Bright lights, big city: influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes

LARS A. MEYER1 AND S. MAŽEKA P. SULLIVAN

School of Environment and Natural Resources, Ohio State University, 2021 Coffey Road, Columbus, Ohio 43210 USA

Abstract. Cities produce considerable ecological light pollution (ELP), yet the effects of artificial night lighting on biological communities and ecosystem function have not been fully explored. From June 2010 to June 2011, we surveyed aquatic emergent insects, riparian arthropods entering the water, and riparian spiders of the family Tetragnathidae at nine stream reaches representing common ambient ELP levels of Columbus, Ohio, USA, streams (low, 0.1–0.5 lux; moderate, 0.6–2.0 lux; high, 2.1–4.0 lux). In August 2011, we experimentally increased light levels at the low- and moderate-treatment reaches to 10–12 lux to represent urban streams exposed to extremely high levels of ELP. Although season exerted the dominant influence on invertebrate fluxes over the course of the year, when analyzed by season, we found that light strongly influenced multiple invertebrate responses. The experimental light addition resulted in a 44\% decrease in tetragnathid spider density ($P = 0.035$), decreases of 16\% in family richness ($P = 0.040$) and 76\% in mean body size ($P = 0.022$) of aquatic emergent insects, and a 309\% increase in mean body size of terrestrial arthropods ($P = 0.015$). Our results provide evidence that artificial light sources can alter community structure and ecosystem function in streams via changes in reciprocal aquatic-terrestrial fluxes of invertebrates.

Key words: ecological light pollution; ecosystem function; stream–riparian invertebrate fluxes; tetragnathid spiders; urban streams.

INTRODUCTION

Streams and their adjacent riparian zones are tightly linked through reciprocal exchanges of invertebrate prey (Nakano and Murakami 2001, reviewed in Baxter et al. 2005). For instance, ~80% of the diet of some stream fishes is composed of terrestrial arthropods (Nakano et al. 1999a). Conversely, aquatic invertebrates that emerge from the stream as adults provide important subsidies to riparian and terrestrial food webs (Akamatsu et al. 2004, Power et al. 2004). For example, certain groups of riparian spiders are highly reliant on aquatic emergent insects (Sanzone et al. 2003, Burdon and Harding 2008) and the abundance of some families of riparian web-weaving spiders (e.g., Tetragnathidae) has been shown to be tightly linked to emergent insect abundance and distribution (Kato et al. 2003).

Under natural light regimes, terrestrial invertebrate inputs to streams typically peak during the day (Angradi and Griffith 1990, Nakano et al. 1999b). While there is variability in the timing of emergence events (Morgan and Waddell 1961), emergence and flight often follow a diel pattern, with greatest activity from late evening to early morning (Harper et al. 1983, Jackson 1988, Bernáth et al. 2004). However, increases in artificial night lighting (e.g., roadway, security lighting, and other urban light sources) have dramatically altered natural light levels (Smith 2009, Hölker et al. 2010), yet only recently have the ecological implications of night lighting been considered as a serious conservation concern (reviewed in Longcore and Rich 2004, Rich and Longcore 2006). The influence of elevated night lighting on reciprocal stream–riparian invertebrate exchanges remains unresolved.

For invertebrates, artificial night lighting has been shown to strongly affect terrestrial and aquatic taxa at both individual and population levels (Frank 1988, Scheibe 1999, Eisenbeis and Hänel 2009). For example, artificial night lighting has been shown to attract postemergent aquatic insects, thereby disrupting their dispersal patterns, and in some cases, serving as ecological traps leading to direct mortality and increased predation (Eisenbeis 2006, Horvath et al. 2009). Changes in artificial lighting can also disrupt predator–prey relationships (reviewed in Perkin et al. 2011). Elevated light levels are known to dampen invertebrate drift rates (Bishop 1969), but also may extend or improve fish foraging opportunities (Moore et al. 2006, Nightingale et al. 2006). This may be a considerable advantage to inverteivore fishes (Tabor et al. 2004), especially in small streams where they are the top predators. Thus, artificial lighting may reduce population sizes of aquatic invertebrates through predation-induced mortality. Conversely, the reflection of light off...
the water’s surface may attract terrestrial insects to the water (Schwind 1991), leading to increases in terrestrial prey subsidies for stream fish and releasing benthic insects from predation pressure.

Artificial night lighting has also been implicated in altering higher levels of biological organization such as community composition. Recently, Davies et al. (2012) showed that the relative abundance of ground-dwelling invertebrate scavengers and predators was higher under street lights than between them. Potential consequences on ecosystem function are also possible (Perkin et al. 2011). For example, Moore et al. (2000) attributed increased algal biomass and lower water quality in a suburban lake to artificial lighting via reduced nighttime algal grazing activity by zooplankton.

To better understand the effects of artificial night lighting on linked stream–riparian ecosystems, we tested the hypothesis that ecological light pollution (ELP; sensu Longcore and Rich 2004) alters reciprocal stream–riparian invertebrate fluxes as evidenced by (1) lower community diversity of both aquatic and terrestrial invertebrates, (2) greater density and biomass of aquatic emergent insects and terrestrial arthropods entering the stream, and (3) a decrease in tetragnathid spider density. We tested this hypothesis through observational and experimental components of a study that compared linked stream–riparian invertebrate responses across artificial light levels representing low to extremely high urban ELP.

**METHODS**

In June 2010, we scouted potential study reaches within the Slate Run subcatchment of the Scioto River basin, located within the Columbus, Ohio, Metropolitan Area (CMA) and recorded ambient light (i.e., ELP) during a moonless night using a handheld photometer (Ex-Tech Model 403125; resolution: 0.01 lux, sensitivity \( \pm 3\% \) of the reading; Optimum Energy Products, Calgary, Alberta, Canada). We measured a minimum of three light (lux) measurements at the top, middle, and bottom of each 30-m reach and recorded the average value, from which we categorized ELP into three levels based on the relative range of artificial light levels commonly found in local canopied urban streams: low (0.1–0.5 lux), moderate (0.6–2.0 lux), and high (2.1–4.0 lux). Of the reaches, we selected three of each ELP light level (\( n = 9 \)) that represented minimal variability in stream physicochemical (e.g., water quality, substrate, geomorphology) and riparian (adjacent land use, buffer width, vegetation) characteristics (as shown in Appendix A: Table A1). We estimated mean canopy density within the channel and along the riparian area of each study reach using a handheld densitometer (Graphic Resource Solutions, Arcata, California, USA; Kelley and Krueger 2005, Progar and Moldenke 2009).

At each study reach, we conducted collections of aquatic emergent insects and riparian arthropods entering the stream once every two months from June 2010 to June 2011. For aquatic emergent insects, we used floating Mundie-style emergence traps (Mundie 1964). We anchored three 1-m\(^2\) traps: one each toward the top, middle, and bottom of each study reach and located in dominant flow habitats of the reach (typically a riffle, pool, and a run). For terrestrial arthropods entering the stream, we used floating pan traps (Grigarick 1959). We deployed three rectangular 0.25-m\(^2\) traps under the vegetative canopy along the stream, placed in a similar fashion as the emergent traps at the top, middle, and bottom of each reach. We partially filled the pan traps with water (~4 cm) and a few drops of surfactant (soap) to trap invertebrates (Greenwood et al. 2004). We deployed emergence and pan traps for 10 d during the middle of each sampling month. We collected specimens from the traps approximately every other day and transported them to the laboratory, where they were immediately frozen. Subsequently, we sorted, enumerated, and identified all samples to family using Triplehorn and Johnson (2005), Merritt and Cummins (1996), and Ubick et al. (2005) as guides. All samples were oven dried at 55°C (~48 h) and weighed (g/m\(^2\)) (Sanzone et al. 2003, Akamatsu 2007).

We also surveyed the webs of horizontal orb web-building spiders (Tetragnathidae) by conducting nighttime web counts, a surrogate measure of abundance (Benjamin et al. 2011). We recorded all orb webs within 1 m of the stream edge and up to 2 m in height following Williams et al. (1995).

**Experimental addition of light**

We mimicked elevated light levels to which streams are exposed in highly developed areas of the urban landscape with a modified BACIP (paired before–after, control–impact) experiment (Stewart-Oaten et al. 1986, Downes et al. 2002). The three low (0.1–0.5 lux) sites from 2010 served as the before-control (i.e., representing the lowest light levels in the system) and the moderate (0.6–2.0 lux) sites from 2010 served as the before-impact. Because of a loss of access to one of the moderate sites, we were left with only two before-impact sites. The addition of light in 2011 to both low and moderate light sites (\( n = 5 \)) served as the after-control and after-impact treatments, respectively. Although we did not include an unmanipulated control site in 2011, benthic invertebrate data (2010–2012) from stream monitoring efforts in the same study stream indicate minimal interannual variability in community composition (as shown in Appendix B: Table B1). Additionally, all experimental stream reaches were located in close proximity to one another within the same stream system; thus, any environmental changes between years would presumably have had similar effects on all sites. Flow, precipitation, and temperature were also comparable for the 2010 and 2011 sampling periods (as shown in Appendix B: Table B2).

To determine appropriate ELP levels for the addition of light, we measured light levels at open or partly canopied streams adjacent to restaurants, sports arenas,
roads with dense street lighting, malls and large stores, and other highly developed areas, and found that light levels typically ranged from 8 to 12 lux (7.5–12.2, $\bar{x} = 1.5$, SD = 1.5 lux). To replicate such extreme light levels, we added strings of battery operated white light-emitting diode (LED) lights (broad spectrum) to the five study reaches in early July 2011. At each reach, we wired LEDs into clusters to create “pockets” of diffuse light to simulate infiltration of ELP from artificial sources. We secured light strings to the overhanging foliage longitudinally along the stream channel and laterally across the stream to approximate 10–12 lux as measured 1 m above the stream surface. The light strings were lighted continuously until sampling was completed. During mid-August, we collected aquatic emergent insects and terrestrial arthropods falling into the stream, and we surveyed tetragnathid spider webs following the same protocols described previously.

**Numerical and statistical analysis**

For all reaches, we calculated density (number/m²), biomass (mg/m²), mean body size (biomass ± density), and family richness of both aquatic emergent insects and terrestrial arthropods. Net aquatic–terrestrial invertebrate flux was based on the difference between aquatic emergent insect density and terrestrial arthropod density (i.e., positive values represent a greater aquatic-to-terrestrial invertebrate flux, and negative values indicate a greater terrestrial-to-aquatic flux). We performed repeated-measures analysis of variance (rANOVA) to test for potential differences in aquatic emergent insect and riparian arthropod measures (density, biomass, family richness, net flux) and tetragnathid density within each sampling month (season). In our analysis, the between-subject factor was ELP level, and the within-subject factor was month (June, August, October, December, February, April), and the dependent variables were invertebrate responses. The interaction ELP × month was also included in the models. We followed with linear contrasts for models where ELP was a significant factor.

Subsequently, we ran general linear models (GLMs) for each sampling month to test for the influence of ELP independent of season on aquatic emergent insects, terrestrial arthropods, and tetragnathid spiders. Although we opt not to include canopy cover in the rANOVA models, given the highly correlative relationship between month and canopy cover, we did include canopy cover as a covariate in the GLMs, as the influence of canopy cover on aquatic macroinvertebrates and terrestrial arthropods is well known (Progar and Moldenke 2009, Riley et al. 2009). In all GLMs, “reach” (nested within “ELP”) was included as a random variable. “ELP” was included as a fixed variable, and “canopy” was included as a covariate. Where significant main effects were detected, we conducted linear contrasts between ELP levels.

Lastly, we used paired t tests to test for potential differences between our invertebrate response measures from August 2010 (pre-experimental light addition) and August 2011 (post light addition). We performed all analyses using JMP 9.0 Statistical Discovery Software (SAS Institute 2010).

**RESULTS**

Overall, we recorded 17 281 stream and riparian arthropods, distributed among 35 aquatic and 81 terrestrial families. The diversity and density of stream–riparian invertebrate communities were highly variable across the study sites (as shown in Appendix C: Tables C1 and C2). Although month was the overwhelmingly influential factor on measures of aquatic–terrestrial invertebrate flux considered in this study, light was also influential for many invertebrate responses (Table 1, Fig. 1). When analyzed by sampling month, thereby removing the influence of season, light emerged as a strong predictor of multiple invertebrate responses, particularly during the autumn (Table 2).

For aquatic emergent insects, light alone was not a significant factor in the repeated measures models, although the interaction of light and month was significant (Table 1). For the October sampling period, ELP significantly influenced measures of aquatic emergent insect flux, where linear contrasts showed that the density and richness of aquatic emergent insects was 6.6 ($F^2 = 11.21, df = 1, P < 0.001$) and 2.1 ($F^2 = 7.85, df = 1, P = 0.005$) times lower at low and high ELP reaches than at moderate ELP reaches, respectively. ELP also played a secondary role to season in influencing terrestrial arthropod density and biomass. Light–density relationships were variable by season, with the density of terrestrial arthropods roughly four times higher at high ELP sites in spring/early summer than in late summer/fall (Fig. 1A). Biomass, however, was more consistently greater at high ELP sites over the course of the year (Fig. 1C). Terrestrial inputs of arthropods to the stream, although minor, was the only measurable invertebrate flux from December and February. For these months, light was a significant factor for both terrestrial arthropod density and family richness (Table 2).

We observed the highest net flux value (220.2 individuals/m²) in August, indicating a greater aquatic-to-terrestrial than terrestrial-to-aquatic transfer of invertebrates. Conversely, the greatest terrestrial-to-aquatic flux occurred in October (−134.9 individuals/m²). The net flux rANOVA model was the only model in which the effect strength of light ($F_{1,16} = 2.84$) and light × season ($F_{10,24} = 2.86$) were comparable to that of season ($F_{5,12} = 3.94$). Net flux was also significantly different among all ELP levels, with net flux at high ELP sites exhibiting greater variability than net flux at low and moderate ELP sites from June through October (Fig. 1D). Light was not a significant factor for mean body size of either aquatic emergent insects or terrestrial arthropods (Table 1, Table 2).
Across all study sites, tetragnathid spider activity was greatest in June and August (as shown in Appendix D: Table D1). Both month and ELP influenced the density of Tetragnathidae (Table 1). Over the course of the year, spider density was lowest at high ELP sites (Fig. 1E), differing from both low ($F_{1,16} = 11.52, P = 0.004$) and

### TABLE 1. Repeated-measures analysis of variance for bi-monthly aquatic and terrestrial invertebrate responses to ecological light pollution for study reaches in the Columbus Metropolitan Area, Ohio, USA.

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
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<tr>
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<td>Light × Month</td>
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<td>1.55</td>
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**Notes:** Light levels are: low, 0.1–0.5 lux; moderate, 0.6–2.0 lux; and high, 2.1–4.0 lux. “Terrestrial arthropod” refers to the flux of terrestrial insects and spiders to the stream. Mean body size is the average individual body mass (mg). Net flux is the density of aquatic emergent insects minus the density of terrestrial arthropods falling into the stream.

**Fig. 1.** Significant aquatic–terrestrial invertebrate responses to ecological light pollution (ELP): (A) higher density of terrestrial arthropods falling into the stream in summer and lower density in autumn at high ELP; (B) higher family richness of terrestrial arthropods entering stream in summer at high ELP; (C) higher biomass of terrestrial arthropods falling into the stream in summer at high ELP; (D) differences in net flux (density of aquatic emergent insects minus the density of terrestrial arthropods falling into the stream) among ELP levels from summer through fall, with the greatest variability at high ELP; (E) lower density of spiders of the family Tetragnathidae in summer at high ELP. Light levels not connected by the same lowercase letter are significantly different ($P < 0.05$).
moderate ($F_{1,16} = 19.77, P < 0.001$) ELP sites (Fig. 1E). Collectively, these differences represent a 41% mean annual decrease in spider density between high and low-moderate ELP sites.

Experimental addition of light

We observed consistent invertebrate responses to the August experimental increase of light at low (after-control) and moderate (after-impact) sites (Fig. 2), which strengthened the evidence for light as a significant driving factor of invertebrate responses. Collectively across the five experimental sites, we observed a 44% decrease in tetragnathid spider density ($t = -3.13, df = 1, P = 0.035$; Fig. 2A) compared to spiders densities that were only 19% less at high-light sites vs. low-light sites (i.e., before-control) during August 2010. We also observed a 16% decrease in aquatic emergent insect family richness ($t = -2.99, df = 1, P = 0.040$; Fig. 2B). Contrasting patterns emerged between mean body size (mg) of aquatic emergent insects and terrestrial arthropods entering the stream, whereby body size of emergent insects decreased by 75% ($t = -3.64, df = 1, P = 0.022$; Fig. 2C), while that of terrestrial arthropods increased threefold ($t = 4.10, df = 1, P = 0.015$; Fig. 2D). We also
observed suggestive increases in terrestrial arthropod biomass ($t = 2.47$, $df = 1$, $P = 0.069$) and aquatic:terrestrial net flux ($t = -2.33$, $df = 1$, $P = 0.073$) at extremely high light levels. Although not statistically significant, increases in both terrestrial arthropod biomass and aquatic:terrestrial net flux were consistent with observational results for August.

**DISCUSSION**

The energetic pathways that connect stream and riparian ecosystems can have profound consequences for linked aquatic and terrestrial populations and food web dynamics (Vander Zanden and Sanzone 2004, Baxter et al. 2005, Sullivan and Rodewald 2012). Across the course of the year, we observed significant differences in multiple invertebrate response measures among ambient urban light levels. The experimental addition of light prompted strong responses of tetragnathid spiders, aquatic emergent insect family richness, and mean body size of both aquatic emergent insects and terrestrial arthropods and helped to confirm or clarify patterns observed in the observational component of the study. We provide initial evidence that ecological light pollution can significantly influence stream–riparian invertebrate community characteristics, cross-boundary invertebrate fluxes, and riparian spiders that rely on these fluxes.

There was significant variability in terrestrial arthropod responses to light across the year. Although we expected that high ELP levels would associate with a greater relative input of terrestrial arthropods entering the stream, we observed this pattern only in spring and early summer (Fig. 1A, C). Artificial lighting has been shown to disrupt nocturnal navigation and migration in some arthropods by masking the physical properties (i.e., polarization) of the moon’s naturally reflected light (Horvath et al. 2009) and is widely known to attract phototaxic insects (Horvath et al. 2011, Egri et al. 2012). An increase in artificial lighting reflecting off the water’s surface may thusly attract terrestrial arthropods to the stream, a pattern weakly supported by a positive response of terrestrial arthropod biomass to the experimental increase in light ($P = 0.069$). This increase in terrestrial arthropod biomass appears to be largely driven by an increase in mean body size of the terrestrial arthropod community (Fig. 2D). In our study system, common large-bodied taxa include predators and scavengers such as rove beetles (Staphylinidae), assassin bugs (Reduviidae), and wolf spiders (Lycosidae) that are likely attracted to highly lit areas by an increase in invertebrate prey abundance. Similarly, Davies et al.

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**Fig. 2.** Responses of aquatic and terrestrial invertebrates to experimental light addition (based on paired t tests): (A) density of spiders of the family Tetragnathidae decreased by 44%; (B) family richness of aquatic emergent insects decreased by 16%; (C) body size of aquatic emergent insects decreased by 76%; (D) body size of terrestrial arthropods entering stream increased by 309%. Low (after-control) ELP sites are shown with X’s at the mean, and moderate (after-impact) ELP sites are shown with a dash at the mean; error bars are ±SE.
alterations in community structure extend beyondbrate communities under street lamps. Light-induced
(2012) found an increase in the relative abundance of
flying species avoid lights (Blake et al. 1994, Rydell and
2010), and fast-flying species of bats have been shown to
gather around lights to feed on insects whereas slower
flying species avoid lights (Blake et al. 1994, Rydell and
Baagøe 1996).
Our hypothesis that increased ELP would result in
decreases in aquatic emergent insect diversity, but with
increases in density and biomass, was only partially
supported. Across the year, light alone was not a
significant predictor of aquatic emergent insect respons-
es, although the interaction of light and month was
influential. With elevated light, a greater terrestrial-to-
aquatic flux of larger bodied individuals may lead to
preferential selection of terrestrial arthropods by stream
fish, thereby releasing benthic invertebrates from high
predation pressure and leading to greater densities of
aquatic emergent insects (Baxter et al. 2004), particu-
larly during the summer months when terrestrial
invertebrate activity tends to be highest.
Although there was no effect of light on aquatic
emergent insect body size during the observational
component of the study, the addition of light prompted
a strong decrease in mean body size (Fig. 2C), indicating
a potential threshold response to light. Given that the
common invertivore fish species found in the study
system (e.g., creek chub [Semotilus atromaculatus] and
green sunfish [Lepomis cyanellus]) are visual predators,
larger bodied benthic invertebrates (e.g., Corydalidae,
Sialidae, Coenagrionidae, Perlidae) might be expected to
be disproportionately depredated over small-bodied
groups such as Chironomidae, Simuliidae, and Baetidae
(Newman and Waters 1984, Rincón and Lobón-Cerviá
smaller body sizes may also relate to higher relative
abundances of armored grazers (e.g., glossosomatid
caddisflies), which would, in turn, affect algal growth
and instream primary productivity. This community-
wide shift in body size was also reflected in the
significant decrease we observed in aquatic emergent
insect family richness (Fig. 2B).
Even at low light levels, our results were not
consistent with the scenario in which the forest feeds
stream food webs during the summer, and that
conversely, the stream fuels terrestrial food webs from
fall to spring (Power 2001). Measurable differences in
net flux estimates among light levels provided evidence
that artificial lighting may shift the balance of inverte-
brate feedback loops between the stream and the
riparian zone. In our study, net flux was most variable
at high light levels (Fig. 1D), suggesting that elevated
light levels may lead to exaggerated swings in aquatic-
terrestrial resource pulses across the course of the year.
Consistent with our observational results, experimental
results suggested a 26% increase in the aquatic-to-
terrestrial net flux for August, although this relation-
ships was relatively weak ($P = 0.073$). The precise nature
of these changes will require further investigation.
Tetragnathid spider density showed a strong negative
response to high ELP during their most active months as
well as to the experimental increase of light (Fig. 2A).
Multiple mechanisms are likely responsible. Firstly, the
reductions in both aquatic emergent invertebrate density
and body size that we observed at elevated light levels
likely led to reduced prey availability for spiders.
Concomitantly, light-induced increases in the activity
of terrestrial predators (birds and other invertebrates)
may contribute to reduced tetragnathid density. High
light levels may also inhibit the ability of spiders to
remain hidden, making them more vulnerable to
predation. Finally, high light levels have been shown
to reduce the efficacy of the ventrum spots used to lure
prey in some spiders (Chuang et al. 2008), potentially
forcing emigration to less lit areas.
Collectively, the results of our study enhance our
understanding of the influences of light pollution on
aquatic ecosystems. In interpreting the results, we
propose the following caveats. First, our study system
is located in a major metropolitan area with substantial
skyglow, thus precluding any zero-light study sites.
Second, although low-pressure sodium lights are the
most widely used lighting in our study system, a variety
of other lighting types (e.g., high-pressure sodium lights,
metal halide lights, mercury vapor) are found through-
out the greater CMA. We did not quantify the spectral
quality of the ambient light at our study sites, although
we recognize the potential importance of spectral range
and intensity to ecological responses (Frank 1988,
Moore et al. 2006). A knowledge of spectral composi-
tion of ambient light would be useful for further elucidating mechanisms behind our observed responses.
To our knowledge, our findings provide the first
evidence that artificial night lighting affects ecosystem-function by significantly altering fluxes of organisms and
nutrients between terrestrial and aquatic systems. In
addition, this study documents shifts in community
characteristics (e.g., biomass, density, diversity, body
size), supporting recent work that ELP affects higher
levels of biological organization (Nightingale et al. 2006,
Eisenbeis and Hänel 2009, Davies et al. 2012). As the
world’s populations continue to urbanize, the potential
for ELP to influence communities and ecosystems at
broader spatial scales also increases. We believe that
research addressing the influence of artificial night
lighting on biodiversity, food webs, ecological networks,
and ecosystem function will have significant conserva-
tion benefits. Within this framework, additional research
that further explores the effects of ELP in its many
forms (e.g., point source, atmospheric reflection, polar-
ization, spectrum frequency, intensity, length of expo-
sure period) in both aquatic and terrestrial environments will be critical.

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Literature Cited


SUPPLEMENTAL MATERIAL

Appendix A
Stream physicochemical characteristics for study reaches in the Columbus Metropolitan Area, Ohio, USA (Ecological Archives A023-070-A1).

Appendix B
Tables presenting stream benthic invertebrate monitoring data and precipitation and climate data for the Columbus, Ohio, USA, study area (Ecological Archives A023-070-A2).

Appendix C
Tables presenting aquatic insect families captured in emergent traps and terrestrial arthropod families captured in pan traps (Ecological Archives A023-070-A3).

Appendix D
Summary statistics of invertebrate responses for Columbus, Ohio, study reaches (Ecological Archives A023-070-A4).