Original research article

Cross-ecosystem effects of light pollution and invasive signal crayfish on riparian spiders

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ABSTRACT

Ecosystems face multiple abiotic and biotic stressors that interact and extend beyond ecosystem boundaries. Both artificial light at night (ALAN) and invasive species are major threats to freshwater biodiversity in Europe. We used a riparian stream mesocosm facility, with 16 replicated units each containing an artificial flume and adjacent terrestrial habitat, to investigate the effects of ALAN, the invasive signal crayfish *Pacifastacus leniusculus* and their interaction. We specifically addressed their impact on aquatic insect emergence and the potential bottom-up control of riparian spiders. As expected, crayfish reduced insect emergence by 35 % after one-week, while ALAN had no significant effect. Moreover, spider numbers, particularly of riparian Tetragnathidae *Pachygnatha degeeri* and *Tetragnatha extensa*, correlated positively with insect emergence, indicating indirect negative effects of the crayfish. During the first week of our experiment, spider numbers increased by 22 % in pitfall traps exposed to ALAN, but decreased by 25 % in suction samples. This difference is likely driven by differences in species composition between the two sampling methods. All in all, the direction and strength of crayfish and ALAN effects were taxon- and time-dependent. This study provides evidence that the impact of signal crayfish can extend beyond aquatic systems and suggests that the effects of crayfish invasion and ALAN are largely independent.

1. Introduction

Global change drivers such as landscape alterations, invasive species and global warming typically co-occur (Fischer and Lindenmayer, 2007). Thus, ecosystems are increasingly exposed to multiple stressors, which can result in synergistic, additive or antagonistic effects (Ormerod et al., 2010; Birk et al., 2020). Such interactive effects of multiple stressors greatly complicate

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predictions of their joint impact, and adaptive ecosystem management. From a meta-ecosystem perspective, effects of multiple stressors in source ecosystems may cascade into the recipient food webs causing bottom-up and top-down effects (Osakpolor et al., 2021). For example, stressors can alter the quantity and quality of fluxes of nutrients and energy subsidizing the receiving food webs (Polis et al., 1997).

Streams and their riparian areas are among the most altered ecosystems globally, and are exposed to a variety of co-occurring abiotic and biotic anthropogenic stressors (Schulz et al., 2015; Larsen et al., 2016; Kraus et al., 2020; Brauns et al., 2022; Schulz et al., 2024). As some riparian insectivores, such as spiders, depend on aquatic emergent insects as high-quality prey (Kato et al., 2003; Kowarik et al., 2021; Parmar et al., 2022), stressor-induced changes in emergence can translate to a shift in spider distribution and abundance (Graf et al., 2019; Kowarik et al., 2023), diet (Krell et al., 2015; Graf et al., 2020; Kolbenschlag et al., 2023), or body condition (Pietz et al., 2023).

Artificial light at night (ALAN) emitted from street lamps and other sources is one of the world's most widespread human-induced landscape changes, affecting aquatic-riparian ecosystems in particular, as human activities are often centered around water bodies (Kummu et al., 2011). Approximately 23 % of the global land area is subjected to ALAN, and global light emissions increase on an annual basis by up to 10 % (Falchi et al., 2016; Falchi and Bará, 2023). Due to the change of natural light/dark cycles, ALAN can affect the circadian rhythm of organisms and their seasonal activities such as animal dispersal, foraging, reproduction and development (Corbet, 1964; Nisimura and Numata, 2001; Degen et al., 2016; Manfrin et al., 2018). Effects of ALAN on organisms have been observed in both aquatic and terrestrial habitats (Longcore and Rich, 2004; Gaston et al., 2015; Hölker et al., 2021; Hölker et al., 2023). In freshwater ecosystems, ALAN can, for example, inhibit zooplankton diel vertical migration, alter aquatic insect larvae drift (Bishop, 1969; Moore et al., 2000, 2006; Schloss and Haney, 2006; Perkin et al., 2014), and affect fish prey selection and predatory success (Tabor et al., 2004; Nelson et al., 2021, 2022). Effects of ALAN in aquatic ecosystems can translate into adjacent terrestrial ecosystems as ALAN alters the quantity and composition of the flux of emerging aquatic insects into the terrestrial systems, though inconsistent in their direction (Meyer and Sullivan, 2013; Manfrin et al., 2017). In presence of ALAN, increased insect emergence has been observed in communities dominated by the tolerant mayfly *Cleon dipterum* (Manfrin et al., 2017). By contrast, a reduction in body size and taxonomic richness of emerging insects were reported elsewhere (Meyer and Sullivan, 2013). In terrestrial ecosystems, ALAN attracts adult aquatic and terrestrial insects, functioning as an ecological trap (Eisenbeis, 2006; Perkin et al., 2011; Manfrin et al., 2017), which can ultimately lure opportunistic terrestrial predators (Meyer and Sullivan, 2013; Manfrin et al., 2017, 2018; Parkinson et al., 2020).

Besides ALAN, invasive species are of global environmental concern (Sala et al., 2000; Johnson et al., 2009; Gallardo et al., 2016; Schirmel et al., 2016). Among those invasive species affecting streams, the signal crayfish *Pacifastacus leniusculus* (Decapoda, Astacidae), native to northwestern parts of North America, has a high potential to adapt to local environmental conditions. This, in combination with its boldness, fast growth rate, high fecundity, early maturation and the high feeding niche plasticity, allows it to outcompete several crayfish species native to Europe (Souty-Grosset et al., 2006; Olsson et al., 2009; Hudina et al., 2012) or to colonize areas where native species have disappeared, as is the case in most of the former range of the noble crayfish (*Astacus astacus*) (Lagrue et al., 2014). The signal crayfish also carries the crayfish plague pathogen, which it is resistant to, further contributing to its success and the decline of the native European crayfish populations (Alderman et al., 1990; Diéguez-Uribeondo, 2006; Schuster et al., 2010). Today the species is widespread in most parts of Europe (Kouba et al., 2014), is invasive in Japan (Azuma et al., 2011), and has the potential to further increase its current distribution range (e.g. Zhang et al., 2020). Moreover, the invasion by the signal crayfish is associated with negative ecological impacts (Vaeßen and Hollert, 2015) as it actively modifies habitats and their suitability for other species (Emery-Butcher et al., 2020). The signal crayfish is omnivorous, feeding on detritus, vascular plants and aquatic insects (Guan and Wiles, 1998), which directly affects benthic communities. They also build burrows, significantly affecting macroinvertebrates (Johnson et al., 2010; Mathers et al., 2016). Besides its unquestionable impact in aquatic systems, the signal crayfish enters riparian zones and its burrowing activities can extend to the river banks (Holdich et al., 2009; 2014), potentially affecting riparian habitat and vegetation structure (Faller et al., 2016). However, the ecological implications of the signal crayfish invasion on connected aquatic and terrestrial meta-ecosystems remain unclear.

In many freshwater habitats influenced by humans, ALAN and invasive species, such as the invasive signal crayfish, can co-occur (Gherardi, 2007; Thomas et al., 2016; Reid et al., 2019). Although there are several studies on the respective impact of these individual stressors either on aquatic or terrestrial ecosystems, their interactive effects on riparian consumers, such as spiders, remain unexplored. To investigate this, we conducted a mesocosm experiment following a fully crossed two-factorial design, in which we determined the responses of spiders to ALAN, to signal crayfish and the joint effect of both stressors. Based on the importance of emergent insects as prey for riparian spiders, we hypothesized that i) the presence of signal crayfish has an indirect negative effect on riparian spider abundance through reduced aquatic insect emergence; ii) ALAN increases spider abundance in the riparian areas because of the increased availability of insects locally attracted to ALAN. Finally, we hypothesized that iii) the effects of the signal crayfish are modulated by the presence of ALAN. We expected that the negative effect of crayfish on aquatic insect emergence, and subsequently on spiders, is reduced by ALAN, since signal crayfish are nocturnal feeders (Guan and Wiles, 1998) and their activity is reduced under ALAN (Thomas et al., 2016). After establishing the treatments, we sampled at two time points (in spring and summer) and were, thus, able to account for possible seasonal differences in spider communities.

2. Methods

2.1. The Riparian Stream Mesocosm (RSM)

The study was conducted between May 17th and July 15th, 2022 at the Riparian Stream Mesocosm (RSM) (fully described by

Rovelli et al., 2024), adjacent to the river Queich in Landau (Rhineland-Palatinate; southwest Germany; 49°12'03.9"N, 8°08'20.1"E). The experimental facility includes 16 replicated RSM units, with each unit containing an artificial flume (15 m long, ~0.8 m wide and ~10 cm deep) and an adjacent terrestrial habitat (~3.8 m width) (Fig. 1a) (see Manfrin et al., 2023; Rovelli et al., 2024). The mean water velocity was 12 cm/s (9–15 cm/s). Each unit is equipped with a tubular frame (height 2 m) covered by a 1-mm mesh net to avoid the exchange of organisms between units. Each flume is independently fed with water pumped from the river Queich, with benthic organisms freely drifting in and out. For this reason, the RSM macroinvertebrate community reflects that of the river Queich.
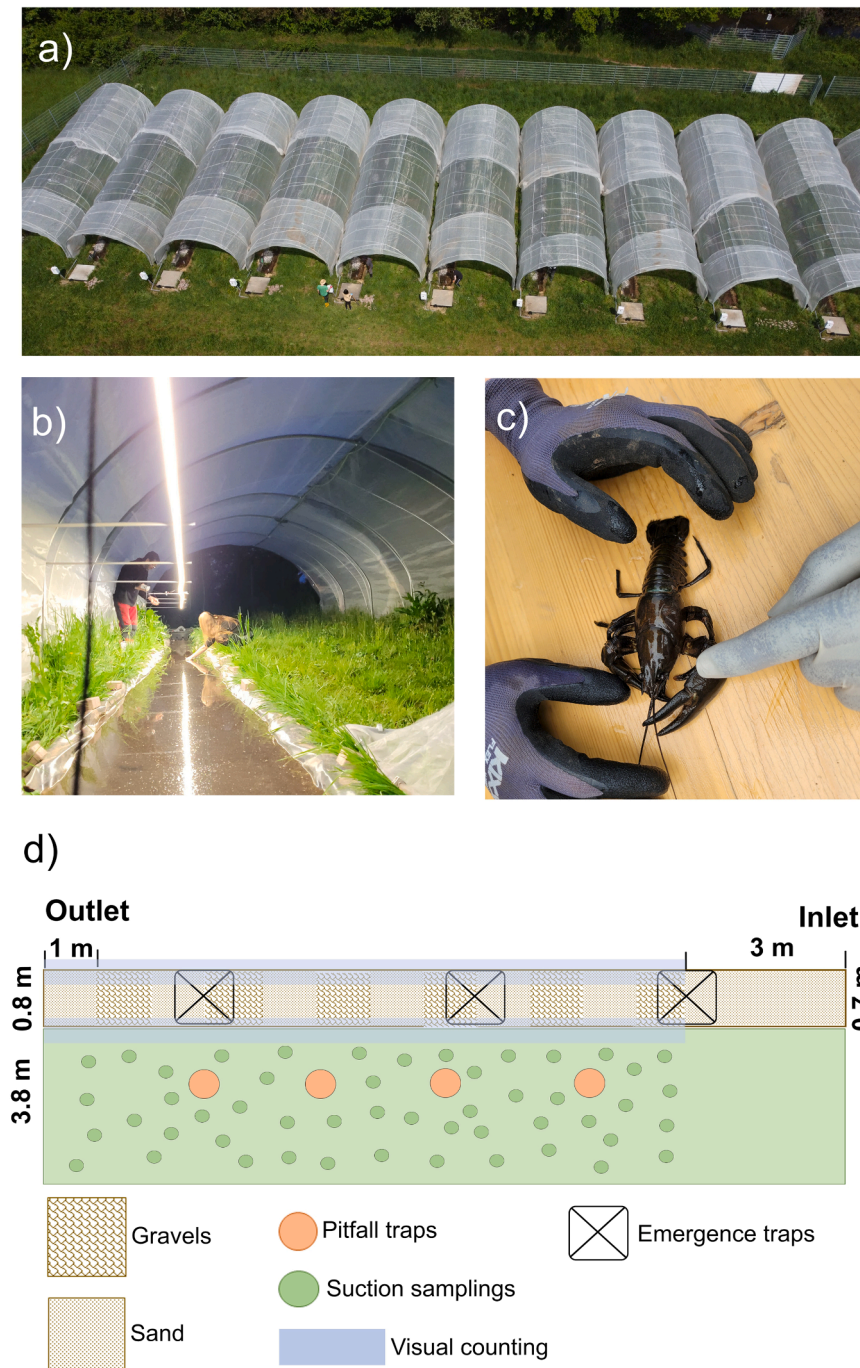

Fig. 1. The Riparian Stream Mesocosm (RSM) in Landau. a) overview, b) example of illuminated RSM unit at night with sampling activities, c) signal crayfish specimen, d) sampling scheme; suction sampling was done at 50 randomly chosen spots in each RSM unit. (Photo in panel a by Carsten Brühl, panel b, c by Alessandro Manfrin).

Perforated metal sheets around the pumping station on the river Queich (holes 6 mm in diameter) prevented larger organisms, such as fish and crayfish, as well as debris, from entering the mesocosm. The terrestrial habitats surrounding the flumes contain the typical riparian vegetation of the surrounding area, including various ground-dwelling and flying terrestrial insect groups as well as different families of free-hunting and web-building spiders. The individual flumes are encased with a pond liner to keep the water level constant and had alternating beds of sand and stone habitats providing a realistic habitat composition. Sand and stone beds were arranged in each flume in a similar manner (Fig. 1d).

2.2. Experimental set-up

The experiment was set up as a fully crossed two-factorial design with four RSM units being randomly assigned to each of the four treatments: signal crayfish, ALAN, the co-occurrence of ALAN and signal crayfish (ALAN:Crayfish), and the control (i.e., neither signal crayfish nor ALAN).

Two 5-m-long LED (4000–4500 K, neutral white, 24 V) light strips (OPT ST4452 company OPTONICA) were plugged together and installed on 15 m plastic strip structures over the center of the flumes, 1 m above the water level (Fig. 1b). The light frame structure was placed over all flumes, but the LED strips were only installed in ALAN treatment units. ALAN at the water surface was set at an intensity of 20 ± 2 lux, which is comparable to typical ALAN levels found in urban and suburban freshwaters (Jechow and Hölker, 2019), and was activated between 9 pm and 6 am.

Signal crayfish (Fig. 1c) were collected daily from the river Queich from early April to mid-May using crayfish traps placed overnight (Peay et al., 2009). Crayfish were kept in a 5000 L tank with constant water flow from the river Queich until the initiation of the experiment. At the start of the experiment, 27 crayfish were introduced in each flume of the respective treatments (i.e., Crayfish, ALAN:Crayfish) at a density of 1.8 ind/m^2, corresponding to the density at which Phillips et al. (2009) observed for the invasive crayfish *Faxonius virilis* a decrease of 70 % of benthic invertebrates and 90 % of periphyton biomass. When introducing the crayfish individuals, an equal distribution regarding sex and carapace length (30–50 mm) was also considered. Five crayfish shelters each made of nine 15-cm-long PVC tubes (3×4 cm wide, 6×5 cm wide) were deployed in each flume. After the first week, dead or missing crayfish were replaced in order to maintain the initial density. Dead individuals were removed from the system. Crayfish presence in the flumes were monitored weekly in the evening using flashlights.

2.3. Sampling and processing of emerging insects

To assess the availability of aquatic prey for riparian spiders, three pyramid-like emergence traps (1 x 1 m surface, 70 cm high) were deployed along each flume, in the upper, middle and downstream reach. Insects that emerged inside the traps were collected using a suction sampler (see Kolbenschlag et al., 2023) and immediately frozen at $-20°$C. Samples were collected after the 1st (24th to the 31st of May of 2022) and 6th week (28th of June to 5th of July of 2022) after the start of the exposure to the treatments. In the laboratory, aquatic insects were sorted and counted under a stereoscopic microscope. The number of emerging insects collected at each observation were averaged between traps of each flume. Emergence was standardized to rates of individuals collected in 1 m^2 over 1 day (ind m^{-2} d^{-1}).

2.4. Sampling and identification of spiders

Spiders were sampled using a) pitfall traps, b) suction sampling and c) visual counting (only the web-building *Tetragnatha* sp.) (Fig. 1d). Four 0.25 L pitfall traps were deployed continuously day and night for 7 days on the 25th of May and the 8th of July 2022, that is the 1st and 7th week of the experiment. Pitfall traps were placed in the riparian area and filled with 0.1 L of a 1:1 propylene glycol:water solution as preservant. A mesh (1×1 cm) was used to cover the trap openings to avoid the trapping of small mammals and crayfish. For data analysis, we pooled the four pitfall traps per RSM unit. The suction samples were taken with a leaf vacuum sampler (SH 86, Stihl®) during diurnal hours (from 7 am to 7 pm), vacuuming for 2–3 seconds at 50 spots per RSM unit. Samples from both pitfall and suction sampling were transferred to 80 % ethanol. Visual counting was conducted near the shore (Fig. 1d) where *Tetragnatha* sp. were visually identified and counted. The visual collection sampling was limited to 20 minutes per flume.

In the laboratory, spiders from the pitfall traps and suction sampling were sorted under stereoscopic microscope (Leica M80) and identified to the species level using taxonomic keys (Roberts, 1995; Nentwig et al., 2024, https://araneae.nmbe.ch/). Due to the difficulty in identification, and because we found it unlikely that they would interact with signal crayfish due to their small body size, Theridiidae and Linyphiidae were only identified to family level, except for the relatively large-bodied genus *Enoplognatha*. Spiders were then categorized into guilds based on their hunting behavior according to Cardoso et al. (2011).

2.5. Data analysis

We used linear models (lm) from the „stat" package (version 4.3.1) for R (R Core Team, 2021) to test differences among main and interacting effects of the treatments on the rate of insect emergence. In these models, we used "ALAN", "crayfish" and their interaction as model predictors. To assess the main and interactive effect of the stressors, the predictors ALAN and crayfish were coded as binary factors (presence $= 1$, absence $= 0$) in all models. The use of the binary factors and the interaction term tests whether the combined effect of ALAN and crayfish differs from the sum of their individual effects, rather than simply comparing the four treatment groups (control, ALAN, crayfish and ALAN + crayfish). We used generalized linear models (glm) from the „stat" package for R to analyze

changes in the total number of spiders (as integers) among treatments, and applied Poisson or negative binomial distributions to account for count data and dispersion. In these models, we included the emergence rate as an additional factor to "ALAN", "crayfish" and their interaction. We ran the models separately for data collected by pitfall trapping and suction sampling and for samples collected after the 1st and 6th (for emergence data) and 1st and 7th week (for spider data) of the experiment to analyze short-term and long-term effects. The same glm models which we used to test the total number of spiders were also used to assess differences in the number of individuals of representative spider taxa, i.e., those with more than 30 individuals being collected over the entire study duration and occurring at least once in each treatment and time point (see Table S1). For each of the representative spider taxa, this analysis was conducted on the total number of spiders collected in both pitfall traps and suction sampling. The same models were also applied to test differences among treatments for the number of *Tetragnatha extensa* and *Tetragnatha montana* collected via visual counting along the shoreline.

Model validation was conducted with visualization of model residuals using the package DHARMa (version 0.4.6, Hartig, 2018) and model residual-fitted values plots. In spider glm models with count data, overdispersion in Poisson models was assessed using Pearson chi-squared statistic (Payne et al., 2018, McCullagh, 2019). In case of detected overdispersion, the model was fit with a negative binomial family (Gelman and Hill, 2006). The package ggplot2 (version 3.4.4, Wickham et al., 2016) for R was used to produce the graphical outputs. We considered p-values < 0.1 as statistically significant.

3. Results

3.1. Emerging aquatic insects

We collected an average of 112 ± 35 individuals of emerging insects per square meter and day after 1 week and 75 ± 41 individuals per square meter and day after 6 weeks, with the majority (98 %) of the emerging insects being Chironomidae. After 1 week, crayfish significantly reduced the average emergence rate by 35 % in comparison to treatments without the crayfish (Table 1; Fig. 2a). In contrast, no significant short-term effects of ALAN nor of an interaction between the crayfish and ALAN were detected (Table 1; Fig. 2a). After 6 weeks, the emergence rate was highly variable between treatments and no significant effects of either crayfish, ALAN nor of their interaction were observed (Table 1; Fig. 2a).

3.2. Spiders

The pitfall traps caught 1593 spiders belonging to 27 taxa and the suction sampling resulted in 1064 spiders belonging to 17 taxa (Table S1). Visual counting resulted in 395 individuals of *T. extensa* and 141 individuals of *T. montana*.

After 1 week, ALAN significantly increased the average number of pitfall-trapped spiders by 22 %, with no significant effect of crayfish or the interaction between the two (Table 1; Fig. 2b). In addition, pitfall-trapped spider numbers after week 1 and week 7

Table 1

Effects of artificial light at night (ALAN), invasive crayfish, and their interaction on the rate of emerging aquatic insects per square meter and day, and total spider numbers. Statistical estimates, standard errors (s.e.) and statistical values from linear models (lm) for aquatic insect emergence rate and generalized linear models (glm) for total number of spider individuals (analyzed separately for pitfall traps and suction sampling) in relation to the treatments (ALAN, Crayfish, ALAN:Crayfish) collected after one week (short-term) and after six weeks (for emergence) and seven weeks (for spiders) (long-term) from the start of the experiment. The estimate represents the estimated change in emergence rate and number of spiders for the treatment in relation to the absence of the treatment (i.e., ALAN, Crayfish, ALAN:Crayfish; negative estimate = decrease; positive estimate = increase).

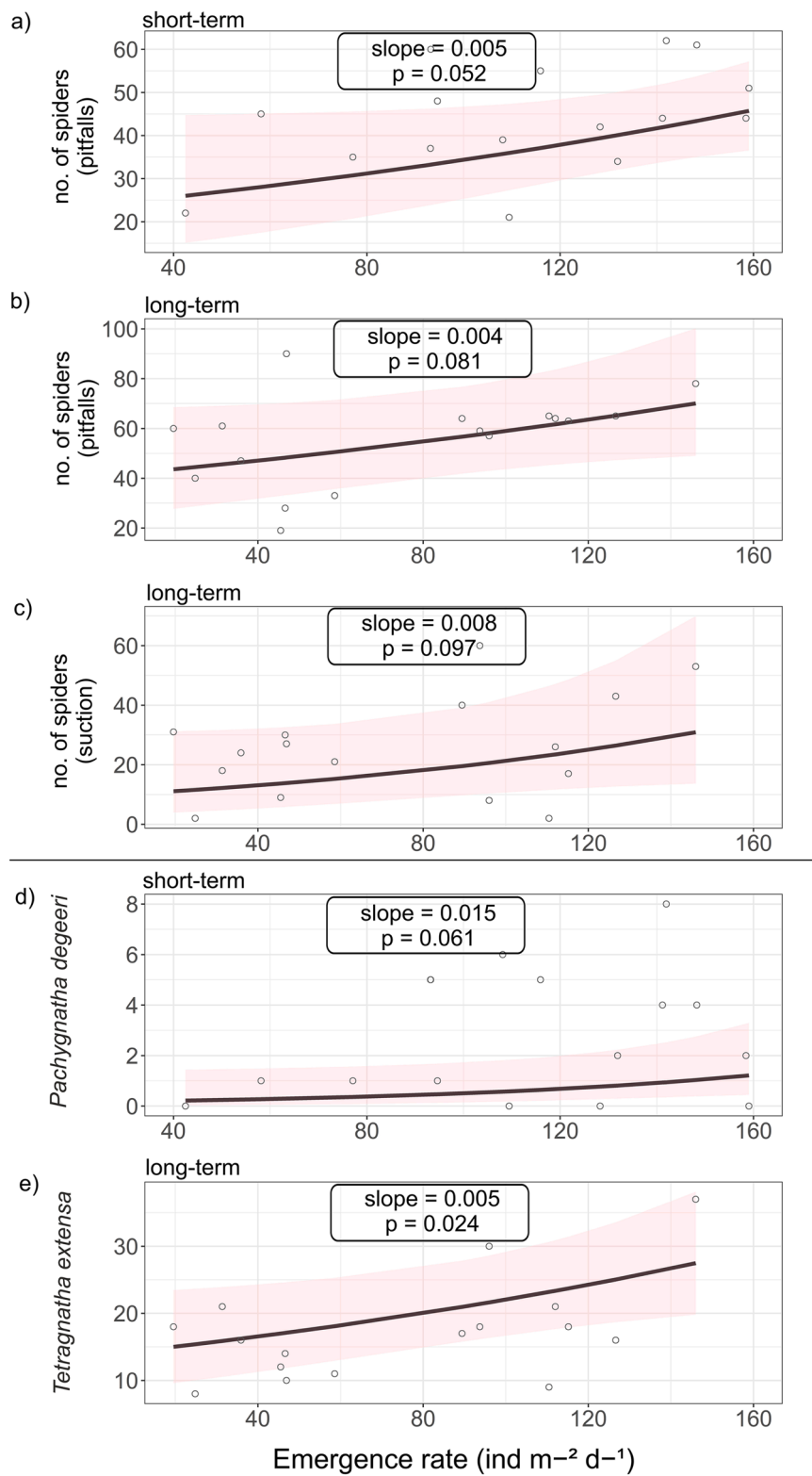| Model	Time	Predictors	Estimate	s.e.	stat. value	p value
Emergence rate (lm)	short-term	ALAN	−15.846	18.203	−0.87	0.401
		Crayfish	**−47.948**	**18.203**	**−2.63**	**0.022**
		ALAN:Crayfish	0.247	25.744	0.01	0.993
	long-term	ALAN	−45.450	29.270	−1.55	0.146
		Crayfish	−25.010	29.270	−0.85	0.410
		ALAN:Crayfish	47.150	41.400	1.14	0.277
Pitfalls - total no. of spiders (glm)	short-term	**ALAN**	**0.312**	**0.155**	**2.02**	**0.044**
		Crayfish	0.072	0.194	0.37	0.709
		ALAN:Crayfish	−0.112	0.217	−0.52	0.607
		Emergence rate	**0.005**	**0.002**	**1.95**	**0.052**
	long-term	ALAN	0.026	0.239	0.11	0.913
		Crayfish	0.145	0.223	0.65	0.514
		ALAN:Crayfish	−0.240	0.324	−0.74	0.459
		Emergence rate	**0.004**	**0.002**	**1.75**	**0.081**
Suction - total no. of spiders (glm)	short-term	**ALAN**	**−0.630**	**0.321**	**−1.97**	**0.049**
		Crayfish	−0.308	0.388	−0.79	0.428
		ALAN:Crayfish	**0.737**	**0.440**	**1.68**	**0.094**
		Emergence rate	0.002	0.005	0.45	0.651
	long-term	ALAN	0.330	0.546	0.61	0.545
		Crayfish	0.440	0.510	0.86	0.388
		ALAN:Crayfish	−0.162	0.735	−0.22	0.825
		Emergence rate	**0.008**	**0.005**	**1.66**	**0.097**
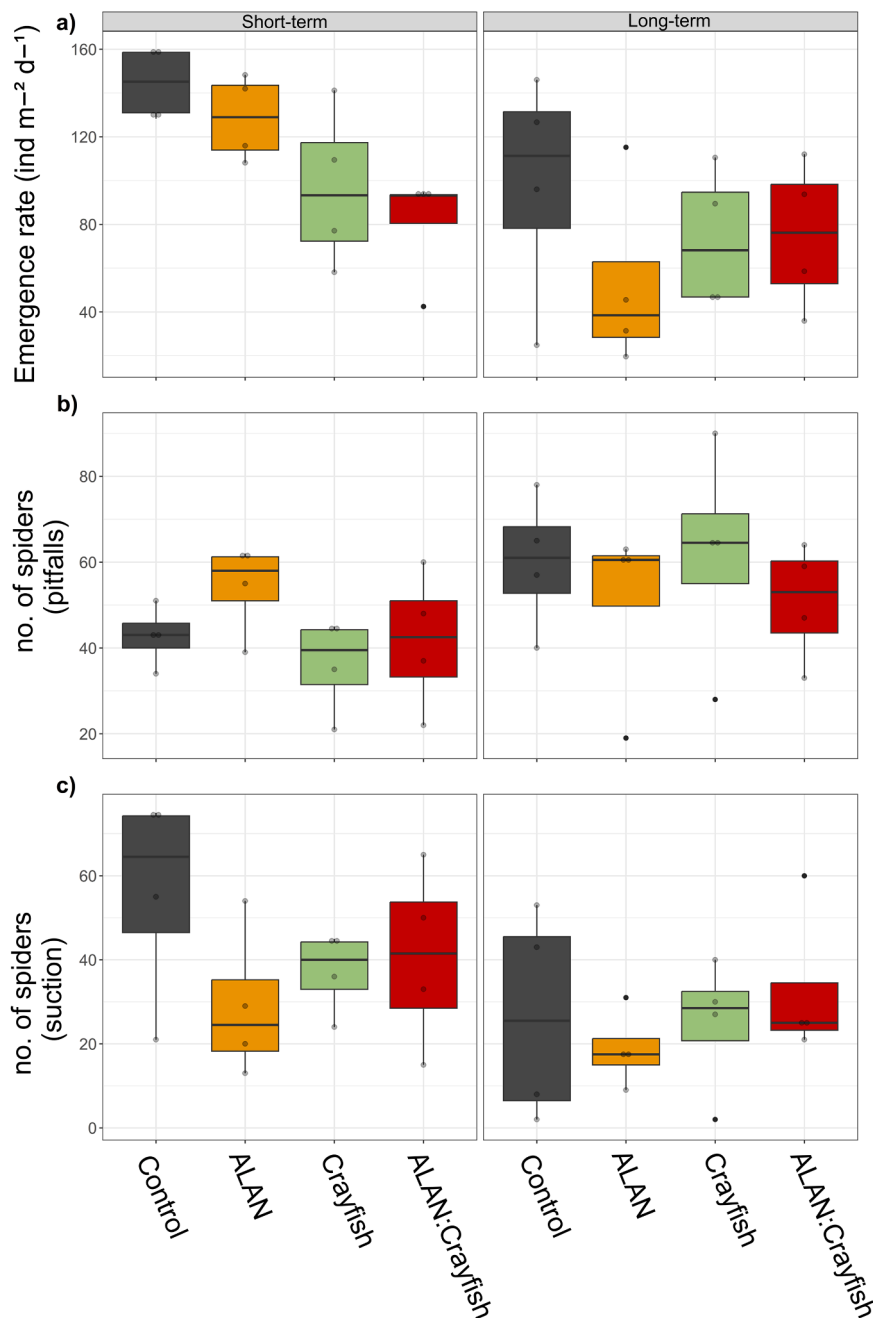
Fig. 2. Rate of (a) emerging aquatic insects per square meter and day, (b) number (no.) of pitfall-trapped spiders, and (c) spiders from suction samples per treatment (i.e., artificial light at night (ALAN), invasive crayfish, and their interaction) and sampling period. (i.e., after one week = short-term; after six and seven weeks = long-term, for emergence and spiders, respectively). The box extends from the first to the third quartile showing the median, whiskers indicate maximum and minimum values.

significantly increased with the number of emerging insects (Table 1; Fig. 3a, b). In contrast, ALAN, the presence of the crayfish and the interaction between crayfish and ALAN had no significant long-term effects on the number of pitfall-trapped spiders (Table 1).

Contrary to the pitfall traps, spider numbers in the suction samples after week 1 were negatively affected by ALAN with 25 % fewer spiders in the ALAN treatments compared to treatments without ALAN (Table 1, Fig. 2c). However, the negative effect of ALAN was particularly strong in the treatments without the crayfish, as indicated by the significant interaction between crayfish and ALAN (Table 1, Fig. 2c). In contrast, crayfish and the emergence rate had no significant short-term effects on the number of spiders in the suction samples (Table 1). Spider numbers from the suction samples significantly increased after week 7 with an increasing emergence rate while ALAN, crayfish and their interaction had no significant long-term effects (Table 1; Fig. 3c).

a)

short-term

slope = 0.005
p = 0.052

no. of spiders
(pitfalls)

b)

long-term

slope = 0.004
p = 0.081

no. of spiders
(pitfalls)

c)

long-term

slope = 0.008
p = 0.097

no. of spiders
(suction)

d)

short-term

slope = 0.015
p = 0.061

Pachygnatha degeeri

e)

long-term

slope = 0.005
p = 0.024

Tetragnatha extensa

Emergence rate (ind m⁻² d⁻¹)

(caption on next page)

Fig. 3. Significant correlations (p < 0.1) (see Fig. S1 for both significant and non-significant correlations) between the observed rate of emerging aquatic insects and the number (no.) of spider individuals for: a) total number of spider individuals from pitfall traps collected after one week (short-term) and b) seven weeks (long-term); c) total number of spider individuals from suction sampling after seven weeks; d) number of *Pachygnatha degeeri* after one week; e) number of *Tetragnatha extensa* after seven weeks. The black line represents model-predicted mean values, while the shaded pink area indicates the 95 % confidence interval. Observed values are shown as empty circles. The text boxes show the slope of the x-y relation (coefficient of change of the respective generalized linear model) and the statistical significance of the model (see Table 2).

The effects of emergence rate and treatments varied among spider taxa and time of exposure (Table 2). *Pachygnatha degeeri* (ground-hunter) and *T. extensa* (orb web weaver) showed a significant positive correlation with the emergence rate (Table 2, Fig. 3d, e) after week 1 and 7, respectively. For *P. degeeri* we observed a 240 % increase in individuals when exposed to ALAN after week 1 compared to

Table 2

Effects of artificial light at night (ALAN), invasive crayfish, and their interaction on number of individuals of single spider taxa collected after one week (short-term) and after seven weeks (long-term). Statistical estimates, standard errors (s.e.) and statistical values from generalized linear models (glm) for number of individuals for the most representative spider taxa (> 30 individuals collected and at least more than 1 individual collected at each sampling time) from pitfall traps and suction samples and for *Tetragnatha montana, T. extensa* from visual counting. Factors with p value < 0.1 are indicated in bold. The estimate represents the estimated change in number of spiders for the treatment in relation to the absence of the treatment (i.e., ALAN, Crayfish, ALAN:Crayfish; negative estimate = decrease; positive estimate = increase) or for one-unit increase in emergence rate (positively or negatively correlated).

Species	Time	Variable (model)	Estimate	s.e.	stat. value	p value
Linyphiidae	short-term	ALAN	−0.391	0.36	−1.10	0.273
Sheet web weavers		Crayfish	−0.280	0.43	−0.64	0.519
		ALAN:Crayfish	0.226	0.49	0.46	0.646
		Emergence rate	0.002	0.01	0.42	0.674
	long-term	ALAN	0.140	0.43	0.33	0.746
		Crayfish	0.064	0.41	0.16	0.874
		ALAN:Crayfish	−0.089	0.59	−0.15	0.879
		Emergence rate	0.006	0.01	1.54	0.123
Pachygnatha degeeri	short-term	**ALAN**	**1.975**	**0.55**	**3.57**	**< 0.001**
Ground hunters		Crayfish	1.027	0.71	1.46	0.146
		ALAN:Crayfish	−1.074	0.75	−1.44	0.150
		Emergence rate	**0.015**	**0.01**	**1.87**	**0.061**
	long-term	ALAN	0.048	0.41	0.12	0.907
		Crayfish	0.459	0.38	1.21	0.228
		ALAN:Crayfish	−0.523	0.56	−0.94	0.348
		Emergence rate	0.002	0.01	0.50	0.615
Pardosa palustris	short-term	ALAN	0.330	0.33	1.00	0.318
Ground hunters		Crayfish	0.212	0.41	0.52	0.603
		ALAN:Crayfish	−0.323	0.46	−0.70	0.484
		Emergence rate	0.006	0.01	1.07	0.287
	long-term	ALAN	0.198	0.35	0.57	0.569
		Crayfish	**0.577**	**0.30**	**1.91**	**0.056**
		ALAN:Crayfish	**−1.029**	**0.47**	**−2.17**	**0.030**
		Emergence rate	0.002	0.01	0.69	0.491
Pardosa agrestis	short-term	ALAN	−0.008	0.99	−0.01	0.994
Ground hunters		Crayfish	−0.680	1.34	−0.51	0.611
		ALAN:Crayfish	0.836	1.52	0.55	0.582
		Emergence rate	0.014	0.02	0.75	0.455
	long-term	ALAN	0.696	1.33	0.52	0.600
		Crayfish	**1.947**	**1.13**	**1.72**	**0.086**
		ALAN:Crayfish	−1.256	1.50	−0.84	0.403
		Emergence rate	0.000	0.01	0.01	0.994
Tetragnatha extensa	short-term	ALAN	−0.129	0.28	−0.47	0.640
Orb web weavers		Crayfish	−0.027	0.33	−0.08	0.934
		ALAN:Crayfish	0.366	0.37	0.99	0.321
		Emergence rate	0.001	0.01	0.21	0.831
	long-term	ALAN	−0.024	0.23	−0.10	0.918
		Crayfish	**−0.443**	**0.23**	**−1.94**	**0.053**
		ALAN:Crayfish	0.285	0.33	0.87	0.383
		Emergence rate	**0.005**	**0.01**	**2.26**	**0.024**
Tetragnatha montana	short-term	ALAN	0.288	0.44	0.66	0.511
Orb web weavers		Crayfish	0.643	0.49	1.31	0.190
		ALAN:Crayfish	−0.100	0.57	−0.18	0.859
		Emergence rate	0.007	0.01	1.09	0.276
	long-term	ALAN	−0.058	0.33	−0.18	0.861
		Crayfish	0.120	0.30	0.40	0.693
		ALAN:Crayfish	−0.066	0.44	−0.15	0.881
		Emergence rate	−0.002	0.01	−0.79	0.429

treatments without ALAN (Table 2, Fig. 4b). No other taxa were significantly affected by ALAN in our experiment. In the presence of crayfish, we observed 27 % fewer *Tetragnatha extensa* spiders than in treatments without crayfish after week 7 (Table 2, Fig. 4e), while the number of individuals of both *Pardosa palustris* and *Pardosa agrestis* (ground hunters) was 15 % and 267 % higher in the presence of crayfish compared to treatments without crayfish, respectively (Table 2, Fig. 4c, d). However, the positive effect of the crayfish on *P. palustris* after 7 weeks occurred mainly in the treatment without ALAN, as indicated by the significant interaction between ALAN and crayfish (Table 2, Fig. 4c). Linyphiidae and *T. montana* were not significantly affected by any of the predictors (Table 2, Fig. 4a, f).
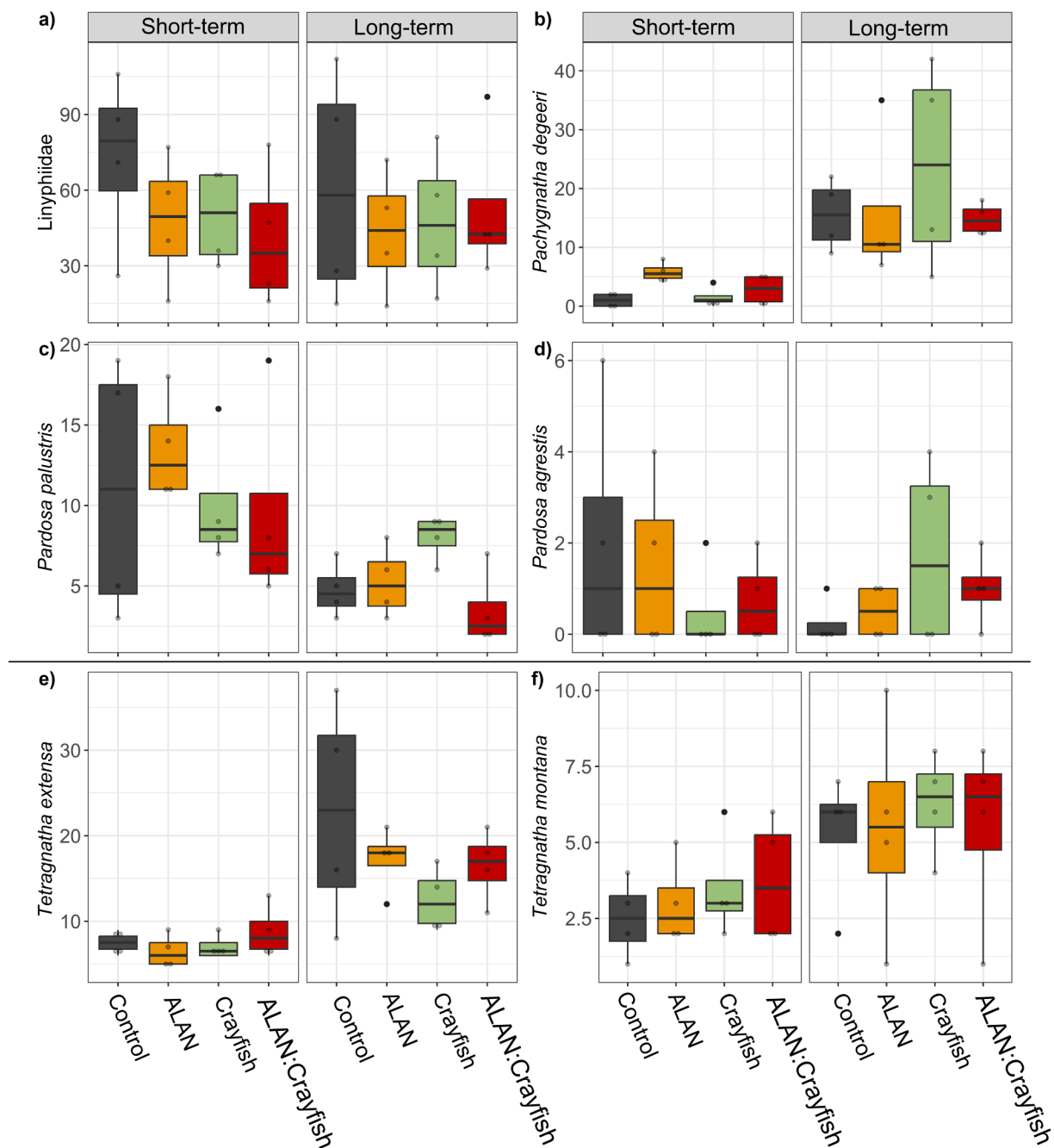
Fig. 4. Number of (a-d) spider individuals of representative taxa (> 30 individuals collected and at least more than one individual collected per treatment and sampling period) and (e, f) number of spiders belonging to the two Tetragnathidae species visually counted among treatments (i.e., artificial light at night (ALAN), invasive crayfish, and their interaction) and time points (i.e., after one week = short-term; after seven weeks = long-term). The box extends from the first to the third quartile showing the median, whiskers indicate maximum and minimum values. Values refer to pitfall and suction samples pooled together.

4. Discussion

We investigated the response of riparian spiders to artificial light at night (ALAN), the invasive signal crayfish and their interaction in a large mesocosm experiment. To better understand whether the observed effects in spiders resulted from changes in prey availability, we also assessed alterations in aquatic insect emergence.

As expected, we found that the crayfish resulted in a significant reduction (*ca.* 35 %) of aquatic insect emergence. This may have been triggered by increased predation by the crayfish (Vaeßen and Hollert, 2015; Mathers et al., 2016; Galib et al., 2022) or by stimulated drift of the emergent insect larvae to avoid predation (Hammock and Wetzel, 2013). As a consequence, we assumed that the signal crayfish would reduce riparian spider abundance, because many riparian spiders - especially web-building species - rely on emerging insect prey, which often make up a large part of their diet (Lafage et al., 2019; Bollinger et al., 2023; Nash et al., 2023). Indeed, we found positive associations between the emergence rate and the total number of spiders both from pitfall trap and suction sampling, which was particularly evident in the ground hunter *P. degeeri* and in the web-building spider *T. extensa*. Alterations in the availability of aquatic prey can profoundly influence riparian spider communities (Kato et al., 2003; Iwata, 2007; Burdon and Harding, 2008; Graf et al., 2019). Additionally, a reduction in insect emergence was previously attributed to a decrease in aquatic insects in the diet of *Tetragnatha* sp. (Gergs et al., 2014), while Manfrin et al. (2018) found that an increased availability of aquatic prey in summer would result in a higher intake of aquatic prey in the diet of *Pachygnatha* sp., which could explain why the number of spiders in our study increased with higher emergence rates.

We further observed that the direction and strength of crayfish impacts (potentially acting via alterations of emergence) on riparian spiders were taxon- and time-dependent. Crayfish negatively affected the spiders with the highest reliance on emergent insects, namely *T. extensa,* which were significantly less abundant at mesocosms with crayfish after 7 weeks. Many long-jawed orb weaver (Tetragnathidae) spiders are typical riparian species consuming high proportions of aquatic emerging insects as prey (Gergs et al., 2014; Bollinger et al., 2023). At the same time, there were also spider species which were not affected by the presence of the signal crayfish, or even increased in number. For example, we found a positive effect of signal crayfish presence on both *Pardosa* spp. at the end of the experiment. These ground-hunting wolf spiders are more related to terrestrial prey and flexible in their use of aquatic prey, potentially switching to a higher consumption of terrestrial prey when emergence is reduced (Graf et al., 2020; Bollinger et al., 2023; Marker et al., 2023). Our results indicate that the impact of aquatic invaders, such as the signal crayfish, is not restricted to aquatic systems but extends to terrestrial systems, affecting the abundance of riparian predators and potentially altering predator-prey interactions (Gergs et al., 2014; Koel et al., 2019; Orihuela-Torres et al., 2022). The signal crayfish is the most widespread invasive crayfish in Europe, being present in 27 European countries (Holdich et al., 2009). Due to its widespread distribution and its potential to further expand its range (e.g. Zhang et al., 2020), it can be assumed that the influence of the signal crayfish on aquatic and riparian ecosystems is more extensive than previously perceived.

We cannot exclude that the effects of the invasive signal crayfish on riparian spiders observed here would manifest similarly with the exclusive presence of the native noble crayfish (*Astacus astacus*). Signal and noble crayfish have been found to exhibit a considerable degree of ecological niche overlap in lake littoral areas (Ercoli et al., 2014; 2015a). On the other hand, Chucholl and Chucholl (2021) found that invasive signal crayfish have higher impacts on stream macroinvertebrates and leaf litter breakdown compared to the noble crayfish. Similarly, Ercoli et al. (2015b) found that boreal lakes invaded by signal crayfish had lower sublittoral macroinvertebrate density compared to lakes inhabited by noble crayfish or those without crayfish presence, indicating stronger negative effects by the signal crayfish on benthic community structure than by the native species. Furthermore, the signal crayfish has been found to exhibit greater plasticity with respect to habitat utilization and feeding (Olsson et al., 2009) and tends to occur at higher densities than the native species (Galib et al., 2022). Still, we cannot conclude that the 35 % reduction in insect emergence, and the resulting cascading effects on the riparian spider community observed in this study, are specific to the invasive signal crayfish. Several indications suggest that the invasive signal crayfish may exert a stronger impact on freshwater communities and aquatic-terrestrial interactions than the native crayfish, highlighting the need for further research on this topic.

In contrast to the presence of the signal crayfish, we expected ALAN to increase spider abundance due to increased prey availability by stimulating insect emergence and attracting adult insects (Manfrin et al., 2017). However, contrary to our hypothesis, the effect of ALAN on the aquatic insect emergence was rather low and statistically insignificant. The increased emergence found in ALAN-exposed ditches by Manfrin et al. (2017) was observed in communities dominated by mayflies. In our study, the aquatic insect community was mainly composed of Chironomidae, which may show different behavioral (e.g., drift) and physiological (e.g., larval development) responses to ALAN. Indeed, altered natural light cycles may reduce the survival of aquatic larvae (Armitage, 1995; Kaiser et al., 2016) or alter larval development and, thus, emergence timing (Pinder et al., 1993). In our experiment, the frames encasing the RSM units restricted the influx of flying insects from other areas, preventing new Chironomidae females from depositing eggs in the flumes, and not attracting other prey for the spiders in addition to the emergence. This limited the increase in local aquatic insect larvae densities in the system from external sources.

Despite the fact that ALAN did not result in a higher aquatic emergence, we found that ALAN still affected spider abundance and composition. Interestingly, we found that exposure to ALAN for one week resulted in a higher number of pitfall-trapped spiders but in a lower number of individuals collected via suction sampling. Such a difference might be explained by the different composition of species characterizing the pitfall and suction samples. Also, the observed difference might be explained by the fact that pitfall traps collected spiders active both during day and night, while the suction sampling was only performed during the day. Spiders captured with pitfall traps were mainly wolf spiders (Lycosidae), which include both nocturnal and diurnal ground-hunters (Krumpalova and Tuf, 2013) (Table S1). ALAN may not be a direct stressor for these spiders, as also observed in previous studies where no effects of ALAN on wolf spiders of the genus *Pardosa* were observed (Manfrin et al., 2017). ALAN may allow diurnal spiders to also be active at

night extending their temporal niche (Owens and Lewis, 2018; Grubisic and van Grunsven, 2021). At the same time, ALAN might boost spider activity during the day, with species benefitting from the presence of exhausted or moribund insects that were attracted to the lights the night before (Davies et al., 2012; Manfrin et al., 2017). Suction samples, on the other hand, mainly recorded web-building spiders (e.g., species from families such as Linyphiidae and Theridiidae), which are assumed to be more active during the day (Król et al., 2018). In this case, the reduction observed under ALAN might be due to increased interference with free-hunting spiders.

A positive effect of ALAN was particularly evident in the ground hunting spider *P. degeeri* at the beginning of the experiment. This result aligns with Manfrin et al. (2017), where the abundance of several night-active ground-dwelling predators, including *Pachygnatha clercki*, increased under ALAN and their activity was extended into the day. While most species of Tetragnathidae are web building sit-and-wait predators, *Pachygnatha* spp. do not use webs but are active hunters (Narimanov et al., 2021). *Pachygnatha clercki* has anatomical eye features that allow high visual efficiency at low light levels (Land, 1985), and *P. degeeri* may have benefited from the increased light levels provided by ALAN for similar reasons. It is important to note that while ALAN can create foraging opportunities for spiders, secondary predators such as bats can also be attracted to these prey hotspots (Voigt et al., 2020; Barré et al., 2022). For this reason, the attraction and foraging opportunity created by ALAN may ultimately turn into a disadvantage if higher predators also make use of it.

Finally, we hypothesized that the effects of the signal crayfish on emerging insects, and subsequently on riparian spiders, would be lower when combined with ALAN. However, we did not observe the expected interactive effects of ALAN and crayfish. Our results suggest that even when exposed to ALAN, the invasive signal crayfish still engage in foraging despite the light. ALAN does not seem to significantly alter the invasive crayfish behavior, as they do not appear to prioritize avoiding light over hunting. The only significant interacting effect of ALAN and crayfish was found on *P. palustris* after 7 weeks of experiment. The co-occurrence of ALAN and the signal crayfish in this case led to a lower number of *P. palustris* compared to the control and to treatments in which there was no co-occurrence of stressors (Fig. 4c). These results could not be directly related to the activity of crayfish, ALAN or changes in availability of insect emergence; it may well be that this taxon was affected indirectly by the joint effect of ALAN and crayfish on other food sources or on the competitive behavior of *P. palustris* with other ground-dwelling taxa. We did not sample terrestrial prey in this study and it may be possible that ground-dwelling arthropods in the RSM riparian meadow were also affected by ALAN (Davies et al., 2012; Manfrin et al., 2017), crayfish or their co-occurrence. Investigating these mechanisms may be important to understand whether the effects of ALAN and crayfish propagate further into the riparian food web (Leroux and Loreau, 2008, Osakpolor et al., 2023).

5. Conclusion

Our study shows that the presence of signal crayfish reduced aquatic insect emergence, inducing cascading effects on riparian spider populations. Additionally, effects of ALAN and crayfish were taxon- and time-dependent, and ALAN did not mitigate crayfish-induced effects. The widespread presence of ALAN along freshwater ecosystems is likely to co-occur with the colonization by the invasive signal crayfish. ALAN and the invasive crayfish had different effects on emerging aquatic insects and their riparian predators. The lack of clear interactive effects of these two anthropogenic stressors can largely be explained by the fact that prey (emerging insects) and predators (riparian spiders) were each affected by only one of the stressors. Our study demonstrates that effects of anthropogenic stressors can propagate between aquatic-terrestrial meta-ecosystems. This can have global implications for riparian food webs and the overall diversity of aquatic-riparian meta-ecosystems, considering the widespread presence of these two anthropogenic stressors. The presence of ALAN and crayfish should therefore be considered in environmental management strategies to protect not only freshwater biodiversity but also riparian biodiversity and ecosystem functioning.

Ethical statement

This study was conducted in accordance with ethical guidelines and regulations. For studies involving animals, all procedures followed ethical standards for animal welfare. No ethical concerns are associated with this research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03577.

Data availability

Data will be made available on request.

References

Alderman, D.J., Holdich, D., Reeve, I., 1990. Signal crayfish as vectors in crayfish plague in Britain. Aquaculture 86, 3–6.

Armitage, P.D., 1995. Behaviour and ecology of adults. In the Chironomidae: Biology and ecology of non-biting midges. Springer Netherlands, Dordrecht, pp. 194–224.

Azuma, N., Usio, N., Korenaga, T., Koizumi, I., Takamura, N., 2011. Genetic population structure of the invasive signal crayfish *Pacifastacus leniusculus* in Japan inferred from newly developed microsatellite markers. Plankton Benthos Res. 6 (4), 187–194.

Barré, K., Vernet, A., Azam, C., Le Viol, I., Dumont, A., Deana, T., Vincent, S., Challéat, S., Kerbiriou, C., 2022. Landscape composition drives the impacts of artificial light at night on insectivorous bats. Environ. Pollut. 292, 118394.

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nat. Ecol. Evol. 4 (8), 1060–1068.

Bishop, J.E., 1969. Light control of aquatic insect activity and drift. Ecology 50 (3), 371–380.

Bollinger, E., Zubrod, J.P., Englert, D., Graf, N., Weisner, O., Kolb, S., Schäfer, R.B., Entling, M.H., Schulz, R., 2023. The influence of season, hunting mode, and habitat specialization on riparian spiders as key predators in the aquatic-terrestrial linkage. Sci. Rep. 13 (1), 22950.

Brauns, M., Allen, D.C., Boëchat, I.G., Cross, W.F., Ferreira, V., Graeber, D., Patrick, C.J., Peipoch, M., von Schiller, D., Gücker, B., 2022. A global synthesis of human impacts on the multifunctionality of streams and rivers. Glob. Change Biol. 28 (16), 4783–4793.

Burdon, F.J., Harding, J.S., 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. Freshw. Biol. 53 (2), 330–346.

Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global patterns of guild composition and functional diversity of spiders. PloS One 6 (6), e21710.

Chucholl, F., Chucholl, C., 2021. Differences in the functional responses of four invasive and one native crayfish species suggest invader-specific ecological impacts. Freshw. Biol. 66 (11), 2051–2063.

Corbet, P.S., 1964. Temporal patterns of emergence in aquatic insects. Can. Èntomol. 96 (1-2), 264–279.

Davies, T.W., Bennie, J., Gaston, K.J., 2012. Street lighting changes the composition of invertebrate communities. Biol. Lett. 8 (5), 764–767.

Degen, T., Mitesser, O., Perkin, E.K., Weiß, N.S., Oehlert, M., Mattig, E., Hölker, F., 2016. Street lighting: sex-independent impacts on moth movement. J. Anim. Ecol. 85 (5), 1352–1360.

Diéguez-Uribeondo, J., 2006. The dispersion of the Aphanomyces astaci-carrier *Pacifastacus leniusculus* by humans represents the main cause of disappearance of the indigenous crayfish *Austropotamobius pallipes* in Navarra. Bull. Français De. la Pêche Et. De. la Piscic. (380-381), 1303–1312.

Eisenbeis, G., Rich, C., Longcore, T., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. Ecol. Conséq. Artif. night Light. 2, 191–198.

Emery-Butcher, H.E., Beatty, S.J., Robson, B.J., 2020. The impacts of invasive ecosystem engineers in freshwaters: a review. Freshw. Biol. 65 (5), 999–1015.

Ercoli, F., Ruokonen, T.J., Hämäläinen, H., Jones, R.I., 2014. Does the introduced signal crayfish occupy an equivalent trophic niche to the lost native noble crayfish in boreal lakes? Biol. Invasions 16, 2025–2036.

Ercoli, F., Ruokonen, T.J., Koistinen, S., Jones, R.I., Hämäläinen, H., 2015b. The introduced signal crayfish and native noble crayfish have different effects on sublittoral macroinvertebrate assemblages in boreal lakes. Freshw. Biol. 60 (8), 1688–1698.

Ercoli, F., Ruokonen, T.J., Erkamo, E., Jones, R.I., Hämäläinen, H., 2015a. Comparing the effects of introduced signal crayfish and native noble crayfish on the littoral invertebrate assemblages of boreal lakes. Freshw. Sci. 34 (2), 555–563.

Falchi, F., Bará, S., 2023. Light pollution is skyrocketing. Science 379 (6629), 234–235.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B.A., Rybnikova, N.A., Furgoni, R., 2016. The new world atlas of artificial night sky brightness. Sci. Adv. 2, e1600377.

Faller, M., Harvey, G.L., Henshaw, A.J., Bertoldi, W., Bruno, M.C., England, J., 2016. River bank burrowing by invasive crayfish: spatial distribution, biophysical controls and biogeomorphic significance. Sci. Total Environ. 569, 1190–1200.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Glob. Ecol. Biogeogr. 16 (3), 265–280.

Galib, S.M., Sun, J., Gröcke, D.R., Lucas, M.C., 2022. Ecosystem effects of invasive crayfish increase with crayfish density. Freshw. Biol. 67 (6), 1005–1019.

Gallardo, B., Clavero, M., Sánchez, M.I., Vilà, M., 2016. Global ecological impacts of invasive species in aquatic ecosystems. Glob. Change Biol. 22 (1), 151–163.

Gaston, K.J., Visser, M.E., Hölker, F., 2015. The biological impacts of artificial light at night: the research challenge. Philos. Trans. R. Soc. B: Biol. Sci. 370 (1667), 20140133.

Gelman, A., Hill, J., 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge university press.

Gergs, R., Koester, M., Schulz, R.S., Schulz, R., 2014. Potential alteration of cross-ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the terrestrial food web. Freshw. Biol. 59 (12), 2645–2655.

Gherardi, F., 2007. Biological invasions in inland waters: an overview. Biol. invaders Inland Water.: Profiles, Distrib., Threats 3–25.

Graf, N., Battes, K.P., Cimpean, M., Dittrich, P., Entling, M.H., Link, M., Scharmüller, A., Schreiner, V.C., Szöcs, E., Schäfer, R.B., 2019. Do agricultural pesticides in streams influence riparian spiders? Sci. Total Environ. 660, 126–135.

Graf, N., Battes, K.P., Cimpean, M., Entling, M.H., Frisch, K., Link, M., Scharmüller, A., Schreiner, V.C., Szöcs, E., Zubrod, J.P., Schäfer, R.B., 2020. Relationship between agricultural pesticides and the diet of riparian spiders in the field. Environ. Sci. Eur. 32, 1–12.

Grubisic, M., van Grunsven, R.H., 2021. Artificial light at night disrupts species interactions and changes insect communities. Curr. Opin. Insect Sci. 47, 136–141.

Guan, R.Z., Wiles, P.R., 1998. Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. Aquaculture 169 (3-4), 177–193.

Hammock, B.G., Wetzel, W.C., 2013. The relative importance of drift causes for stream insect herbivores across a canopy gradient. Oikos 122 (11), 1586–1593.

Hartig, F., 2018. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R. Packag Version 020.

Holdich, D.M., Reynolds, J.D., Souty-Grosset, C., Sibley, P.J., 2009. A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. Knowl. Manag. Aquat. Ecosyst. (394-395), 11.

Holdich, D.M., James, J., Jackson, C., Peay, S., 2014. The North American signal crayfish, with particular reference to its success as an invasive species in Great Britain. Ethol. Ecol. Evol. 26 (2-3), 232–262.

Hölker, F., Bolliger, J., Davies, T.W., Giavi, S., Jechow, A., Kalinkat, G., Longcore, T., Spoelstra, K., Tidau, S., Visser, M.E., Knop, E., 2021. 11 pressing research questions on how light pollution affects biodiversity. Front. Ecol. Evol. 9, 767177.

Hölker, F., Jechow, A., Schroer, S., Tockner, K., Gessner, M.O., 2023. Light pollution of freshwater ecosystems: principles, ecological impacts and remedies. Philos. Trans. R. Soc. B 378 (1892), 20220360.

Hudina, S., Hock, K., Žganec, K., Lucić, A., 2012. Changes in population characteristics and structure of the signal crayfish at the edge of its invasive range in a European river. Ann. De. Limnol. -Int. J. Limnol. 48 (1), 3–11.

Iwata, T., 2007. Linking stream habitats and spider distribution: spatial variations in trophic transfer across a forest–stream boundary. Ecol. Res. 22, 619–628.

Jechow, A., Hölker, F., 2019. How dark is a river? Artificial light at night in aquatic systems and the need for comprehensive night-time light measurements. Wiley Interdiscip. Rev.: Water 6 (6), e1388.

Johnson, M.F., Rice, S.P., Reid, I., 2010. Topographic disturbance of subaqueous gravel substrates by signal crayfish (*Pacifastacus leniusculus*). Geomorphology 123 (3-4), 269–278.

Johnson, P.T., Olden, J.D., Solomon, C.T., Vander Zanden, M.J., 2009. Interactions among invaders: community and ecosystem effects of multiple invasive species in an experimental aquatic system. Oecologia 159, 161–170.

Kaiser, T.S., Poehn, B., Szkiba, D., Preussner, M., Sedlazeck, F.J., Zrim, A., Neumann, T., Nguyen, L.T., Betancourt, A.J., Hummel, T., Vogel, H., 2016. The genomic basis of circadian and circalunar timing adaptations in a midge. Nature 540 (7631), 69–73.

Kato, C., Iwata, T., Nakano, S., Kishi, D., 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. Oikos 103 (1), 113–120.

Koel, T.M., Tronstad, L.M., Arnold, J.L., Gunther, K.A., Smith, D.W., Syslo, J.M., White, P.J., 2019. Predatory fish invasion induces within and across ecosystem effects in Yellowstone National Park. Sci. Adv. 5, eaav1139.

Kolbenschlag, S., Bollinger, E., Gerstle, V., Brühl, C.A., Entling, M.H., Schulz, R., Bundschuh, M., 2023. Impact across ecosystem boundaries–Does Bti application change quality and composition of the diet of riparian spiders? Sci. Total Environ. 873, 162351.

Kouba, A., Petrusek, A., Kozák, P., 2014. Continental-wide distribution of crayfish species in Europe: update and maps. Knowl. Manag. Aquat. Ecosyst. (413), 05.

Kowarik, C., Martin-Creuzburg, D., Robinson, C.T., 2021. Cross-ecosystem linkages: transfer of polyunsaturated fatty acids from streams to riparian spiders via emergent insects. Front. Ecol. Evol. 9, 707570.

Kowarik, C., Martin-Creuzburg, D., Mathers, K.L., Weber, C., Robinson, C.T., 2023. Stream degradation affects aquatic resource subsidies to riparian ground-dwelling spiders. Sci. Total Environ. 855, 158658.

Kraus, J.M., Walters, D.M., Mills, M.A., 2020. Switzerland. Contaminants and Ecological Subsidies: Land–Water Interface. Springer Scientific, Cham.

Krell, B., Röder, N., Link, M., Gergs, R., Entling, M.H., Schäfer, R.B., 2015. Aquatic prey subsidies to riparian spiders in a stream with different land use types. Limnologica 51, 1–7.

Król, A., Hajdamowicz, I., Tkaczuk, C., 2018. Diel and seasonal activity of ground dwelling spiders (Araneae) in a sandy grassland habitat. Turk. J. Zool. 42 (4), 439–448.

Krumpalova, Z., Tuf, I.H., 2013. Circadian rhythms of ground living spiders: mechanisms of coexistence strategy based on the body size. Pol. J. Ecol. 61 (3), 575–586.

Kummu, M., De Moel, H., Ward, P.J., Varis, O., 2011. How close do we live to water? A global analysis of population distance to freshwater bodies. PloS One 6 (6), e20578.

Lafage, D., Djoudi, E.A., Perrin, G., Gallet, S., Pétillon, J., 2019. Responses of ground-dwelling spider assemblages to changes in vegetation from wet oligotrophic habitats of Western France. Arthropod-Plant Interact. 13, 653–662.

Lagrue, C., Podgorniak, T., Lecerf, A., Bollache, L., 2014. An invasive species may be better than none: invasive signal and native noble crayfish have similar community effects. Freshw. Biol. 59 (9), 1982–1995.

Land, M.F., 1985. The morphology and optics of spider eyes. In Neurobiology of arachnids. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 53–78.

Larsen, S., Muehlbauer, J.D., Marti, E., 2016. Resource subsidies between stream and terrestrial ecosystems under global change. Glob. Change Biol. 22 (7), 2489–2504.

Leroux, S.J., Loreau, M., 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecol. Lett. 11 (11), 1147–1156.

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2 (4), 191–198.

Manfrin, A., Singer, G., Larsen, S., Weiß, N., Van Grunsven, R.H., Weiß, N.S., Wohlfahrt, S., Monaghan, M.T., Hölker, F., 2017. Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. Front. Environ. Sci. 5, 61.

Manfrin, A., Lehmann, D., van Grunsven, R.H., Larsen, S., Syväranta, J., Wharton, G., Voigt, C.C., Monaghan, M.T., Hölker, F., 2018. Dietary changes in predators and scavengers in a nocturnally illuminated riparian ecosystem. Oikos 127 (7), 960–969.

Manfrin, A., Schirmel, J., Mendoza-Lera, C., Ahmed, A., Bohde, R., Brunn, M., Brühl, C.A., Buchmann, C., Bundschuh, M., Burgis, F., Diehl, D., Entling, M.H., Ganglo, C., Geissler, S., Gerstle, V., Girardi, J.P., Graf, T., Huszarik, M., Jamin, J., Joschko, T.J., Jungkunst, H.F., Knäbel, A., Kolbenschlag, S., Lorke, A., Muñoz, K., Ogbeide, C., Osakpolor, S.E., Pietz, S., Riess, K., Roodt, A.P., Rovelli, L., Röder, N., Rösch, V., Schaumann, G.E., Schäfer, R.B., Schmitt, T., Schmitz, D., Schützenmeister, K., Schwenk, K., Stehle, S., Schulz, R., 2023. SystemLink: Moving beyond Aquatic–Terrestrial Interactions to Incorporate Food Web Studies. Limnol. Oceanogr. Bullettin 77–81.

Marker, J., Bergman, E., Bowes, R.E., Lafage, D., 2023. Small stream predators rely heavily on terrestrial matter energy input in the fall, regardless of riparian buffer size. Food Webs 36, e00302.

Mathers, K.L., Chadd, R.P., Dunbar, M.J., Extence, C.A., Reeds, J., Rice, S.P., Wood, P.J., 2016. The long-term effects of invasive signal crayfish (*Pacifastacus leniusculus*) on instream macroinvertebrate communities. Sci. Total Environ. 556, 207–218.

McCullagh, P., 2019. Generalized linear models. Routledge.

Meyer, L.A., Sullivan, S.M.P., 2013. Bright lights, big city: influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. Ecol. Appl. 23 (6), 1322–1330.

Moore, M.V., Pierce, S.M., Walsh, H.M., Kvalvik, S.K., Lim, J.D., 2000. Urban light pollution alters the diel vertical migration of *Daphnia*. Int. Ver. F. üR. Theor. und Angew. Limnol.: Verh. 27 (2), 779–782.

Moore, M.V., Kohler, S.J., Cheers, M.S., 2006. Artificial light at night in freshwater habitats and its potential ecological effects. In: Rich, C., Longcore, T. (Eds.), Ecological consequences of artificial night lighting. Island Press, Washington, pp. 365–384.

Narimanov, N., Hatamli, K., Entling, M.H., 2021. Prey naïveté rather than enemy release dominates the relation of an invasive spider toward a native predator. Ecol. Evol. 11 (16), 11200–11206.

Nash, L.N., Kratina, P., Recalde, F.C., Jones, J.I., Izzo, T., Romero, G.Q., 2023. Tropical and temperate differences in the trophic structure and aquatic prey use of riparian predators. Ecol. Lett. 26 (12), 2122–2134.

Nelson, T.R., Michel, C.J., Gary, M.P., Lehman, B.M., Demetras, N.J., Hammen, J.J., Horn, M.J., 2021. Effects of artificial lighting at night on predator density and salmonid predation. Trans. Am. Fish. Soc. 150 (2), 147–159.

Nelson, T.R., Michel, C.J., Gary, M.P., Lehman, B.M., Demetras, N.J., Dudley, P.N., Hammen, J.J., Horn, M.J., 2022. Riverine fish density, predator–prey interactions, and their relationships with artificial light at night. Ecosphere 13 (10), e4261.

Nentwig, W., Blick, T., Bosmans, R., Gloor, D., Hänggi, A. and Kropf, C., 2024. Spiders of Europe. Version {09}.2024. Online at ⟨https://www.araneae.nmbe.ch⟩. https://doi.org/10.24436/1.

Nisimura, T., Numata, H., 2001. Endogenous timing mechanism controlling the circannual pupation rhythm of the varied carpet beetle *Anthrenus verbasci*. J. Comp. Physiol. A 187, 433–440.

Olsson, K., Stenroth, P., Nyström, P.E.R., Granéli, W., 2009. Invasions and niche width: does niche width of an introduced crayfish differ from a native crayfish? Freshw. Biol. 54 (8), 1731–1740.

Orihuela-Torres, A., Perez-Garcia, J.M., Sanchez-Zapata, J.A., Botella, F., Sebastian-Gonzalez, E., 2022. Scavenger guild and consumption patterns of an invasive alien fish species in a Mediterranean wetland. Ecol. Evol. 12, e9133.

Ormerod, S.J., Dobson, M., Hildrew, A.G., Townsend, C., 2010. Multiple stressors in freshwater ecosystems. Freshw. Biol. 55, 1–4.

Osakpolor, S.E., Kattwinkel, M., Schirmel, J., Feckler, A., Manfrin, A., Schäfer, R.B., 2021. Mini-review of process-based food web models and their application in aquatic-terrestrial meta-ecosystems. Ecol. Model. 458, 109710.

Osakpolor, S.E., Manfrin, A., Leroux, S.J., Schäfer, R.B., 2023. Cascading impacts of changes in subsidy quality on recipient ecosystem functioning. Ecology 104 (5), e4023.

Owens, A.C., Lewis, S.M., 2018. The impact of artificial light at night on nocturnal insects: a review and synthesis. Ecol. Evol. 8 (22), 11337–11358.

Parkinson, E., Lawson, J., Tiegs, S.D., 2020. Artificial light at night at the terrestrial-aquatic interface: Effects on predators and fluxes of insect prey. PLoS One 15 (10), e0240138.

Parmar, T.P., Kindinger, A.L., Mathieu-Resuge, M., Twining, C.W., Shipley, J.R., Kainz, M.J., Martin-Creuzburg, D., 2022. Fatty acid composition differs between emergent aquatic and terrestrial insects—A detailed single system approach. Front. Ecol. Evol. 10, 952292.

Payne, E.H., Gebregziabher, M., Hardin, J.W., Ramakrishnan, V., Egede, L.E., 2018. An empirical approach to determine a threshold for assessing overdispersion in Poisson and negative binomial models for count data. Commun. Stat. -Simul. Comput. 47 (6), 1722–1738.

Peay, S., Guthrie, N., Spees, J., Nilsson, E., Bradley, P., 2009. The impact of signal crayfish (*Pacifastacus leniusculus*) on the recruitment of salmonid fish in a headwater stream in Yorkshire, England. Knowl. Manag. Aquat. Ecosyst. (394-395), 12.

Perkin, E.K., Hölker, F., Richardson, J.S., Sadler, J.P., Wolter, C., Tockner, K., 2011. The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. Ecosphere 2 (11), 1–16.

Perkin, E.K., Hölker, F., Tockner, K., Richardson, J.S., 2014. Artificial light as a disturbance to light-naïve streams. Freshw. Biol. 59 (11), 2235–2244.

Phillips, I.D., Vinebrooke, R.D., Turner, M.A., 2009. Experimental reintroduction of the crayfish species *Orconectes virilis* into formerly acidified Lake 302S (Experimental Lakes Area, Canada). Can. J. Fish. Aquat. Sci. 66 (11), 1892–1902.

Pietz, S., Kolbenschlag, S., Roeder, N., Roodt, A.P., Steinmetz, Z., Manfrin, A., Schwenk, K., Schulz, R., Schaefer, R.B., Zubrod, J.P., Bundschuh, M., 2023. Subsidy quality affects common riparian web-building spiders: consequences of aquatic contamination and food resource. Environ. Toxicol. Chem. 42 (6), 1346–1358.

Pinder, A.M., Trayler, K.M., Mercer, J.W., Arena, J., Davis, J.A., 1993. Diel periodicities of adult emergence of some chironomids (Diptera: Chironomidae) and a mayfly (Ephemeroptera: Caenidae) at a Western Australian Wetland. Aust. J. Entomol. 32 (2), 129–135.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. 28 (1), 289–316.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL ⟨https://www.R-project. org/⟩.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94 (3), 849–873.

Roberts, M.J., 1995. Spiders of Britain & Northern Europe. HarperCollins Publishers.

Rovelli, L., Mendoza-Lera, C., Manfrin, A., 2024. Organic Matter accumulation and hydrology as drivers of greenhouse gas dynamics in newly developed artificial channels. Environ. Sci. Technol. 58 (19), 8360–8371.

Sala, O.E., Stuart Chapin, F.I.I.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., 2000. Global biodiversity scenarios for the year 2100. science 287 (5459), 1770–1774.

Schirmel, J., Bundschuh, M., Entling, M.H., Kowarik, I., Buchholz, S., 2016. Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. Glob. Change Biol. 22 (2), 594–603.

Schloss, A.L., Haney, J.F., 2006. Clouds, shadows or twilight? Mayfly nymphs recognise the difference. Freshw. Biol. 51 (6), 1079–1089.

Schulz, R., Bundschuh, M., Gergs, R., Brühl, C.A., Diehl, D., Entling, M.H., Fahse, L., Frör, O., Jungkunst, H.F., Lorke, A., Schäfer, R.B., 2015. Review on environmental alterations propagating from aquatic to terrestrial ecosystems. Sci. Total Environ. 538, 246–261.

Schulz, R., Bundschuh, M., Entling, M.H., Jungkunst, H.F., Lorke, A., Schwenk, K., Schäfer, R.B., 2024. A synthesis of anthropogenic stress effects on emergence-mediated aquatic-terrestrial linkages and riparian food webs. Sci. Total Environ. 908, 168186.

Schuster, G.A., Taylor, C.A. & Cordeiro, J. 2010. *Pacifastacus leniusculus*. The IUCN Red List of Threatened Species 2010: e.T153648A4526314.

Souty-Grosset, C., Haffner, P., Reynolds, J.D., Noel, P.Y., Holdich, D.M., 2006. Atlas of crayfish in Europe. Muséum national d'Histoire naturelle, Paris, p. 188.

Tabor, R.A., Brown, G.S., Luiting, V.T., 2004. The effect of light intensity on sockeye salmon fry migratory behavior and predation by cottids in the Cedar River, Washington. North Am. J. Fish. Manag. 24 (1), 128–145.

Thomas, J., James, J., Newman, R.C., Riley, W.D., Griffiths, S.W., Cable, J., 2016. The impact of streetlights on an aquatic invasive species: artificial light at night alters signal crayfish behaviour. Appl. Anim. Behav. Sci. 176, 143–149.

Vaeßen, S., Hollert, H., 2015. Impacts of the North American signal crayfish (*Pacifastacus leniusculus*) on European ecosystems. Environ. Sci. Eur. 27 (1), 1–6.

Voigt, C.C., Scholl, J.M., Bauer, J., Teige, T., Yovel, Y., Kramer-Schadt, S., Gras, P., 2020. Movement responses of common noctule bats to the illuminated urban landscape. Landsc. Ecol. 35, 189–201.

Wickham, H., Chang, W., Wickham, M.H., 2016. Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics. Version 2 (1), 1–189.

Zhang, Z., Capinha, C., Usio, N., Weterings, R., Liu, X., Li, Y., Landeria, J.M., Zhou, Q., Yokota, M., 2020. Impacts of climate change on the global potential distribution of two notorious invasive crayfishes. Freshw. Biol. 65 (3), 353–365.