1 Fig. A1 for fat extraction methodology).

We used an elemental analyser (Flash EA; Thermo Finnigan, Bremen, Germany) connected via a continuous flow system to an isotope ratio mass spectrometer (Delta V Advantage, Thermo Finnigan, Bremen, Germany) to analyse the $\delta^{13}C$ of CO_2 gas obtained after sample combustion. The sample isotope ratios were compared with international standards (USGS-24) within each run (Gonfiantini et al. 1995, Voigt et al. 2003). The notation used (δ) expresses sample carbon isotope ratios as parts per thousand (‰) differences to international standards of Vienna Pee Dee Belemnite (Slater et al. 2001). The instrument precision assessed as the standard deviation of internal standards within each run was always better than 0.1‰.

Statistical analyses

Because our aim was to test whether consumer diet shifted as a result of changing relative abundances of aquatic and terrestrial prey, prey taxa were pooled and classified as aquatic or terrestrial in origin. Pooling multiple source species into biologically meaningful groups is the recommended practise when within-group isotopic variation is smaller than between-group variation, providing more constrained and less diffuse solutions of models using isotope values (Phillips et al. 2005, Phillips et al. 2014). We also corrected consumer $\delta^{13}C$ for trophic fractionation by 1 ‰ (DeNiro and Epstein 1978, Akamatsu et al. 2004).

Differences in prey and consumer $\delta^{13}C$ were analysed with linear mixed-effect (LME) models using the lme4 package (Bates et al. 2007) for R (R Core Team 2015). Fixed factors for the prey model were “habitat” (aquatic or terrestrial), “site” (control or treatment), “season” (spring: May – June; summer: July – August; autumn: September – October) and their interactions. Fixed factors for the consumer model were “taxa” (i.e. *P. clercki*, *P. prativaga*, Opiliones), “site”, “season” and their interactions. As post-hoc pairwise comparison, another LME model was used for each of the three consumer taxa within each season, in which “site” was a unique fixed factor. All LME models considered “trap” nested in “site” as random factors to account for multiple observations. Each LME model was compared with a reduced model (i.e. without the fixed factors) using a likelihood ratio test (Pinheiro and Bates 1995). The distribution of residuals was assessed using Wilk-Shapiro tests (Shapiro and Wilk 1965) and qq-plots (Wilk and Gnanadesikan 1968). To control for inflated false discovery rates, we used Benjamini-Hochberg corrected α-values (Waite and Campbell 2006).

In addition to LME models testing for significance, we used model-based estimates of the relative contribution of aquatic and terrestrial food sources to consumer diets using the mixing model package SIAR (Parnell and Jackson 2013) for R. SIAR uses Bayesian inference to calculate the most likely set of dietary proportional contributions given the isotopic ratios in a set of possible food sources and consumers (Parnell et al. 2010). This generates potential dietary solutions as Dirichlet probability distributions with mean, mode, and levels of uncertainty (95% credibility intervals). We ran 1 million iterations, thinned by 300 and with an initial discard of the first 40,000 iterations. Control and treatment sites were compared across the three seasons in 2013.

Results

$\delta^{13}C$ was significantly lower in aquatic prey (-34.0 ± 2.2‰) compared to terrestrial prey (-26.5 ± 1.24‰) (Table 1; Fig. 2a, b; Supplementary material Appendix 1 Table A1). There were no significant differences in prey $\delta^{13}C$ mean values between control and lit sites (Fig. 2a, b; Table 1). In each consumer taxon, mean $\delta^{13}C$ was more similar to that of terrestrial prey then aquatic prey in both control and lit sites (Fig. 3a, b, c; Supplementary material Appendix 1 Table A1). Nonetheless, consumer $\delta^{13}C$ values varied between sites and among seasons (Table 1). The effect of treatment differed across taxa (site x taxa interaction; Table 1; Fig. 3a, b, c) and among seasons (site x season interaction; Table 1; Fig. 3a, b, c). In *P. clercki*, $\delta^{13}C$ was 0.3 ‰ higher at the lit site than at the control site in spring ($F_{1, 40} = 5.04$; p =0.02) but was 0.7 ‰ lower at the lit site in summer ($F_{1, 36} = 8.20$; p =0.007) (Fig. 3a). In *P.*

prativaga, δ^{13}C was 0.7‰ higher at the lit site in spring ($F_{1,40} = 16.7$; $p < 0.001$) (Fig. 3b). In Opiliones, there were no differences among sites and seasons (Fig. 3c).

Bayesian mixing models (SIAR) indicated that the contribution of terrestrial-derived carbon to consumer diet in both control and treatment site ranged from 67-80% (aquatic-derived carbon ranged from 20-32% in the control site and 20-34% in the treatment site) with variation occurring among taxa and seasons (see Fig. 4a, b, c; Supplementary material Appendix 1 Table A2). In summer, *P. clercki* at the lit site exhibited an increase in aquatic prey intake compared to the control site (from 21% to 34%) (Fig. 4a; Supplementary material Appendix 1 Table A2), whereas the contribution of aquatic prey to the diet of *P. prativaga* and Opiliones (*N. sempronii* and *P. opilio* in summer*)* was similar at both sites (Fig. 4b, c; Supplementary material Appendix 1 Table A2). In spring, Bayesian mixing models showed increased terrestrial prey intake at the lit site in *P. clerckii* (from 70% to 74%), Opiliones (from 68% to 72%) and *P. prativaga* (from 68% to 77%) (Fig. 4a, b, c; Supplementary material Appendix 1 Table A2). In autumn, mixing models also indicated increased terrestrial prey intake at the lit site in *P. prativaga* (from 67% to 72%) and Opiliones (from 68% to 75%) (Fig. 4b, c; Supplementary material Appendix 1 Table A2).

Discussion

Aquatic subsidies are an important component of terrestrial ecosystems (Collier et al. 2002, Sabo and Power 2002, Sanzone et al. 2003, Kato et al. 2003, Paetzold et al. 2011). This study is among the first *in situ* experiments to test the effects of ALAN on aquatic subsidies. The effort and cost associated with such large-scale experiments often limits the assessment of un-replicated large-scale perturbations. However, responses observed in our large-scale natural scenario were preferred over small-scale laboratory experiments because we felt that the complexity of the research question could not be adequately addressed using laboratory experiments (Carpenter 1990, Carpenter 1996, Skelly and Kiesecker 2001, Davies and Gray 2015, Barley and Meeuwig 2017). All the statistical results were obtained using analytical approaches that accounted for potential spatial and temporal relation (i.e. random effects). Bayesian statistic was used as non-frequentist analysis (Oksanen et al. 2001). These considerations, along with the detailed measurements of both biotic and abiotic components collected before and after the start of the experiment (see Holzauer et al. 2015), allows us to ascribe the observed ecological changes to ALAN with confidence.

Terrestrial and aquatic prey species differed in $\delta^{13}C$, allowing us to differentiate those two source categories in the diet of our consumers, as expected (Kato et al. 2004). We observed no direct effect of ALAN on $\delta^{13}C$ values of either aquatic or terrestrial prey, suggesting that ALAN did not affect their isotopic composition. We therefore conclude that changes in $\delta^{13}C$ observed in the consumers in the treatment site resulted from changes in prey consumption.

The proportion of aquatic prey (20 - 33%) in the diet of the riparian consumers at the control site indicates that aquatic insects were an important food source. These proportions are comparable to those observed in riparian canopies and forests in northern temperate regions (Briers et al. 2005, Krell et al. 2015), but lower than those observed in riparian areas of desert streams (Sanzone et al. 2003). The degree to which consumers respond to aquatic subsidies depends on the ratio of aquatic to terrestrial resources in the recipient habitat (Marczak et al. 2007). This ratio can strongly differ among habitats. For instance, stronger gradients in productivity exist between aquatic and riparian zones in desert areas compared to temperate zones, with temperate riparian zones generally being more productive. In desert areas, the aquatic insect contribution for active-hunting spiders (i.e. not using webs) can reach 70% while in temperate zones, as in our case, aquatic insects can contribute from 15 to 50 % (Sanzone et al. 2003, Briers et al. 2005, Krell et al. 2015). In our control site, the spring and autumn values for the proportion of aquatic prey (30-33%) were higher than in summer (20-24%). This pattern indicates a seasonal change in consumer diet that may be explained by the seasonal availability of aquatic (emerging and flying) and terrestrial prey (flying and ground-dwelling) caught during the experiment at the control site (Supplementary material Appendix 1 Table A3). The relationship found between prey availability and prey consumption from generalist predators was similar to what has been found in other studies (Kato et al. 2004, Paetzold et al. 2005, 2006). A seasonal pulse of aquatic subsidies is particularly common at northern temperate latitudes. In such regions, water temperature and photoperiod play an important role in regulating aquatic insect emergence and are seasonally variable (Corbet 1964, Brittain 1982, Paezold et al. 2005).

When exposed to ALAN in our study, *P. clercki* increased its assimilation of aquatic-derived carbon in summer according to both the isotopic signature and the Bayesian analysis of the diet. We propose that this shift in the spider diet was due to the large number of aquatic insects attracted to the light sources during the summer season. The number of aquatic insects caught at the treatment site at this time was approximately 25 times higher than in spring and 130 times higher than in autumn, and 87% of all collected insects (8000 individuals) were aquatic, compared to 15% (140 individuals) caught at the control site (Manfrin et al. 2017, Supplementary material Appendix 1 Table A3). *P. clercki* is primarily a night-active spider, but extended its activity into the day when exposed to ALAN (Manfrin et al. 2017). It may be that *P. clercki* consumed exhausted or dead aquatic insects lying on the ground after flying around the lamps during the night. Although spiders rarely feed on dead prey, von Berg et al. (2012) found that 38% of the specimens of *Pachygnatha degeeri* opportunistically scavenged when dead prey were available. Alternatively, the illumination treatment might have exhausted the local terrestrial community (Eisenbeis 2006) thereby inevitably increasing the relative contribution of the aquatic subsidy, even if this in itself remains the same. Given the large number of aquatic insects in the traps, and no decrease in the number of terrestrial insects in the traps over the years (data not shown) we believe this to be a less likely explanation.

The increased assimilation of aquatic-derived carbon found in *P. clercki* in summer was not observed in *P. prativaga* and Opiliones during the same period. Although the terrestrial prey did not increase as much as the aquatic prey did, they showed a marked increase in number in the lit traps (Supplementary material Appendix 1 Table A3). These taxa might simply have maintained their preference for larger-sized terrestrial prey over the numerous but smaller aquatic prey (Briers et al. 2005). In contrast to *P. clercki*, *P. prativaga* and Opiliones did not exploit the additional extra hours of hunting-activity during the day (Manfrin et al. 2017), and therefore may not have utilized dead insects on the ground from the night before. Alternatively, the carbon derived from aquatic prey in summer, might not have been integrated into consumer tissues. These taxa may have allocated most of the food intake in this period to reproduction as metabolic carbon instead of structural carbon for somatic growth (Jespersen and Toft 2003, Bragg and Holmberg 2009). The isotopic signatures and analysis of the diet composition suggest an increased terrestrial prey intake by *P. clercki* in spring and in *P. prativaga* and Opiliones (*R. triangularis* and *N. sempronii*) in spring and autumn when exposed to ALAN. The aquatic insects collected in the eclector traps (predominantly Chironomidae and *Cloeon* sp.) were smaller than many terrestrial taxa available as prey. Also, ALAN has been found to decrease mean body size and taxonomic richness (family-level) in emerging aquatic insects (Meyer and Sullivan 2013) leading to a community of aquatic prey that is dominated by even smaller individuals compared to natural conditions. This difference in biomass might explain why consumers increased the terrestrial prey intake under artificial illumination, with an overall lower number of available prey (in both spring and autumn) than in summer or with similar availability between aquatic and terrestrial prey in autumn (Manfrin et al. 2017, Supplementary material Appendix 1 Table A3). Dietary changes were species-specific and seasonably variable, indicating that the effects of artificial might strongly depend on the phenology of the subsidy sources and on both the phenology and feeding strategies of the consumers.

Our results provide evidence that ALAN can influence the dietary composition of secondary consumers increasing their aquatic carbon assimilation as result of the increased flux of aquatic insects into riparian areas. However, such dietary changes were not consistent, varying among taxa and seasons. This was probably due to the relative high availability of terrestrial insects (highly productive) in the riparian zones of the study area. Because the effects of trophic subsidies on recipient ecosystems are usually stronger when the receiving system has low levels of resources (Marczak et al. 2007), in urban and semi-urban areas, where the pool of potential terrestrial prey in riparian areas is poor, the effects of ALAN on locally productive water bodies might have stronger effects.

A shift to more reliance on an aquatic- or terrestrial-derived diet can affect the flow of energy through the food-web. It is well known that spiders are important biological control agents (Riechert et al. 1984, Hodge 1999, Marc et al. 1999, Henschel et al. 2001). Dietary shifts observed under ALAN, arising from a temporary disproportionate availability of a specific prey type (e.g. aquatic prey), might release predatory pressure from species causing a displacement of predator-prey dynamics. In the case of semi-urban and agricultural areas, this might have consequences for the natural control of invertebrate pest populations (e.g. Aphidae, Auchenorrhyncha) by predation (Dixon 2000, Hassell 1978, Polis and Strong 1996).

We assessed ALAN in the field and specifically in the context of an aquatic-terrestrial ecotone. The experimental erection of street lights in a previously ALAN-naïve area allowed us (1) to disentangle the effects of ALAN from other aspects of urbanization such as pollution, noise, and habitat alteration; and (2) to minimize the effects of potential long-term adaptations that may have already occurred in areas that have been lit for many generations. No isotope data were available from the period prior to illumination, thus we could not test whether the difference in diet composition existed prior to the treatment. Manfrin et al. (2017) observed no differences in consumer community composition and prey availability between the two sites prior to illumination. We therefore assumed that invertebrate consumers had the same diet composition.

Our findings raise a number of new research questions that can now be studied mechanistically at smaller scales. We used high-pressure sodium lamps, which are considered to be relatively 'insect friendly' (Eisenbeis et al. 2006). The current increase in illumination and the global shift to the use of LED lamps with an emission peak in blue (Kyba et al. 2017) are both expected to increase the impact of

ALAN given the sensitivity of nocturnal invertebrates to short wavelength light (van Langevelde 2011, van Grunsven et al 2014, Pawson and Bader 2014). Our earlier work found that high-pressure sodium lights resulted in a shift in the biomass exchange between adjacent ecosystems (Manfrin et al. 2017), and here we observed a change in the diet composition of riparian consumers and conclude that is was due to this shift. This might have implications for ecosystem functioning and suggest we considering the potential ecological impacts of ALAN in lighting policy and landscape planning.

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Figures and Tables

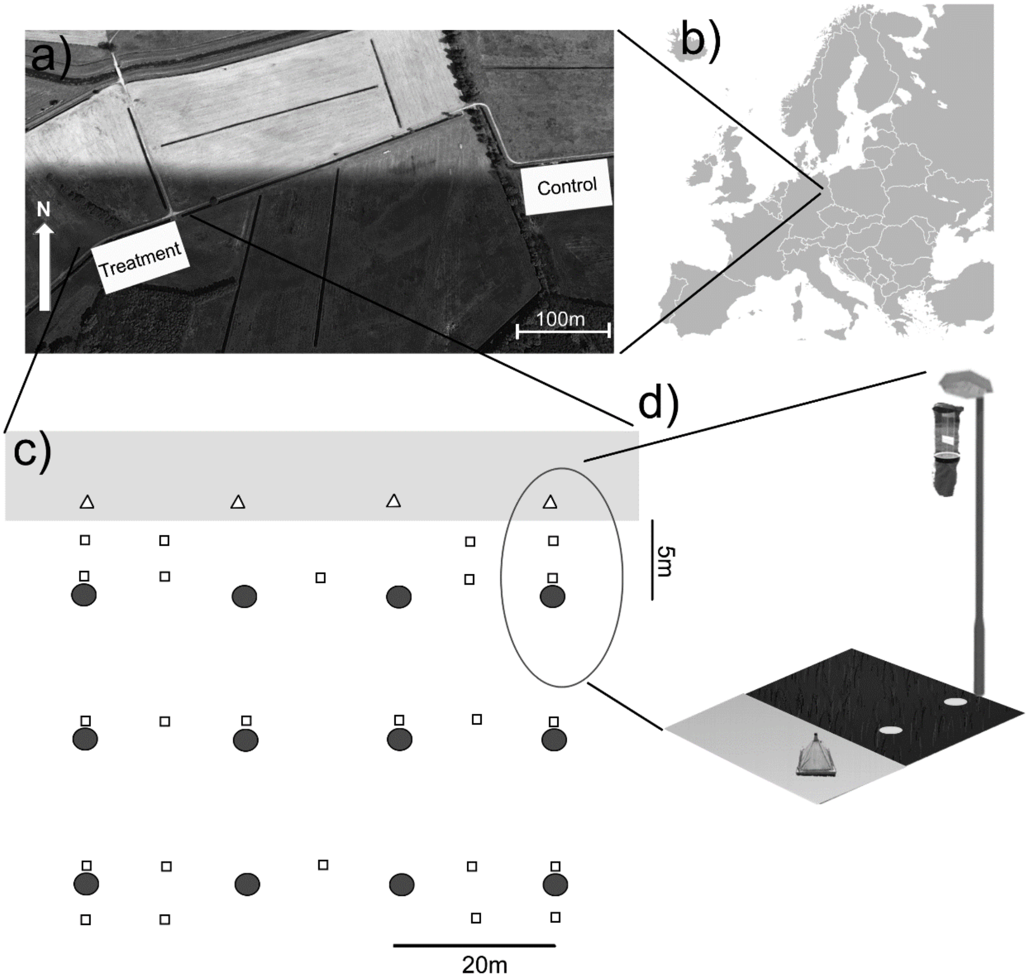

Figure 1. Study area in the Westhavelland (Brandenburg; 52° 68’ 53’’ N, 12° 44’ 32’’ E) depicting treatment and control sites (each 60 x 40 m) located along an agricultural drainage ditch (a, b). The lower panels (c, d) depict the treatment site with streetlamps and sampling traps. Floating pyramidal emergence traps (triangles, *n* = 4) were placed adjacent to a lamp on the water surface of the drainage ditch. Air eclector traps were mounted below each lamp (grey circles, *n* = 12). Pitfall traps (quadrats, *n* = 24) were placed on the ground in multiple locations. The structural design of the control site was identical to the treatment site, yet streetlights were not switched on. Map data by Google Earth Pro (2011) (a) and Wiki-vr (https://en.wikipedia.org/wiki/File:Europe_blank_map.png) (b).

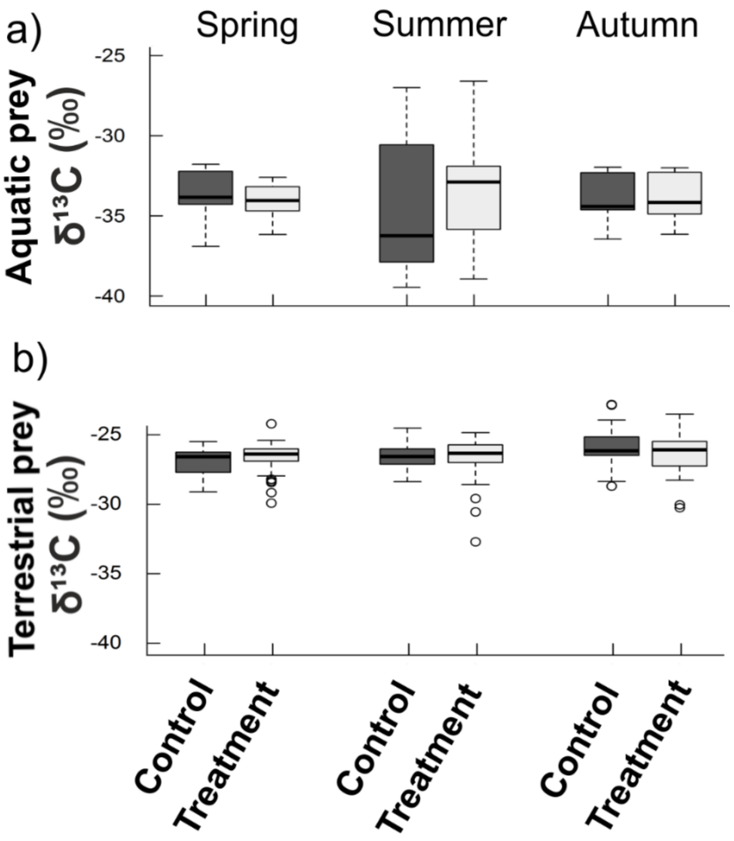

Figure 2. Comparison δ^{13}C values between control and treatment sites is depicted for aquatic (a) and terrestrial (b) prey over the three seasons in 2013. Box plots depict the 25, 50 and 75 percentiles, and whiskers the highest and lowest values excluding outliers.

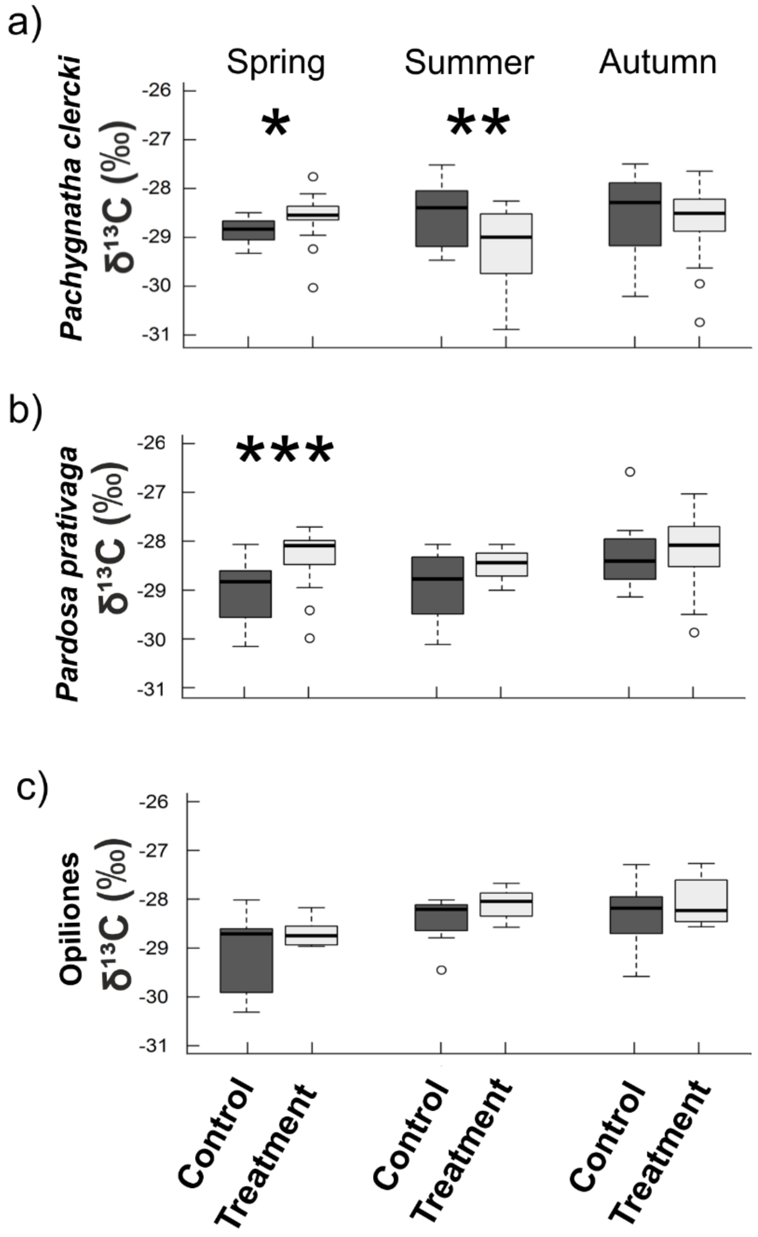

Figure 3. Comparison δ^{13}C values between control and treatment sites is depicted for consumer taxa (a, b, c) over the three seasons in 2013. Box plots depict the 25, 50 and 75 percentiles, and whiskers the highest and lowest values excluding outliers. In case of significant LME interaction, asterisks are used to indicate significant difference in the pairwise comparisons (*** = <0.001; ** = <0.01). A lower value indicates a larger proportion of aquatic prey in the diet.

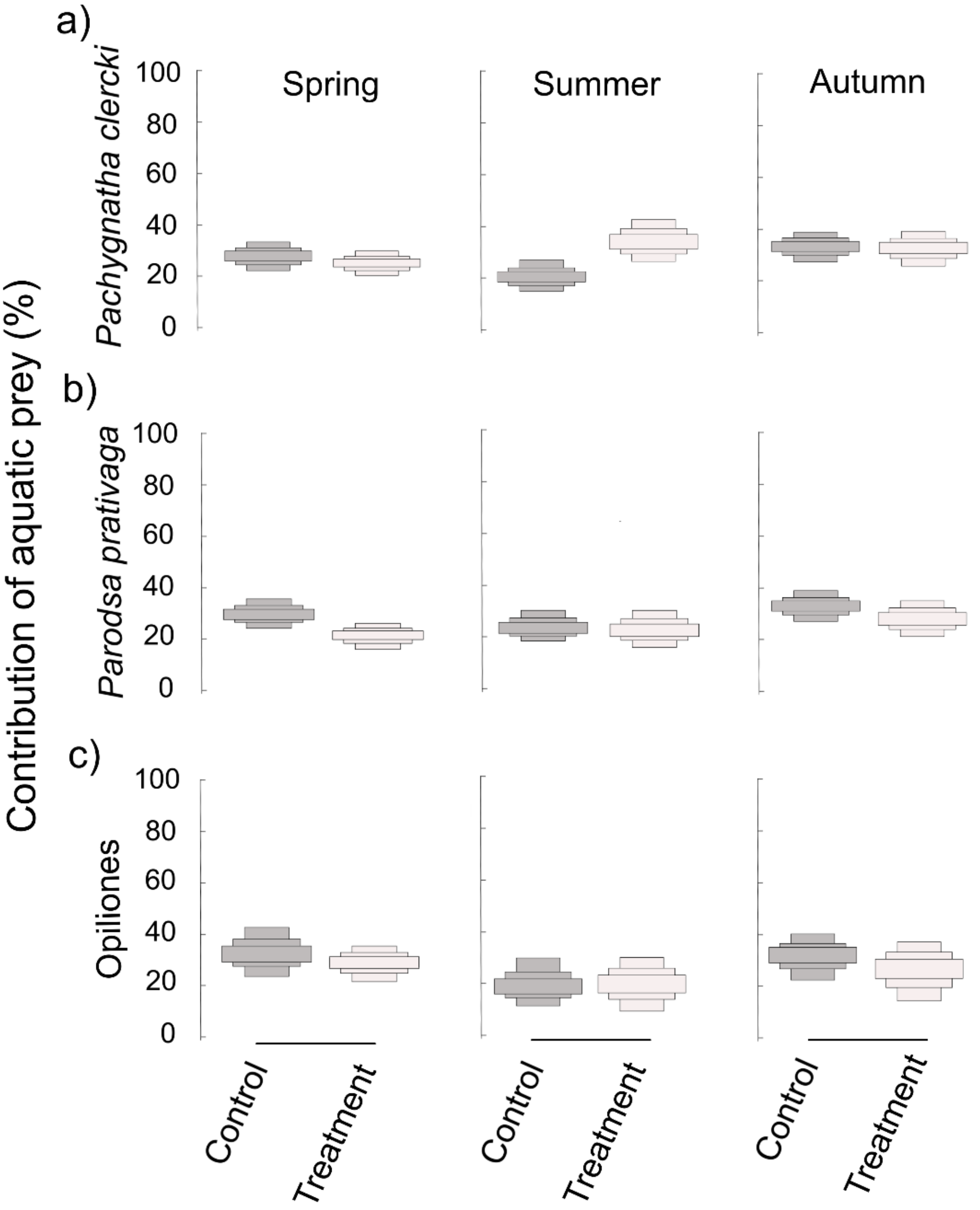

Figure 4. Comparison of relative contribution (%) of aquatic prey to the diets of the consumer taxa (a, b, c) based on Bayesian isotope mixing models (SIAR) on $\delta^{13}C$ values. The plots show 95% (middle rectangle), 75% and 25% (external rectangles) credibility intervals. Data are shown for control and treatment site across the three seasons in 2013.

Table 1. Results of linear mixed-effect models (LME) for prey and consumers using δ13C as a dependent variable. Independent variables for food sources and consumers are shown in the table. Asterisks are used to indicate significant main effect (*** = <0.001; ** = <0.01; * = <0.05).

Model	X^2	Factors	*F*- statistic
Prey	351.35***	Site	$F_{1,29}$=0.40
		Habitat	$F_{1,110}$=754.22***
		Season	$F_{2,531}$=5.78**
		Site x Habitat	$F_{1,110}$=0.34
		Site x Season	$F_{2,531}$=0.05
		Habitat x Season	$F_{2,534}$=1.54
		Site x Habitat x Season	$F_{2,534}$=1.94
Consumers	63.19***	Site	$F_{1,293}$=7.86**
		Taxa	$F_{2,293}$=4.65*
		Season	$F_{2,293}$=8.95***
		Site x Taxa	$F_{2,293}$=8.04***
		Site x Season	$F_{2,293}$=2.73*
		Taxa x Season	$F_{4,293}$=2.95*
		Site x Taxa x Season	$F_{4,293}$=1.48

Appendix 1

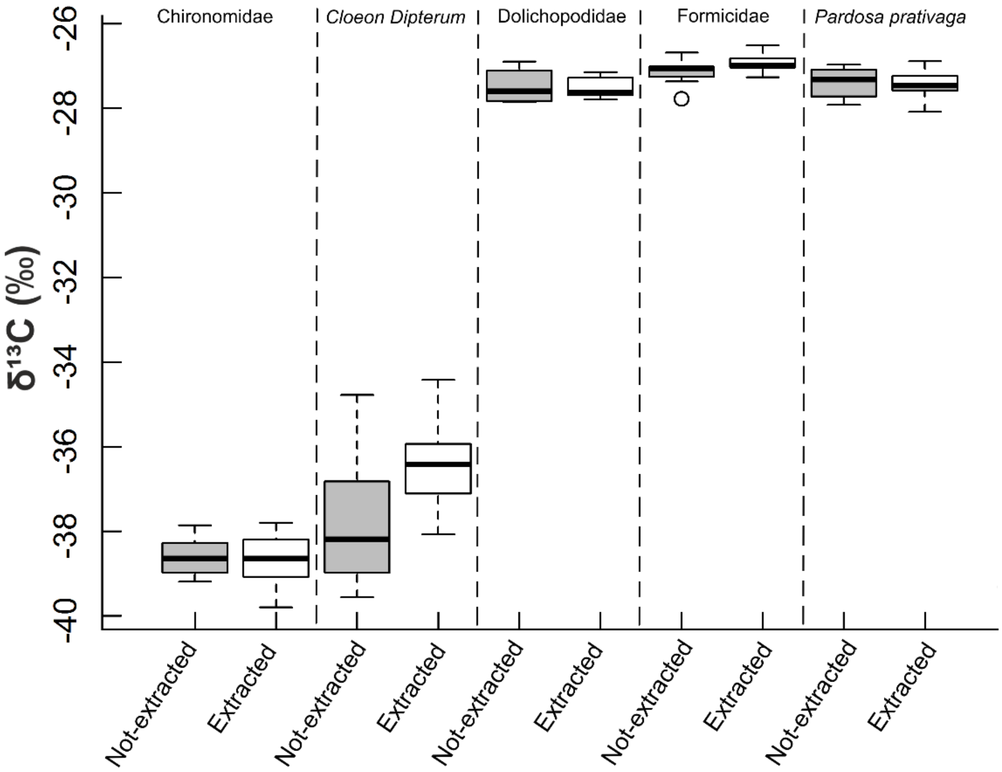

Figure A1. Comparison showing no significant difference in $\delta^{13}C$ values for samples in which lipids were extracted with samples in which *were not (t-test >0.05).* 10 individuals for each of the 5 selected taxa and condition were analysed. Lipids were removed by Soxhlet extraction using a chloroform/methanol 2:1 solution and a Soxtherm Type SE406 (C. Gerhardt GmbH & Co. KG, Königswinter, Germany). Box plots depict the 25, 50 and 75 percentiles, and whiskers the greatest and least values excluding outliers.

Table A1. Stable carbon ($\delta^{13}C$) isotope ratios (Mean ± SD) and number of samples analysed for each source and consumer taxon in control and treatment site and across the three seasons in 2013.

Group	Species	Season	Site	N	$\delta^{13}C$ (‰) Mean ± SD
Aquatic prey	Chironomidae	Spring	Control	4	-32.56 ± 1.05
			Treatment	4	-35.50 ± 0.62
	Cloeon dipterum		Control	10	-33.99 ± 1.24
			Treatment	20	-33.93 ± 0.97
	Chironomidae	Summer	Control	10	-36.82 ± 3.10
			Treatment	7	-37.55 ± 1.06
	Hydrophilidae		Control	5	-30.15 ± 3.58
			Treatment	20	-31.80 ± 1.57
	Cloeon dipterum		Control	0	_
			Treatment	12	-34.91 ± 2.13
	Chironomidae	Autumn	Control	5	-35.34 ± 1.40
			Treatment	9	-34.92 ± 1.22
	Cloeon dipterum		Control	10	-34.67 ± 0.19
			Treatment	10	-34.80 ± 0.36
	Erythromma najas		Control	10	-34.42 ± 0.23
			Treatment	10	-34.20 ± 0.22
	Limnephilus binotatus		Control	10	-32.14 ± 0.11
			Treatment	10	-32.11 ± 0.05
Terrestrial prey	Auchenorrhyncha	Spring	Control	5	-27.83 ± 1.20
			Treatment	10	-27.45 ± 1.37
	Chrysomelidae		Control	6	-28.51 ± 0.16
			Treatment	8	-27.90 ± 0.62
	Formicidae		Control	10	-26.55 ± 0.39
			Treatment	20	-26.19 ± 0.54
	Linyphiidae		Control	12	-26.36 ± 0.42
			Treatment	18	-26.46 ± 0.54
	Auchenorrhyncha	Summer	Control	20	-26.85 ± 0.92
			Treatment	20	-26.37 ± 1.88
	Formicidae		Control	15	-26.29 ± 0.57

			Treatment	20	-26.29 ± 0.62
	Linyphiidae		Control	15	-26.86 ± 0.66
			Treatment	20	-26.22 ± 0.59
	Stenorrhyncha		Control	6	-26.56 ± 0.91
			Treatment	5	-27.13 ± 1.19
	Auchenorrhyncha	Autumn	Control	20	-26.26 ± 1.62
			Treatment	20	-26.92 ± 1.77
	Formicidae		Control	20	-26.53 ± 0.48
			Treatment	20	-26.28 ± 0.65
	Linyphiidae		Control	20	-26.14 ± 0.72
			Treatment	20	-25.86 ± 0.48
	Stenorrhyncha		Control	20	-25.26 ± 1.37
			Treatment	20	-25.29 ± 2.05
Consumers	*Pachygnatha clercki*	Spring	Control	20	-28.89 ± 0.26
			Treatment	20	-28.62 ± 0.46
		Summer	Control	18	-28.54 ± 0.64
			Treatment	18	-29.19 ± 0.75
		Autumn	Control	20	-28.59 ± 0.80
			Treatment	20	-28.69 ± 0.75
	Pardosa prativaga	Spring	Control	20	-29.04 ± 0.52
			Treatment	20	-28.36 ± 0.53
		Summer	Control	20	-28.91 ± 0.58
			Treatment	20	-28.42 ± 0.43
		Autumn	Control	20	-28.50 ± 0.80
			Treatment	20	-28.24 ± 0.71
	Rilaena triangularis	Spring	Control	10	-29.09 ± 0.82
			Treatment	10	-28.72 ± 0.24
	Nelima sempronii/ Phalangium opilio	Summer	Control	9	-28.47 ± 0.44
			Treatment	10	-28.12 ± 0.29
	Nelima sempronii	Autumn	Control	10	-28.36 ± 0.63
			Treatment	8	-28.06 ± 0.47

Table A2. Bayesian mixing model statistics obtained from SIAR for the relative contribution of aquatic and terrestrial food sources to the diet of the analysed consumers for control and treatment site across the three seasons in 2013. Contribution values are shown as mode and mean and 95% credibility intervals are given.

Consumers	Season	Site	Prey	min (95%)	Mode	Mean	Max (95%)
Pachygnatha clercki	Spring	Control	Terr	0.66	0.70	0.71	0.77
			Aqua	0.23	0.30	0.29	0.34
		Treatment	Terr	0.69	0.74	0.74	0.79
			Aqua	0.21	0.26	0.26	0.31
	Summer	Control	Terr	0.73	0.79	0.79	0.84
			Aqua	0.16	0.21	0.21	0.27
		Treatment	Terr	0.57	0.67	0.65	0.73
			Aqua	0.27	0.34	0.35	0.43
	Autumn	Control	Terr	0.61	0.67	0.66	0.72
			Aqua	0.28	0.33	0.34	0.39
		Treatment	Terr	0.61	0.67	0.67	0.74
			Aqua	0.26	0.33	0.33	0.39
Pardosa prativaga	Spring	Control	Terr	0.63	0.68	0.69	0.75
			Aqua	0.25	0.32	0.31	0.37
		Treatment	Terr	0.72	0.77	0.77	0.82
			Aqua	0.18	0.23	0.23	0.28
	Summer	Control	Terr	0.69	0.76	0.75	0.81
			Aqua	0.19	0.24	0.25	0.31
		Treatment	Terr	0.69	0.77	0.76	0.83
			Aqua	0.17	0.23	0.24	0.31
	Autumn	Control	Terr	0.62	0.67	0.68	0.73
			Aqua	0.27	0.33	0.32	0.38
		Treatment	Terr	0.66	0.72	0.73	0.79
			Aqua	0.21	0.28	0.27	0.34
Opiliones	Spring	Control	Terr	0.58	0.68	0.68	0.77
			Aqua	0.23	0.32	0.32	0.42
		Treatment	Terr	0.65	0.72	0.72	0.79
			Aqua	0.21	0.28	0.28	0.35
	Summer	Control	Terr	0.70	0.80	0.79	0.88

		Aqua	0.12	0.20	0.21	0.30
	Treatment	Terr	0.69	0.80	0.80	0.90
		Aqua	0.10	0.20	0.20	0.31
Autumn	Control	Terr	0.61	0.68	0.69	0.77
		Aqua	0.23	0.32	0.31	0.39
	Treatment	Terr	0.63	0.75	0.74	0.86
		Aqua	0.14	0.25	0.26	0.37

Table A3. Number of individuals caught per hour of trap operation (CPUE; catch per unit effort) for aquatic and terrestrial adult flying insects and proportion (% of CPUE) of aquatic compared to terrestrial insects collected in the air eclector traps at the control and treatment site during the three seasons in 2013. Vales are shown as means and standard deviations.

Sites	Season	CPUE aquatic	CPUE terrestrial	% aquatic
Control	Spring	0.44 ± 0.30	0.12 ± 0.16	72 ± 31
	Summer	0.87 ± 0.94	0.75 ± 0.73	49 ± 33
	Fall	0.09 ± 0.12	0.17 ± 0.09	26 ± 26
Treatment	Spring	10.30 ± 4.91	1.73 ± 1.29	85 ± 11
	Summer	281.69 ± 443.92	35.26 ± 44.45	64 ± 27
	Fall	1.24 ± 0.77	0.73 ± 0.29	60 ± 15