Do the ecological impacts of dam removal extend across the aquatic–terrestrial boundary?

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Abstract. The longitudinal influences of dam removal on river ecosystems are increasingly well described, but impacts to aquatic–terrestrial connectivity are largely unknown. Before and four successive years after dam removal, we quantified density and trophic metrics of nearshore tetragnathid spiders and riparian swallows and their potential emergent-aquatic insect prey at two experimental reaches located within the former impoundment (one unrestored, one with channel restoration) and one control reach above an intact lowhead dam. We observed substantial annual variability in response variables; however, few patterns appear to be strongly linked to dam removal. We found negligible changes in emergent-insect biomass or community structure, although there were slight changes in the relative abundance of feeding modes (e.g., increased predators, decreased collector-gatherers). The most pronounced response was a ~9.9 times average decline in spider densities after dam removal at the restored reach. Stable-isotope analysis (\(^{13}C, {^{15}}N\)) indicated that changes in aquatically-derived energy (i.e., nutritional subsidies derived from aquatic primary producers) to riparian consumers generally showed comparable patterns system-wide; swallow aquatically-derived energy declined more in the restored vs. control reach by the final year of the study. Trophic position (TP) of spiders showed little change post-dam removal, while swallow TP converged slightly between control and experimental reaches after dam removal. Collectively, we interpret our results as evidence that lowhead dam removal can prompt relatively nuanced shifts in aquatic–terrestrial trophic dynamics, regardless of intensive channel-restoration activities. In contrast, we found that broader-scale forcings (e.g., discharge, regional temperature) may be more influential in governing cross-boundary trophic interactions than the perturbations related to lowhead dam removal. This study furthers current understanding of the effects of dam removal on integrative, food-web metrics of ecosystem structure and function.

Key words: aerial insectivorous birds; aquatic-insect emergence; in-stream perturbations; nearshore spiders; nutritional subsidies; riparian; stable isotopes.

INTRODUCTION

Dams affect geomorphic, chemical, and biological processes of streams and rivers (Ligon et al. 1995, Doyle et al. 2005, Nilsson et al. 2005). The majority of dams are small (<7.5 m in height; U.S. Army Corps of Engineers 2013), which, despite their size, can have measurable influences on rivers (Csiki and Rhoads 2010). Removal of both large and smaller, lowhead dams, is becoming a popular restoration method to reestablish upstream–downstream connectivity of flow, sediment regimes, and organisms (Poff and Hart 2002, Bellmore et al. 2017a); the majority of dams that are removed are <8 m in height (Bellmore et al. 2017a). In-stream
longitudinal responses to the suite of perturbations related to dam removal, while still understudied, are increasingly documented (Bednarek 2001, Doyle et al. 2005, Gardner et al. 2013, Bellmore et al. 2017a). However, the effects of dam removal on lateral connectivity with riparian ecosystems are not well described, particularly in the context of biotic coupling via food-web interactions between rivers and terrestrial riparian zones (Schulz et al. 2015). Understanding how dam removal affects these lateral interactions across ecosystem boundaries is critical to understanding the broader ecological implications of this restoration process.

Streams and their adjacent riparian zones are linked through exchanges of organic matter (i.e., energy), biota, and nutrients; reciprocal transfers of energy through these linkages are essential to maintain ecosystem functions (reviewed in Baxter et al. 2005). Terrestrial-to-aquatic transfers of energy are widely recognized (Covich et al. 1999, Power et al. 2004), yet reverse, aquatic-to-terrestrial energy flows also provide important nutritional subsidies to riparian and terrestrial food webs (Power and Rainey 2000, Henschel et al. 2001, reviewed in Baxter et al. 2005, Kautza and Sullivan 2016). Prey items represent critical energetic connections between aquatic and terrestrial ecosystems. In particular, aquatic insects emerging from streams as adults (hereafter “emergent insects”) constitute a key nutritional subsidy for a suite of terrestrial consumers (Murakami and Nakano 2002, reviewed in Baxter et al. 2005). Behavioral studies suggest that the timing and location of emergent insects affect the movement and distribution of these consumers, including riparian spiders (Kato et al. 2003, Power et al. 2004) and birds (Iwata et al. 2003, Alberts et al. 2013) that rely on emergent insects as a food resource (Sanzone et al. 2003).

A suite of changes to within-channel structure and function of rivers can occur after a dam is removed, and these changes are typically observed over differing timescales (i.e., pulse vs. press disturbance; Stanley et al. 2010). For example, immediately after the dam is removed, there can be an initial flush of stored sediments and nutrients (Magilligan et al. 2016a), channel constriction leading to newly exposed riparian zones, and reduced water depth (Stanley et al. 2002). These initial effects can alter macroinvertebrate community composition (Orr et al. 2008, Renófalt et al. 2013, Sullivan and Manning 2017) and lead to shifts from lentic to lotic fish assemblages (Dorobek et al. 2015). Over variable timescales, newly exposed sediments become revegetated (Orr and Stanley 2006) and channel morphology continues to adjust (Gartner et al. 2015). Despite a relatively robust framework for the physical effects of dam removal, and the potential spatial and temporal scope of these perturbations, our understanding of their effects on integrative metrics of ecosystem structure and function (Palmer and Febria 2012), such as food-web dynamics across the aquatic–terrestrial boundary, remains unresolved (but see Schulz et al. 2015). Further, there is a need to understand how restoration, including via dam removal, can affect river food webs both within the stream channel (Bellmore et al. 2017b) and across ecosystem boundaries.

We hypothesized that because dam removal can prompt several changes to in-stream ecosystem structure that are likely to affect aquatic–terrestrial linkages (reviewed by Schulz et al. 2015), these changes would extend laterally from the river to affect adjacent riparian consumers via trophic pathways. For example, emergent aquatic-insect fluxes to riparian zones have been modeled previously to scale linearly with ecosystem size (i.e., stream width; Gratton and Vander Zanden 2009). Thus, river channel constriction post-dam removal (e.g., reduced ecosystem size) could disrupt insect prey emergence. Along with the potential for changes to insect fluxes, if dam removal affects basal-resource supply to primary consumers (increased fine sediments vs. stimulated algal growth; e.g., Gray and Ward 1982), then changes to benthic insect diets (and in turn adult, emergent insects) could affect riparian consumers.

We tested our overall hypothesis by comparing several responses related to aquatic–terrestrial connectivity before (2 yr) and after (4 yr) dam removal in two reaches encompassing the former impoundment, and in one control reach above an intact dam in the same system. We evaluated changes to aquatic–terrestrial linkages, including the biomass and composition of emergent insects, and the density and trophic measures of nearshore spiders and riparian swallows (consumer reliance on aquatically-derived
energy [i.e., derived from primary producer pathways] and number of trophic transfers from the base of the food web, hereafter trophic position [TP]). Because spiders depend on riparian habitat structure to build webs and intercept insects (Kato et al. 2003), we expected that tetragnathid spider density would track nearshore vegetation and habitat complexity: Initial decreases in spider density would correspond with nearshore vegetation losses following the rapid, post-dam removal reduction in channel width, but would subsequently increase as exposed riparian areas developed vegetation. Based on findings by Kautza and Sullivan (2016)—who found that Chironomidae in dammed river reaches transported more aquatically-derived energy to terrestrial consumers than in free-flowing reaches—we predicted that dam removal would prompt a decrease in spider and swallow reliance on aquatically-derived energy. Further, we expected that shifts in emergent-insect community taxonomic or functional structure (e.g., functional feeding groups) following dam removal (Sullivan and Manning 2017) would modify food-web pathways leading to alterations in tetragnathid spider and swallow TP.

Because of the unreplicated nature of our large, natural experiment on the fifth-order Olentangy River (Ohio, USA), we also compared a subset of responses with the same measures in free-flowing reaches upstream and downstream of the dam removal reaches in the same river system, and in a separate sub-watershed not influenced by dam removals (Fig. 1b, c). Additionally, we considered broad, system-wide influences (e.g., streamflow, regional temperature, and precipitation) as potential controls on trophic responses.

MATERIALS AND METHODS

Site description and experimental approach

The Olentangy River is a 156-km tributary of the Scioto River, with a drainage area of 1406 km² (Fig. 1a). The lower Olentangy River flows through the city of Columbus, Ohio, where it enters the Scioto River. Our study followed a modified BACI (before-after, control-impact) design (Downes et al. 2002) with three 300-m reaches within a 2.6 river-km (rkm) segment upstream of the 5th Avenue Dam, which was removed in the summer of 2012 (Figs. 1b, 2). Our control reach was located above an intact low-head dam of comparable age and height to the 5th Avenue Dam (Fig. 1b). Two experimental reaches were situated 1.3 and 2.2 rkm upstream of the former 5th Avenue Dam. One was intensively restored, including channel reconfiguration, floodplain wetland redevelopment, and native riparian vegetation plantings (Ohio Environmental Protection Agency 2011); this reach was located entirely within the scope of influence of these restoration activities (Figs. 1b, 2). The other experimental reach was left to readjust without interventions (hereafter, restored and unrestored, respectively). Three 100-m sub-sites (i.e., for reach-level replication) were established at upstream, middle, and downstream locations of each study reach.

Two years of before data relative to emergent insects, tetragnathid spiders, and swallows were available from two reaches (control reach and restored reach) as part of ongoing food-web research in the same river system (see Alberts et al. 2013, Kautza and Sullivan 2016, Tagwireyi and Sullivan 2016). Coordinated data collection (emergent insects, tetragnathid spiders) was conducted at each sub-site in June and August 2011–2012 (pre-dam removal) and 2013–2016 (post-dam removal). For swallows, post-dam removal data were also collected, but at the reach (vs. sub-site) level, and no samples were collected at the control reach and unrestored reach in 2013.

Large, unreplicated studies or experiments, including many opportunistic dam-removal studies, are constrained by multiple factors that limit the availability or practicality of replicate study sites. For example, typically only one dam is removed at a time within a watershed, and both the location and timing of dam removal can be problematic for implementing conventional experimental designs. Our study was not unique in this regard, and so we were unable to fully separate dam-removal effects from other interannual effects. Nevertheless, our design that included two experimental sites and a control, as well as both pre- and post-dam removal data extending across six years, is consistent with dam-removal studies in the literature (Tullos et al. 2014, Kornis et al. 2015, Claeson and Coffin 2016). Whereas we used an experimental design
that was amenable to traditional hypothesis testing in the strictest sense, we also considered the implications of potential trends in our data in the context of both pre-dam removal data collected as part of this study, as well as complementary data examining similar responses in nearshore spiders, riparian swallows, and emergent insects from free-flowing reaches of the same river system (Kautza and Sullivan 2016, Tagwireyi and Sullivan 2016).

**Emergent insects**

Following Kautza and Sullivan (2015), we deployed six 1-m² Mundie-style emergent-insect traps (Mundie 1964) along transects (two per transect, one located toward the left bank and one toward the right bank) for ten days at each of the three reaches. These two samples were combined for each transect. After five and ten days of deployment, we sorted and enumerated all emergent insects to family according to Triplhorn and Johnson (2005) and Merritt et al. (2008). From these data, we calculated biomass flux (mg·m⁻²·d⁻¹) and mean body size (biomass/density) of individual insects (mg). We also categorized insects based on their feeding modes during larval or nymphal stages (collector-gatherer, collector-filterer, predator, herbivore) based on Poff et al. (2006) and Merritt et al. (2008). Parasitic wasps (e.g., family Braconidae) were excluded from this trait analysis. We processed a subset of the emergent-insect community (the numerically dominant family observed in the study: midges of the family Chironomidae) for stable-isotope analysis (see Methods: Stable-isotope analysis).

**Tetragnathid spiders**

Following methods outlined in Meyer and Sullivan (2013) and Tagwireyi and Sullivan (2016),
we surveyed riparian tetragnathid spiders on both sides of the river at night (21:00–24:00 hours), along 30-m riparian segments parallel to the shoreline and centered at each of the three transects per study reach. Within each survey location, all horizontal orb webs within one horizontal m and two vertical m of the river were counted and considered evidence of one tetragnathid spider (Williams et al. 1995, Benjamin et al. 2011). Five to ten individual spiders were collected for subsequent isotopic analysis (see Methods: Stable-isotope analysis).

**Riparian swallows**

We captured aerial insectivorous riparian swallow species of the family Hirundinidae (majority [88%] were Tree Swallows [*Tachycineta bicolor*]) during the breeding season (June–July in our study area). We used mist nets or nest boxes (see Alberts et al. 2013 for detailed methods related to nest boxes) to capture at least six individuals (usually >15). Briefly, we positioned mist nets (2.7 × 12 m, 30 mm mesh size) nearshore or across sections of the river to intercept birds, according to observations of their behavior and flight patterns. We set and monitored mist nets during the morning, and late afternoon/evening when birds are most active. We drew blood from the jugular vein of swallows for stable-isotope analysis (see Methods: Stable-isotope analysis) following methods outlined in Sullivan and Vierling (2012) and Alberts et al. (2013).
Periphyton and detritus

We sampled periphyton annually by scrubbing 15 haphazardly collected cobbles across each reach with a small nylon brush (Finlay et al. 1999). We collected three detrital samples by hand from representative habitats across the reach. Detritus was frozen in plastic sleeves until processing. Coarse particulate matter was manually removed from periphyton samples, resulting in samples predominantly composed of benthic algae (i.e., diatoms). Fine particulate matter (particles <1 mm) was sieved from detritus.

Discharge, temperature, and precipitation

We evaluated annual differences in discharge \( (m^3s^{-1}) \) in the Olentangy River during the study period using publically available stage data (USGS site 03226800), coinciding with the periods immediately before, during, and after our samples were taken (May 1–September 1 of each study year). We used median daily discharge for this period and assessed relationships between discharge and consumer responses such as reliance on aquatically-derived energy. We also accessed local climatological data for 2011–2016 from the National Centers for Environmental Information (ncdc.noaa.gov) from The Ohio State University Airport (Columbus, Ohio; Station ID: WBAN:04804) and computed mean annual temperature and cumulative precipitation for each year of the study.

Stable-isotope analysis

Naturally abundant stable-isotope (carbon \( [\delta^{13}C] \) and nitrogen \( [\delta^{15}N] \)) signatures of detritus, periphyton, nearshore tetragnathid spiders, and riparian swallows were estimated following methods outlined in Kautza and Sullivan (2016). Spiders, detritus, and periphyton were sampled concomitantly, in early or late summer (June, August) of each year of the study, before and after dam removal, whereas swallows were sampled during the breeding season (late May through early July). Briefly, detritus, spider, and swallow (blood) samples were dried (60°C for 48 h) and homogenized with a ball mill or mortar and pestle, and packaged in tin capsules. Likewise, periphyton samples were filtered onto GF/F filters, dried, and packaged into tin capsules for analysis. All samples were analyzed at the Washington State University Stable Isotope Core Facility (Pullman, Washington, USA).

We first estimated emergent insect, riparian spider, and swallow TP using a two-source food-web model (periphyton and detritus) and \( \delta^{15}N \) and \( \delta^{13}C \) signatures of collected consumers (Post 2002). However, recognizing that our focus on periphyton alone may have missed additional contributions of other aquatic primary producers (e.g., phytoplankton, macrophytes; see Kautza and Sullivan 2016), we updated our models with a 4-source model (detritus, periphyton, phytoplankton, macrophytes) based on data collected prior to dam removal from 12 dammed and free-flowing sites in the Scioto-Olentangy river system from 2011 to 2013 (\( n = 36; \) see Kautza and Sullivan 2016 for details about sampling sites and methods). Thus,

\[
TP = \lambda + \frac{\delta_{\text{consumer}} - [\delta_{\text{peri}}\alpha + \delta_{\text{phyto}}\beta + \delta_{\text{mac}}\gamma + \delta_{\text{det}}\{1 - \alpha - \beta - \gamma\}]}{\Delta_n}
\] (1)

where \( \lambda \) is the TP of basal resources (i.e., 1); \( \delta_{\text{consumer}} \) is the isotopic signature for the consumer (\( \delta^{15}N \)); \( \delta_{\text{peri}} \), \( \delta_{\text{phyto}} \), \( \delta_{\text{mac}} \), and \( \delta_{\text{det}} \) are the signatures of primary producers (periphyton, phytoplankton, macrophytes) and conditioned detritus, respectively; \( \alpha \), \( \beta \), and \( \gamma \) are the proportion of N from the three respective primary producers; and \( \Delta_n \) is an estimate of trophic enrichment for \( \delta^{15}N \) per trophic level (Post 2002). We estimated total aquatic contributions (i.e., \( \alpha \), \( \beta \), and \( \gamma \)) to the diets of riparian spiders, and swallows using a four-end-member Bayesian mixing model (with the package siar in R; Parnell et al. 2013, R Development Core Team 2016). This Bayesian mixing-model approach allows for uncertainty in isotopic signatures of basal resources, consumers, and trophic enrichment. The trophic discrimination factors we used for riparian spiders and swallows were based on those that have been used previously in this study system (i.e., \( 6\%_o \pm 1\%_o \) for \( \delta^{15}N \),
Statistical analysis

While these 4-source models are partially based on surrogate data collected prior to dam removal, we found negligible differences among years or reaches for periphyton and terrestrial detritus $\delta^{13}C$ and nitrogen $\delta^{15}N$ signatures (see Appendix S1: Fig. S1a–d), supporting the assumption that the isotopic signatures from phytoplankton and macrophytes also remained similar in space and time.

We used Bayesian inference to assess the effects of dam removal on emergent insects and riparian consumers. We opted for Bayesian inference vs. traditional null-hypothesis testing because we were interested in the probability of shifts in emergent insects, consumer diets, and trophic interactions given the data (vs. the probability of our data given the null hypothesis is true, i.e., a $P$-value), and because Bayesian inference is better equipped to deal with assumptions that were violated by the inherent limitations of our study that are common to large, unreplicated designs (see Site Description and Experimental Approach; reviewed by Barley and Meeuwig 2017). Therefore, we used the posterior probability estimates of diet contributions generated by the mixing models, and their 95% credible intervals, to evaluate the probability of differences among control, restored, and unrestored reaches before vs. after dam removal. In a similar way, we modeled TP and the corresponding 95% credible intervals (using Eq. 1) with the posterior probabilities of diet contributions from the Bayesian mixing models. We compared reach-level total aquatic contributions (periphyton + phytoplankton + macrophytes) and TP means and 95% credible intervals from year to year, and among control vs. restored, and unrestored reaches. In each case, the 95% credible intervals of aquatic contribution and TP presented here can be interpreted as the probability of a parameter estimate ($\Theta$), given the data, $y$ (i.e., $p(\Theta|y)$), or the joint posterior distribution; similarly, the degree to which 95% credible intervals for reach/year values of total aquatic contributions and TP overlap can be interpreted as the probability of the difference between a specific reach/year comparison (i.e., if 95% CIs do not overlap, then the probability of a difference between two groups approaches 0.95).

We also used Bayesian inference to evaluate the effects of dam removal on spider density and emergent-insect parameters (e.g., total flux [biomass m$^{-2}$ d$^{-1}$], mean individual body size); we visually inspected for patterns among years and reaches for the relative abundance of emergent-insect feeding modes. To estimate spider density and emergence flux, we used the software JAGS coupled with the package ‘rjags’ (Plummer 2016) and MCMC from uninformative normal prior distributions, to fit hierarchical models with posterior probabilities for group-level (reach/year) parameters and their 95% credible intervals. We used a Poisson distribution and log-link function for the likelihood for spider density, along with uninformative uniform prior distributions (Kéry and Schaub 2012). The resulting parameter estimates and their 95% credible intervals for each reach and year were also interpreted as described above.

We used non-metric multidimensional scaling followed by analysis of similarities (ANOSIM; 999 permutations) to assess differences among emergent-insect communities before vs. after dam removal and across all reaches. We examined the relationship between emergent insects and terrestrial consumers by testing for associations between the relative abundance of different feeding modes, and the respective $\delta^{13}C$ signatures of the dominant family of emergent insects (Chironomidae) and terrestrial consumers. Correlations between Chironomidae $\delta^{13}C$ and consumer $\delta^{13}C$ imply an energetic reliance on these emergent insects (e.g., Sullivan 2013). We used major axis (MA) fits (Warton et al. 2006) to evaluate the degree to which emergent-insect $\delta^{13}C$ and consumer $\delta^{13}C$ were related. We deemed MA the most appropriate test in this case because
residuals in the direction of both the $x$ variable (Chironomidae $\delta^{13}C$) and the $y$ variable (consumer $\delta^{13}C$) contain underlying error, and are needed for interpreting the slope. We visually assessed associations between factors such as discharge, mean annual temperature, and cumulative precipitation and consumer reliance on aquatically-derived energy and TP.

**RESULTS**

**Emergent insects**

There were no pronounced changes in emergent-insect community composition across all years and reaches (Fig. 3a; ANOSIM $R = 0.088$, $P = 0.295$ [Year], ANOSIM $R = -0.336$, $P = 1.00$ [Reach]), nor any changes in mean insect body size among reaches (Appendix S1: Fig. S2a). Collector-gatherer was the dominant feeding mode of emergent insects (mean = 73.6% of total emergent biomass flux), followed by predators (21.4%), collector-filterers (1.9%), and herbivores (1.2%). Consistent with this, the dominant emergent-insect family throughout the study was Chironomidae (mean relative biomass flux = 68.7%), which are predominantly collector-gatherers in our study system (Appendix S1: Fig. S2b). There were modest changes to the relative abundance of different insect feeding modes; predators and herbivores tended to increase in both restored and unrestored reaches (Fig. 3b, c), whereas collector-filterers showed no clear pattern (Fig. 3d) and collector-gatherers tended to decrease comparably in both the restored and unrestored reaches (excluding 2014, Fig. 3e). There was a slight decrease in emergent-insect biomass flux immediately after dam removal in both the restored and unrestored reach compared to the control (Fig. 3f), particularly for Chironomidae in the restored reach relative to the unrestored reach (Appendix S1: Fig. S2c).

**Basal-resource isotopic signatures**

There was reasonable separation among basal resources (e.g., between periphyton and detritus $\delta^{13}C$) across all years and reaches: periphyton mean $= -20.96^{\%}_{o/o} \pm 3.54^{\%}_{o/o}$; detritus mean $= -28.34^{\%}_{o/o} \pm 0.86^{\%}_{o/o}$; Fig. 4). Periphyton, macrophyte, and phytoplankton $\delta^{15}N$ was more enriched compared to detritus (e.g., periphyton mean $= 9.23^{\%}_{o/o} \pm 1.49^{\%}_{o/o}$; detritus mean $= 4.61^{\%}_{o/o} \pm 1.59^{\%}_{o/o}$) across all years and reaches (Fig. 4a–f). Collectively, the isotopic distribution of our basal resources allowed for confidence in our mixing models. Further, all models converged based on visual assessment of trace plots, and checking for r-hat values <1.1 (Kéry and Schaub 2012).

**Spider density**

Nearshore spider densities declined system-wide post-dam removal (Fig. 5a, b). Overall, spider densities were $9.9 \times$ lower after dam removal in the restored reach, and this decline was 3.7 times greater than the decline observed in the control reach. Reductions in spider densities were most pronounced in the restored reach in the first two years after dam removal (Fig. 5a, b), where spider densities declined by 21.9 times and 22.4 times in 2013 and 2014, respectively (Fig. 5b). In contrast, spider densities in the unrestored reach showed comparable patterns through time at the control reach (Fig. 5b).

**Consumers and emergent insects**

We found evidence that riparian spiders were partially reliant on emerging Chironomidae, according to the positive relationship between their respective $\delta^{13}C$ signatures ($R^2 = 0.30$; Fig. 6a). There was also visual indication that spider and Chironomidae $\delta^{13}C$ became more closely aligned after dam removal in the restored reach (Fig. 6a). Consistent with this, the absolute values of residuals between observed $\delta^{13}C$ and MA fitted values approached zero in 2013–2016 (decreased from 1.625 [before] to 0.086 [2016]) for the restored reach. Residuals in the unrestored reach tended to be higher than the restored reach (mean = 0.804), but were still lower than pre-dam removal values, particularly in 2014 (residual = 0.096) and 2016 (0.383). The control reach had residuals that were consistent across years, but they tended to increase slightly after dam removal (residuals = 0.57 [before], 0.867 [after]).

In contrast, swallow $\delta^{13}C$ was negatively correlated with Chironomidae $\delta^{13}C$ ($R^2 = 0.35$; Fig. 6b), and this relationship remained consistent before vs. after dam removal; that is, Chironomidae became more enriched with $^{13}C$ while swallows became more depleted, suggesting that Chironomidae were not a predominant dietary component for swallows. There was a stronger,
Fig. 3. (a–f) Non-metric multidimensional scaling plot of emergent-insect community composition by year and time (a); relative abundance (%) of emergent insects with predatory (b), herbivorous (c), filtering (d), and gathering (e) feeding modes (based on Poff et al. 2006, Merritt et al. 2008); and emergence biomass flux (f). In (a), black, red, gray, and blue symbols denote the year (PRE, 2013–2015, respectively), and the reaches are indicated with shapes (control = circles, unrestored = squares, restored = triangles). In (b–f), open, gray, and black circles indicate the control, unrestored, and restored reaches, respectively, and the vertical lines indicate date of dam removal.
Fig. 4. (a–f) Stable-isotope biplots depicting $\delta^{13}$C and $\delta^{15}$N of riparian swallows (blue closed circles) and spiders (black closed circles), emergent insects (Chironomidae [gray open circles]), and basal resources (periphyton [green open circles], detritus [brown open circles]) directly measured in this study. The biplots shown in (a–f) represent each year of the study (2011–2016, respectively; 2011–2012 are pre-dam removal, 2013 and later are post-dam removal). Each point in the biplots represents the mean isotopic signature for each basal resource or consumer in a given reach; circles, squares, and triangles denote the control, unrestored, and restored reaches, respectively. The open red and green circles with $x$ and $y$ standard error bars indicate the isotopic signatures for phytoplankton and macrophytes, respectively, from 12 reaches in the Scioto-Olentangy River system sampled before dam removal (2011–2013; mean ± 1 standard error from Kautza and Sullivan 2016; $n = 36$ in both cases).
negative relationship between Chironomidae $\delta^{13}C$ and swallow $\delta^{13}C$ in the restored reach based on visual inspection of the graph and analysis of the residuals of the MA fit. Observed $\delta^{13}C$ values for the restored reach were consistently closer to fitted values compared to the control reach (mean residual = 0.826 [restored], 1.030 [control]), and the same was true (although to a greater degree) for the unrestored reach (mean residual = 0.432 [unrestored]).

Riparian consumer diet and trophic responses

Spider reliance on aquatically-derived energy (i.e., total derived from periphyton, phytoplankton, and macrophytes) was variable in the restored reach compared to the control reach prior to dam removal (Fig. 7a). Total aquatically-derived energy differed the most among reaches in the initial year following dam removal. In the restored reach, aquatically-derived energy decreased ~2 times to levels comparable to two years prior to dam removal, whereas the unrestored and control reaches remained higher (~52–65% energy derived from aquatic primary producers; Fig. 7a). After the second year post-dam removal, aquatically-derived energy was more comparable among reaches, and was within the range of values for free-flowing reaches in the Scioto River system (43–74%; Fig. 7a). Despite slight changes in aquatically-derived energy, spider TP was similar across years and reaches, and comparable to observed values in from free-flowing reaches of the Scioto River, particularly after dam removal (post-dam TP range = 1.79–1.95; Fig. 7b).

Swallow reliance on aquatically-derived energy was lower than that of spiders and was slightly lower in the restored (vs. control) reach in the year prior to dam removal (Fig. 7c). Two years after dam removal, swallow reliance on aquatically-derived energy increased across all reaches; this increase was most pronounced in the restored reach (Fig. 7c). In the final year of the study, swallow reliance on aquatically-derived energy generally remained within (control, unrestored) or decreased below (restored) the range of values found in free-flowing reaches of the Scioto River that were outside the influence of the dam removal (Fig. 7c). Similar to spider TP, swallow TP was generally comparable across years and reaches although there was a visual trend toward increased TP in the restored reach post-dam removal, with mean values falling squarely within the range of free-flowing
reaches outside the scope of influence of the dam removal (Fig. 7d).

**Discharge, temperature, and precipitation**

Median daily discharge in the Olentangy River from May through September across all years was 3.32 m$^3$s$^{-1}$. Median discharge was 1.89 times higher after dam removal, compared to the same time period in 2011 and 2012. Mean annual (air) temperatures were comparable pre- and post-dam removal (11.6°C before vs. 11.0°C after, on average). Cumulative annual precipitation after dam removal was also comparable to, but slightly lower than, before dam removal (238 cm before vs. 205 cm after, on average). We visually assessed relationships between trophic responses of spiders and swallows to discharge and local climatological data (mean annual temperature, cumulative precipitation) from each year of the study (Appendix S1: Figs. S3–S5). Spider reliance on aquatically-derived energy (total from phytoplankton, periphyton, and macrophytes) showed a negative association with discharge, and a positive association with mean annual temperature (Appendix S1: Figs. S3a, S4a). In contrast, swallow reliance on aquatically-derived energy showed the opposite associations (positive with discharge, negative with temperature), driven by the year with the highest median daily discharge and coldest mean annual temperature (2014; Appendix S1: Figs. S3b, S4b). Trophic position of both spiders and swallows showed few clear patterns with either discharge or regional climate variables, with the exception of lower spider TP in the year with highest cumulative precipitation (Appendix S1: Fig. S5c).

**DISCUSSION**

Dam removal is an increasingly common restoration tool that aims to improve several aspects of river functioning, including flow regime, and upstream–downstream connectivity (O’Connor et al. 2015, Magilligan et al. 2016b). As the number of dam-removal projects continues to expand—roughly doubling every decade

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**Fig. 6.** (a–b) Spider (a) and swallow (b) $\delta^{13}C$ as a function of $\delta^{13}C$ signatures of emergent insects (family: Chironomidae) across all years of the study. Points are reach-/year-level mean $\delta^{13}C$ values. Major axis fits are shown with solid lines, indicating significant associations between $\delta^{13}C$ of emergent Chironomidae and spiders (a; $P = 0.014$) and swallows (b; $P = 0.025$). Open, closed, and gray circles denote values from the control, restored, and unrestored reaches, respectively. Triangles in (a) indicate values from free-flowing reaches of the Scioto River (REF; i.e., reference). Points from the restored reach with corresponding years are labeled to illustrate degree of alignment between $\delta^{13}C$ signatures of Chironomidae and spiders/swallows through time.
since 1986 (O’Connor et al. 2015)—understanding the many-faceted effects on river ecosystem structure and function is critical. Furthermore, most dam-removal studies focus on one response measure (e.g., one taxon; Bellmore et al. 2017a), limiting our understanding of potential changes that represent a higher level of ecosystem integration.
In this study, we investigated the potential impacts of dam removal on trophic interactions across river–riparian boundaries. Although we observed substantial variability in observed responses over time, in general, comparable patterns in emergent insect, spider, and swallow trophic dynamics between control and experimental reaches may implicate broader-scale controls, with initial support for discharge and temperature. However, several responses linked to dam removal did emerge, that is, where more pronounced changes were observed at the experimental vs. control reaches. For instance, we documented declines in tetragnathid spider density, which are likely attributable as much to changes in river channel width and nearshore habitat structure/vegetation as to in-stream changes (S. M. P. Sullivan, unpublished data; see further discussion below). There was also initial evidence for declines in the contribution of aquatically-derived energy to both spider and swallow diets either immediately (for spiders) or within 4 yr after dam removal. Our study, representing multiple years and several reaches, points to the inherent complexity of ecological responses to dam removal where the interplay between dam characteristics (e.g., lowhead, run-of-river vs. large, storage dams) and the ecosystem and landscape context in which the dam removal occurs needs to be considered (Foley et al. 2017).

**Dam removal and aquatic–terrestrial trophic linkages**

Overall, our observations did not strongly support the hypothesis that dam removal would alter ecological linkages between aquatic–terrestrial systems via changes in ecosystem size and emergent-insect communities. There are several possible explanations for this result, including a mismatch in timing between the initial effects of dam removal (late summer) and peak insect emergence and riparian consumer activity (late spring and early summer). This mismatch may have muted initial responses to dam removal; however, we found evidence for modest changes in the relative abundance of emergent-insect feeding modes that might be expected to affect terrestrial consumers over longer time scales (5–10 yr). We also attribute the muted nature of observed responses to the physical characteristics of the removed dam. Unlike with larger (>8-m high) storage dams, streamflow, sediment, and organic matter transport are not fully restricted over lowhead, run-of-river dams (Roberts et al. 2007, Tullos et al. 2014). Thus, larval invertebrate drift (and metapopulation dynamics) is also likely only moderately impacted, leading merely to subtle changes in emergent-insect community composition and, in turn, prey subsidies to riparian consumers.

Our clearest lines of evidence for changes in cross-boundary connections after dam removal were the changes to tetragnathid spider density, closer energetic relationships between spiders and Chironomidae, and slight increases in swallow TP in the restored reach consistent with isotopic associations between swallows and Chironomidae. In terms of spider densities, riparian habitat structure on which nearshore spiders depend (Tagwireyi and Sullivan 2016) was especially limited post-dam removal in the restored reach, where we observed the greatest spider declines. In this reach, >95% of the vegetation within 2 m of the river edge remained bare ground up to 2 yr post-dam removal (S. M. P. Sullivan, unpublished data); spiders likely began to recover once this edge habitat was revegetated (increased to 71% herbaceous vegetation, on average, by 2016; Fig. 2d; S. M. P. Sullivan, unpublished data).

There were associations between $\delta^{13}C$ of both riparian consumers and Chironomidae, but in opposing directions. Spider $\delta^{13}C$ was positively associated with Chironomidae $\delta^{13}C$, suggesting that spiders consumed Chironomidae. Swallow $\delta^{13}C$ was negatively associated with Chironomidae $\delta^{13}C$, perhaps because swallows have been shown to actively select for larger-bodied prey (e.g., Odonata; McCarty and Winkler 1999) or because a substantial portion of swallow diet was terrestrial insects (riparian swallows feed on a mixture of aquatic and terrestrial flying insects; Alberts et al. 2013). Reduced swallow reliance on aquatically-derived energy was most evident in the restored reach post-dam removal in the final year of the study, suggesting that in-stream changes to prey communities potentially played a role in shifting the energy basis of swallow diets (Sullivan and Manning 2017). In both cases, trends were evident to a greater degree in the restored reach compared to the unrestored reach, and, in the case of spiders, became more strongly...
aligned post-dam removal. The closer alignment between spider δ13C and Chironomidae δ13C occurred despite lower chironomid biomass flux immediately after dam removal (Fig. 6a; Appendix S1: Fig. S2c).

Our findings generally indicate that consumer reliance on aquatically-derived energy can be highly variable from year to year, particularly for aerial insectivores such as swallows, and that these fluctuations can occur system-wide. Following dam removal, we observed that the mean total contribution of aquatically-derived energy ranged from 0.38 to 0.67 in spiders and 0.14 to 0.93 in swallows. In free-flowing reaches of the same river system, Kautza and Sullivan (2016) found mean total contributions of aquatically-derived energy were between 0.34 and 0.53 to spiders, and from 0.23 to 0.54 to swallows. Although we had expected that the contributions from periphyton- and phytoplankton-derived energy to riparian consumers would increase and decrease, respectively, in response to dam removal in the experimental reaches (both restored and unrestored), this was not the case (Appendix S1: Figs. S6, S7). However, the slight declines in swallow reliance on periphyton-derived energy (Appendix S1: Fig. S7b) and concomitant upwards shifts in TP (Fig. 7d) at the restored reach following dam removal are consistent with a negative relationship between algal-derived pathways and riparian consumer TP reported in Tagwireyi and Sullivan (2016) from work in the same river system. These observations suggest that dam removal can prompt a shift in swallow TP via prey switching to terrestrial (vs. aquatic) flying insects.

We found little evidence that the small shifts in TP of both spiders and swallows were associated with dam removal, and in fact largely converged between control and experimental reaches after dam removal, indicating little to no effect of dam removal on trophic complexity. This pattern is in contrast to findings from companion research on fish-community trophic dynamics in the same study system. For example, Dorobek (2016) observed fish food-chain length was 36% shorter in the restored reach and 25% shorter in the unrestored reach, and implicated reductions in ecosystem size and shifts in fish species richness, body size, and relative abundance of top predators following dam removal as mechanisms. In contrast to fish communities that responded to restored upstream–downstream connectivity after dam removal, upstream flight and dispersal of adult insects was likely unaltered by lowhead dam removal (see Dam removal and aquatic–terrestrial trophic linkages). Thus, as we observed, whole-scale turnover in emergent-insect community composition and, in turn, trophic structure appears unlikely following lowhead dam removal.

**Interactions between dam removal and system-wide drivers**

Several potential drivers that we cannot fully separate from explicit dam-removal effects include those related to climate and hydrology pre- vs. post-dam removal. For example, the reliance of aquatic energy to spider diets was negatively associated with discharge. There was a substantial increase in median discharge (~2 times), which may have affected benthic macroinvertebrates (Sullivan and Manning 2017), among other responses (geomorphic responses, nutrient availability, etc.). We found initial evidence that regional temperature and, to a smaller degree, precipitation may have also driven patterns of aquatic–terrestrial interactions, particularly for spiders, and these variables have also been linked to waterbird ecology in fluvial systems (Sullivan and Vierling 2012). We expect that multiple ecosystem and regional factors could partly drive the patterns of aquatic–terrestrial linkages observed here, but the relative importance of these drivers and predicting their potential interactions with lowhead dam removal remains uncertain.

**Aquatic–terrestrial linkages and dam-removal management**

Run-of-river dams are more numerous than large storage dams (U.S. ACE), and their removal is an important restoration tool. However, the ecological effects of run-of-river dams and their removal on river–riparian communities are likely more limited in scope compared to larger dams (East et al. 2015, Tonra et al. 2015), supporting the muted trophic responses observed in our study. For example, the magnitude of changes before vs. after dam removal is likely to scale with dam size (e.g., hydrology, geomorphic changes, Richter et al. 1996, Major et al. 2017), but the potential for this pattern to emerge for
food-web responses to dam removal is largely unexplored. This remains an important, but unanswered question relative to dam removal as a restoration tool, particularly as the number of dam-removal projects continues to increase (O’Connor et al. 2015).

Currently, post-dam river management focuses on in-stream concerns (e.g., geomorphic changes, elevated turbidity, expansion of invasive fish); lateral effects of dam removal have thus far remained largely outside the scope of such discussions (Tullos et al. 2016). Understanding lateral ecological consequences of dam removal could inform terrestrial conservation and restoration priorities. In terms of conservation, eastern North American aerial insectivorous bird populations (e.g., flycatchers, swallows, swifts, nightjars) have severely declined over the last several decades (Nebel et al. 2010). Many species are linked via habitat or foraging requirements to riparian areas (e.g., Tree Swallows; McCarty 1997, Alberts et al. 2013). Kautza and Sullivan (2016) estimated that ~41% of riparian swallow nutritional subsidies were derived from emergent insects that rely on aquatic primary producers in the Scioto River system of the current study. Furthermore, Twining et al. (2016) found that fatty-acid composition of prey—of which aquatic insects contain higher levels than terrestrial insects—was more important for swallow nestlings than food quantity, highlighting the critical importance of high-quality aquatic habitat for these species. Thus, long-term investigation into the influences of dam removal on these functional aspects of nutritional subsidies to terrestrial consumers will be an important step for associated conservation goals.

Long-term studies of dam removal and associated spatial connectivity (upstream–downstream, lateral) are needed to understand system-wide responses as dam removals become more common. While there remains a need to further explore longitudinal effects of dams and dam removal, shifts in lateral connectivity are a relevant aspect of river–riparian functioning that could potentially interact with dam removal. Greater attention paid to this cross-boundary food-web pathway in newly undammed rivers and their ensuing restoration and management plans (Bellmore et al. 2017a) may provide additional insight into the ecological effects of dam removal.

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LITERATURE CITED

Alberts, J. M., S. M. P. Sullivan, and A. Kautza. 2013. Riparian swallows as integrators of landscape change in a multiuse river system: implications for aquatic-to-terrestrial transfers of contaminants. Science of the Total Environment 463:42–50.

Barley, S. C., and J. J. Meeuwig. 2017. The power and the pitfalls of large-scale, unreplicated natural experiments. Ecosystems 20:331–339.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

Bednarek, A. T. 2001. Undamming rivers: a review of the ecological impacts of dam removal. Environmental Management 27:803–814.

Bellmore, J. R., J. J. Duda, L. S. Craig, S. L. Greene, C. E. Torgersen, M. J. Collins, and K. Vittum. 2017a. Status and trends of dam removal research in the United States. Wiley Interdisciplinary Reviews: Water. https://doi.org/10.1002/wat2.1164

Bellmore, J. R., J. R. Benjamin, M. Newsom, J. A. Boun-
try, and D. Dombroski. 2017b. Incorporating food web dynamics into ecological restoration: a modeling approach for river ecosystems. Ecological Applications 27:814–832.

Benjamin, J. R., K. D. Fausch, and C. V. Baxter. 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. Oecologia 167:503–512.

Claeson, S. M., and B. Coffin. 2016. Physical and biologi-
cal responses to an alternative removal strategy of a moderate-sized dam in Washington, USA. River Research and Applications 32:1143–1152.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems: Zoobenthic species influence energy flows and nutrient cycling. BioScience 49:119–127.
Csiki, S., and B. L. Rhoads. 2010. Hydraulic and geomorphological effects of run-of-river dams. Progress in Physical Geography 34:755–780.

Dorobek, A. C. 2016. Short-term consequences of low-head dam removal for fish community dynamics in an urban river system. Thesis. Ohio State University, Columbus, Ohio, USA.

Dorobek, A. C., S. M. P. Sullivan, and A. Kautza. 2015. Short-term consequences of low-head dam removal for fish assemblages in an urban river system. River Systems 21:125–139.

Downes, B. J., L. A. Barmuta, P. G. Fairweather, D. P. Faith, M. J. Keough, P. S. Lake, B. D. Mapstone, and G. P. Quinn. 2002. Monitoring ecological impacts: concepts and practice in flowing water. Cambridge University Press, New York, New York, USA.

Doyle, M., E. Stanley, C. Orr, A. Selle, S. Sethi, and J. Harbor. 2005. Stream ecosystem response to small dam removal: lessons from the Heartland. Geomorphology 71:227–244.

East, A. E., et al. 2015. Large-scale dam removal on the Elwha River, Washington, USA: river channel and floodplain geomorphic change. Geomorphology 228:765–786.

Finlay, J., M. Power, and G. Cabana. 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnology and Oceanography 44:1198–1203.

Foley, M. M., et al. 2017. Landscape context and the biophysical response of rivers to dam removal in the United States. PLoS ONE 12:e0180107.

Gardner, C., S. M. Coghlan, J. Zydlewski, and R. Saunders. 2013. Distribution and abundance of stream fishes in relation to barriers: implications for monitoring stream recovery after barrier removal. River Research and Applications 29:65–78.

Gartner, J. D., F. J. Magilligan, and C. E. Renshaw. 2015. Predicting the type, location and magnitude of geomorphic responses to dam removal: role of hydrologic and geomorphic constraints. Geomorphology 251:20–30.

Gratton, C., and M. J. Vander Zanden. 2009. Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. Ecology 90:2689–2699.

Gray, L. J., and J. V. Ward. 1982. Effects of sediment releases from a reservoir on stream macroinvertebrates. Hydrobiologia 96:177–184.

Henschel, J. R., D. Mahsberg, and H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. Oikos 93:429–438.

Iwata, T., S. Nakano, and M. Murakami. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. Ecography 26:325–337.

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

Kautza, A., and S. M. P. Sullivan. 2015. Shifts in reciprocal river-riparian arthropod fluxes along an urban-rural landscape gradient. Freshwater Biology 60:2156–2168.

Kautza, A., and S. M. P. Sullivan. 2016. The energetic contributions of aquatic primary producers to terrestrial food webs in a mid-size river system. Ecology 97:694–705.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Elsevier, Waltham, Massachusetts, USA.

Kornis, M. S., B. C. Weidel, S. M. Powers, M. W. Diebel, T. J. Cline, J. M. Fox, and J. F. Kitchell. 2015. Fish community dynamics following dam removal in a fragmented agricultural stream. Aquatic Sciences 77:465–480.

Ligon, F., W. Dietrich, and W. Trush. 1995. Downstream ecological effects of dams. BioScience 45:183–192.

Magilligan, F. J., K. H. Nislow, B. E. Kynard, and A. M. Hackman. 2016a. Immediate changes in stream channel geomorphology, aquatic habitat, and fish assemblages following dam removal in a small upland catchment. Geomorphology 252:158–170.

Magilligan, F. J., B. E. Graber, K. H. Nislow, J. W. Chipman, C. S. Sneddon, and C. A. Fox. 2016b. River restoration by dam removal: enhancing connectivity at watershed scales. Elementa: Science of the Anthropocene 4:00108.

Major, J., A. E. East, J. E. O’Connor, G. E. Grant, A. C. Wilcox, C. S. Magrill, M. J. Collins, and D. D. Tullos. 2017. Geomorphic responses to dam removal in the United States: a two-decade perspective. Pages 355–383 in D. Tsutsumi and J. B. Laronde, editors. Gravel bed rivers and disasters. Wiley, West Sussex, UK.

McCarty, J. P. 1997. Aquatic community characteristics influence the foraging patterns of tree swallows. Condor 99:210–213.

McCarty, J. P., and D. W. Winkler. 1999. Foraging ecology and diet selectivity of tree swallows feeding nestlings. Condor 101:246–254.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. Fourth edition. Kendall Hunt, Dubuque, Iowa, USA.

Meyer, L. A., and S. M. P. Sullivan. 2013. Bright lights, big city: influences of ecological light pollution on reciprocal stream-riparian invertebrate fluxes. Ecological Applications 23:1322–1330.
Mundie, J. H. 1964. A sampler for catching emerging insects and drifting materials in streams. Limnology and Oceanography 9:456–459.

Murakami, M., and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through predation by birds. Ecology Letters 5:333–337.

Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor. 2010. Declines of aerial invertevores in North America follow a geographic gradient. Avian Conservation and Ecology 5:1.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world’s large river systems. Science 308:405–408.

O’Connor, J. E., J. J. Duda, and G. E. Grant. 2015. 1000 dams and counting. Science 348:496–497.

Ohio Environmental Protection Agency. 2011. Environmental assessment: Columbus 5th avenue dam removal and river restoration. Ohio EPA, Ohio, USA. https://www.columbus.gov/uploadedFiles/Public_Utilities/Projects/5th%20dam%20EPA.pdf

Orr, C. H., S. J. Kroiss, K. L. Rogers, and E. H. Stanley. 2008. Downstream benthic responses to small dam removal in a coldwater stream. River Research and Applications 24:804–822.

Orr, C. H., and E. H. Stanley. 2006. Vegetation development and restoration potential of drained reservoirs following dam removal in Wisconsin. River Research and Applications 22:281–295.

Palmer, M. A., and C. M. Febria. 2012. The heartbeat of ecosystems. Science 336:1393.

Parnell, A. C., D. L. Phillips, S. Bearhop, B. X. Semmens, E. J. Ward, J. W. Moore, A. L. Jackson, J. Grey, D. J. Kelly, and R. Inger. 2013. Bayesian stable isotope mixing models. Environmetrics 24:387–399.

Plummer, M. 2016. rjags: Bayesian graphical models using MCMC. R package version 4-6. https://CRAN.R-project.org/package=rjags

Poff, N. L., and D. D. Hart. 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience 52:659–668.

Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B. C. Kondratieff. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. Journal of the North American Benthological Society 25:730–755.

Post, D. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Pages 291–314 in M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. Ecological consequences of habitat heterogeneity. Blackwell Scientific, Oxford, UK.

Power, M. E., W. E. Rainey, M. S. Parker, J. L. Sabo, A. Smyth, S. Khandwala, J. C. Finlay, F. C. McNeely, K. Marsee, and C. Anderson. 2004. River-to-watershed subsidies in an old-growth conifer forest. Pages 217–240 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago, Illinois, USA.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Renfalt, B., A. Lejon, M. Jonsson, and C. Nilsson. 2013. Long-term taxon-specific responses of macroinvertebrates to dam removal in a mid-sized swedish stream. River Research and Applications 29:1082–1089.

Richter, B., J. Baumgartner, J. Powell, and D. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10:1163–1174.

Roberts, S. J., J. F. Gottgens, A. L. Spongberg, J. E. Evans, and N. S. Levine. 2007. Assessing potential removal of low-head dams in urban settings: an example from the Ottawa River, NW Ohio. Environmental Management 39:113–124.

Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank, and N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134:238–250.

Schulz, R., et al. 2015. Review on environmental alterations propagating from aquatic to terrestrial ecosystems. Science of the Total Environment 538:246–261.

Stanley, E. H., M. A. Luebke, M. W. Doyle, and D. W. Marshall. 2002. Short-term changes in channel form and macroinvertebrate communities following low-head dam removal. Journal of the North American Benthological Society 21:172–187.

Stanley, E. H., S. M. Powers, and N. R. Lottig. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. Journal of the North American Benthological Society 29:67–83.

Sullivan, S. M. P. 2013. Stream foodweb delta C-13 and geomorphology are tightly coupled in mountain drainages of northern Idaho. Freshwater Science 32:606–621.

Sullivan, S. M. P., and D. W. P. Manning. 2017. Seasonally distinct taxonomic and functional shifts in macroinvertebrate communities following dam removal. PeerJ 5:e3189.

Sullivan, S. M. P., and K. T. Vierling. 2012. Exploring the influences of multiscale environmental factors
on the American dipper *Cinclus mexicanus*. Ecography 35:624–636.

Tagwireyi, P., and S. M. P. Sullivan. 2016. Distribution and trophic dynamics of riparian tetragnathid spiders in a large river system. Marine and Freshwater Research 67:309–318.

Tonra, C. M., K. Sager-Fradkin, S. A. Morley, J. J. Duda, and P. P. Marra. 2015. The rapid return of marine-derived nutrients to a freshwater food web following dam removal. Biological Conservation 192:130–134.

Triplehorn, C. A., and N. F. Johnson. 2005. Borror and delong’s introduction to the study of insects. Seventh edition. Thomson Brooks/Cole, Belmont, California, USA.

Tullos, D. D., M. J. Collins, J. R. Bellmore, P. J. Connolly, P. B. Shafroth, and A. C. Wilcox. 2016. Synthesis of common management concerns associated with dam removal. Journal of the American Water Resources Association 52: 1179–1206.

Tullos, D. D., D. S. Finn, and C. Walter. 2014. Geomorphic and ecological disturbance and recovery from two small dams and their removal. PLoS ONE 9: e108091.

Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson, and D. W. Winkler. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences USA 113:10920–10925.

US ACE [U.S. Army Corp of Engineers]. 2013. National Inventory of Dams. http://nid.usace.army.mil/

Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. Biological Reviews 81:259–291.

Williams, D. D., L. G. Ambrose, and L. N. Browning. 1995. Trophic dynamics of 2 sympatric species of riparian spider (Araneae, Tetragnathidae). Canadian Journal of Zoology-Revue Canadienne De Zoologie 73:1545–1553.

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