Western North American Naturalist 83(2), © 2023, pp. 207–219

Aquatic insect communities remain impaired following large-scale river restoration

JARED MEEK[1,2,*], JACKSON BIRRELL[1,3], TEAGAN MULFORD[1], DENNIS K. SHIOZAWA[1], AND C. RILEY NELSON[1]

[1]*Department of Biology and Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT*
[2]*Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY*
[3]*Division of Biological Sciences, University of Montana, Missoula, MT*

ABSTRACT.—River manipulation and degradation can cause detrimental impacts on aquatic insect communities. River restoration projects seek to mitigate these human disturbances. Assessing the efficacy of river restoration remains an important goal for river managers and conservation biologists so that improved restoration methods can be used in the future. From 1999 to 2008, the Utah Reclamation Mitigation and Conservation Commission restored a 15-km channelized portion of the Provo River (Wasatch County, Utah, USA). Before (1999) and during (2002) the restoration project, macroinvertebrate samples were collected using modified kick nets from 3 sites within the restored area and 1 site outside the restored area. In 2017, we collected macroinvertebrates from these same sites using identical sampling methods to assess the long-term outcomes of the Provo River Restoration Project through a comparison of macroinvertebrate species richness, Shannon diversity, %EPT (Ephemeroptera, Plecoptera, Trichoptera), functional feeding groups, and habit groups. We show that macroinvertebrate richness and diversity have significantly decreased in the restored reaches of the river, despite the restoration project being completed in 2008. Additionally, we found that EPT taxa declined in the restored reaches and that the community remains dominated by collectors. Our results help quantify the efficacy of the Provo River Restoration Project and highlight the need for additional remediation techniques. Significant reductions in richness, Shannon diversity, and functional feeding group diversity at the reference site suggest that factors unaddressed by the restoration such as river damming, lack of riparian vegetation, maintenance of nonnative fish, nutrient pollution, and climate change may be preventing the full rehabilitation of the river. We discuss potential factors that may be contributing to river degradation in this system and advocate for revised and more holistic river restoration approaches, along with the importance of regular monitoring programs for completed restoration projects.

RESUMEN.—La manipulación y degradación de los ríos puede tener efectos perjudiciales en las comunidades de insectos acuáticos. Los proyectos de restauración de ríos tratan de mitigar estas perturbaciones humanas. Evaluar la eficacia de la restauración de los ríos sigue siendo un objetivo importante para los gestores de ríos y los biólogos conservacionistas, de modo que en el futuro puedan utilizarse mejores métodos de restauración. Entre 1999 y 2008, la Utah Reclamation Mitigation and Conservation Commission restauró una porción canalizada de 15 km del río Provo (condado de Wasatch, Utah, EE.UU.). Antes (1999) y durante (2002) el proyecto de restauración, se recogieron muestras de macroinvertebrados utilizando redes modificadas en tres sitios dentro del área restaurada y un sitio fuera del área restaurada. En 2017, recogimos macroinvertebrados de estos mismos sitios utilizando métodos de muestreo idénticos para evaluar los resultados a largo plazo del Proyecto de Restauración del Río Provo a través de una comparación de la riqueza de especies de macroinvertebrados, la diversidad de Shannon, %EPT (Ephemeroptera, Plecoptera, Trichoptera), grupos de alimentación funcional y grupos de hábitos. Mostramos que la riqueza y diversidad de macroinvertebrados ha disminuido significativamente en los tramos restaurados del río a pesar de que el proyecto de restauración finalizó en 2008. Además, encontramos que los taxones EPT disminuyeron en los tramos restaurados y que la comunidad sigue dominada por recolectores. Nuestros resultados ayudan a cuantificar la eficacia del Proyecto de Restauración del Río Provo, y ponen en evidencia la necesidad de técnicas de remediación adicionales. Las reducciones significativas en la riqueza, la diversidad de Shannon y la diversidad de grupos de alimentación funcionales en el sitio de referencia, sugieren que factores no abordados por la restauración, como el represamiento del río, la falta de vegetación ribereña, el mantenimiento de peces no nativos, la contaminación por nutrientes y el cambio climático pueden impedir la rehabilitación completa del río. Discutimos los factores potenciales que pueden estar contribuyendo a la degradación del río en este sistema y abogamos por enfoques revisados y más holísticos de restauración de ríos, junto con la importancia de programas de monitoreo regulares para proyectos de restauración concluidos.

---

*Corresponding author: jared.meek@columbia.edu

JM orcid.org/0000-0001-8191-4266 JB orcid.org/0000-0001-5339-0717 TM orcid.org/0000-0003-1467-1780

Aquatic insects are integral components of freshwater ecosystems, constituting over 60% of all freshwater species (Dijkstra et al. 2014, Macadam and Stockan 2015). They provide food for terrestrial and aquatic primary consumers, cycle nutrients, and act as ecosystem engineers (Walters et al. 2018, MacDonald et al. 2021). Aquatic insects also increase the economic and recreational value of streams, lakes, and rivers by supporting healthy fisheries (Suter and Cormier 2015). Despite their ecological, economic, aesthetic, and cultural importance, aquatic insects are threatened by a variety of land-use changes and anthropogenic disturbances, including physical river modification and channelization, thermal and hydrological shifts from dams, and nutrient pollution from urban activity and agriculture (Merritt et al. 2008, Elosegi and Sabater 2012). In degraded systems, aquatic insects are often the first organisms to disappear due to their sensitivity to changes in water quality and are thus used as bioindicators of river health (Barbour et al. 1999, DeWalt et al. 2005). Nevertheless, aquatic insects have received relatively little attention in conservation and restoration efforts (Strayer and Dudgeon 2010). Indeed, even as global insect populations are rapidly declining (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019, Wagner et al. 2021), research into the causes and remedies of insect decline has primarily focused on terrestrial taxa (Cardoso and Leather 2019, Harvey et al. 2020). Thus, understanding how aquatic insects and other macroinvertebrates are responding to anthropogenic disturbance is of considerable importance (Bernhardt et al. 2005, Carpenter et al. 2011).

To remedy anthropogenic disturbances of lotic systems, ecologists implement a variety of river restoration techniques, including physical reconstruction and improvement of in-stream habitat, bank stabilization, livestock exclusion and riparian recovery, floodplain reconnection, and water quality enhancement (Bernhardt et al. 2005). Restoration practices that aim to increase habitat heterogeneity by reconfiguring stream channels and adding in-stream features like boulders and logs are particularly common (Harrison et al. 2004, Palmer et al. 2007, 2010, Wohl et al. 2015). However, evidence that habitat heterogeneity is a major driver of species recovery, biodiversity, and stream health is mixed (e.g., Stewart et al. 2009, Whiteway et al. 2010). Indeed, recent studies suggest that physical restructuring methods may be ineffective on their own and that restoring ecological function should be a more explicit priority of restoration efforts (Palmer and Ruhi 2019, Johnson et al. 2020). For example, in a comprehensive review of 78 different restoration projects that sought to restore habitat heterogeneity, Palmer et al. (2010) found that only 2 of the projects resulted in a statistically significant increase in macroinvertebrate diversity and river health. Although the limitations of stream habitat restorations are well understood, assessing their efficacy at local levels remains important so managers can continue to improve river restoration methods.

We sought to determine the efficacy of a restoration project conducted along the Provo River, Utah, USA, from 1999 to 2008 (URMCC 1997). To do so, we compared 5 metrics of macroinvertebrate diversity and river health from collections made before, during, and after the restoration project. In particular, we compared species richness; Shannon diversity; percentage of individuals belonging to Ephemeroptera, Plecoptera, or Trichoptera (%EPT); and the structure of insect functional feeding and habit groups. Although increasing habitat heterogeneity through channel reconfiguration and the addition of in-stream habitat features may promote biotic recovery, these techniques are unlikely to fully rehabilitate a river impaired by dams and nutrient pollution (Lepori et al. 2005, Klein et al. 2007, Miller et al. 2010, Palmer et al. 2010, Nilsson et al. 2015). Due to the continued impacts of dams and agricultural activity near the Provo River watershed, we predicted that the aquatic macroinvertebrate diversity and other metrics of river health in the Provo River would show no significant increase compared to the prerestored river, even after 9 years postrestoration.

STUDY AREA

The Provo River is a Blue Ribbon fishery (UDNR 2021) that flows from its headwaters in the Uinta Mountains down the agricultural Heber Valley, through the urban center of Provo and Orem, and out into Utah Lake. The river has 2 large retention dams, the Deer Creek Dam (completed in 1941) and the Jordanelle Dam (completed in 1993), which separate the stream into 3 segments—the Upper, Middle, and Lower Provo River. Beginning in the 1950s, the Middle Provo River underwent significant alterations

Fig. 1. The Provo River Restoration Project restored meanders and habitat heterogeneity to a 15 km stretch of the Middle Provo River, which had previously been channelized. Sites 1–3 (blue) lie within the restored segment and are referred to as treatment sites; site 4 (red) was never channelized or restored and is referred to as a reference site.

as part of a large-scale water reclamation project (Central Utah Project; Ashley and Jones 2002), including channelization, straightening, and diking. To remedy these ecological impairments and restore the stream's aquatic biodiversity, the Utah Reclamation Mitigation and Conservation Commission (URMCC) restructured 15 km of the Middle Provo, restored habitat heterogeneity by reconstructing meanders, side channels, and eddies, and performed some degree of riparian restoration (URMCC 1997). The Provo River Restoration Project (PRRP) was conducted between 1999 and 2008, and the physical restructuring was modeled after a stretch of river that had never been channelized (i.e., reference reach).

METHODS

Sampling and Identification

Shiozawa and others (Shiozawa et al. 2002, Shiozawa and Weibell 2006) collected aquatic macroinvertebrate samples from 4 different sites along the Middle Provo immediately before and during the PRRP. We returned to these same 4 sites and collected macroinvertebrate samples 9 years after the PRRP was completed. Sites 1–3 are treatment sites that were restored; site 4 is a reference site because it lies within the reference reach—a historically unchannelized section that was neither markedly modified prerestoration nor was directly altered by the PRRP restoration (Fig. 1). Just prior to the restoration, Shiozawa et al. (2002) collected 200 benthic macroinvertebrate samples at 3 of these sites (referred to as “prerestoration” samples, which were sampled between 27 February and 13 March 1999). Another 100 samples per site were collected by Shiozawa et al. (2002) while the restoration was on-going (referred to as “during-restoration” samples, which were sampled between March and April 2002; see Supplementary Material 1 for more details on Shiozawa et al.’s (2002) sampling locations and protocol). We collected 50 macroinvertebrate samples from each site (1–4) between 25 February and 17 March 2017 (referred to as “postrestoration” samples).

We followed the same methodology and sampled at the same sites in 2017 as Shiozawa et al. (2002) sampled in 1999 and 2002. Within a riffled reach at each site, we sampled benthic macroinvertebrates with modified kick nets (253-micron mesh on a 17.5-cm metal frame). Starting downstream, we placed transects 10 m apart and collected samples at 2-m intervals across the stream on each transect, moving upstream until we had collected 50 samples per site. Most of our samples were collected from the main riffle habitat, but this transect protocol ensured that we sampled from a diversity of microhabitats across the river, including slower habitat near the riverbank. We washed the contents of each net into Whirl-Pak® bags and preserved them in 70% ethyl alcohol. At each 2-m interval along the transects, we also made qualitative measurements of abiotic factors, including surface silt cover, substrate compactness, detritus amount and size, and percent vegetation cover (see Supplementary Material 2 for additional details on abiotic sampling methods, protocols, and units).

We obtained raw data from the pre- and during-restoration samples, which included a comprehensive list of all taxa and abiotic measurements collected from each site (URMCC 2002, Shiozawa and Weibell 2006). We used *An Introduction to the Aquatic Insects of North America* (Merritt et al. 2008) to identify our postrestoration samples down to the same taxonomic level as the pre- and during-restoration samples (genus level for those belonging to orders Ephemeroptera, Trichoptera, Plecoptera, Coleoptera, Isopoda, Amphipoda, Rhynchobdellida, Gastropoda, and Bivalvia; family level for those belonging to orders Diptera, Hemiptera, and Nematophora; order level for Acari; class level for Oligochaeta and Ostracoda; phylum for Platyhelminthes; see Supplementary Material 4 for a full taxon list). From these data, we quantified 5 measures of biodiversity, water quality, and stream functional structure: (1) species richness, (2) Shannon diversity, (3) %EPT (a common measure of water quality based on the percentage of individuals belonging to the sensitive insect orders Ephemeroptera, Plecoptera, or Trichoptera), (4) the proportion of macroinvertebrates belonging to 5 functional feeding groups (FFG) (i.e., shredders, collector-filterers, collector-gatherers, predators, and scrapers), and (5) the proportion of macroinvertebrates belonging to 4 habit groups (HG) (i.e., clingers, burrowers, swimmers, and sprawlers). We used Merritt et al. (2008) and Barbour et al. (1999) to assign each species to a FFG and HG. If members of any taxa were included in multiple feeding or habit groups, only the primary group was assigned to the taxa.

We compared these 5 metrics among sampling years to determine how the macroinvertebrate community changed in response to the restoration project. In addition, we compared the species richness from 1999, 2002, and 2017 to a historical macroinvertebrate biodiversity survey at 3 sites on the Middle Provo (Gaufin 1951). Although Gaufin (1951) does not provide precise locations of his 3 sites, we determined that the collections were likely made near site 1, at site 2, and near site 4 of the present study. While Gaufin’s data set is useful for anecdotal comparisons, we did not incorporate it into our statistical analyses because it followed a different sampling protocol—namely nonrandom, unstratified kick samples from various microhabitats at 9 different sites along the Provo River. Lastly, we compared the abiotic factors that were measured across the 3 sampling years to detect potential correlative relationships between changes in the stream’s physical properties and the insect community.

Statistical Analysis

Sample size differed among collection years (1999: 200 samples/site; 2002: 100 samples/site;

TABLE 1. Weighted linear models for the effect of treatment and year on species richness and Shannon diversity. Year had a significant effect in both models.

Response variable and fixed effect	df	Sum squared error	Mean square	*F*	*P*
Species richness					
Treatment	1	0.175	0.023	1.787	0.239
Year	2	0.023	0.088	6.853	0.037
Treatment * Year	2	0.134	0.067	5.232	0.059
Shannon diversity					
Treatment	1	0.001	0.001	0.011	0.920
Year	2	0.880	0.440	9.358	0.020
Treatment * Year	2	0.127	0.063	1.345	0.341

2017: 50 samples/site), which can bias comparisons of species richness and Shannon diversity. Thus, we used the R package '*iNEXT*' (function: iNEXT) (Chao et al. 2014, Hsieh et al. 2016) to construct species accumulation curves in order to estimate species richness (Hill number: $q = 0$) and Shannon diversity (Hill number: $q = 1$) at each site and year at a common sampling effort (R Core Team 2021). iNEXT defines Shannon diversity as the exponential of the Shannon's diversity index, and this metric can be interpreted as the number of common species in an assemblage (Hsieh et al. 2016). Accumulation curves with unconditional confidence intervals (confidence levels of 95%) for each sampling year were interpolated or extrapolated to 100 samples, depending on each year's sample size. Afterward, estimates of richness and Shannon diversity and their unconditional confidence intervals were extracted from the curves. Differences in richness and diversity among individual sites were considered significant if confidence intervals did not overlap—a conservative conclusion when using 95% confidence levels, as we did (Payton et al. 2003, Gotelli and Colwell 2011). Additionally, we used weighted linear regressions to model how richness and Shannon diversity changed over time among reference and treatment sites (function: lm) (R Core Team 2021). Because year likely did not have a linear effect on richness and diversity throughout the sampling period, year was considered a categorical variable in these analyses. Regression lines were thus impossible to generate and were not included in the relevant plots below. Weights of the models were the inverse of the variance of the estimated richness and Shannon diversity values produced by the iNEXT 100-sample accumulation curves.

We tested the effect of treatment and collection year on %EPT using linear mixed effects models with the R package '*nlme*' (function: lme) (Pinheiro et al. 2021, R Core Team 2021). Site was included as a random effect because we were interested only in the effect of year and treatment. Because the FFG and HG data included zero-inflated proportion data, we used a zero-inflated negative binomial mixed model (function: glmm.zinb) in the R package '*NBZIMM*' (Zhang and Yi 2020) to test how the proportion of individuals belonging to different FFGs and HGs differed among years and treatments. Site was also included as a random effect for these analyses.

Changes in abiotic factors over time were analyzed via Kruskal–Wallis rank sum tests (R Core Team 2021). The abiotic data were ordinal and zero-inflated, and Kruskal-Wallis tests are known to handle data with these characteristics well (Mangiafico 2016). However, Kruskal–Wallis tests cannot operate on structured data, so we analyzed the effect of year separately for each site. Because our sample sizes were high, nearly every test generated very low *P* values ($P < 0.01$ or lower). Thus, we also calculated epsilon-squared statistics to determine the effect size of year on each abiotic factor per site with the R package '*rcompanion*' (function: epsilonSquared) (Mangiafico 2016).

RESULTS

We found a significant reduction in species richness and Shannon diversity from 1999 to 2017 when accounting for all sampling sites ($P < 0.03$ and $P < 0.02$, respectively) (Table 1, Fig. 2A, B). Reductions in richness and diversity were not affected by treatment ($P = 0.23$, $P = 0.92$, respectively), though a near-significant interaction among year and treatment was found for richness ($P < 0.06$). At the scale of individual sites, a significant decrease in richness occurred at site 4, the reference site, falling from 37.73 (± 3.11) species in 1999 to 22.87 (± 4.42)

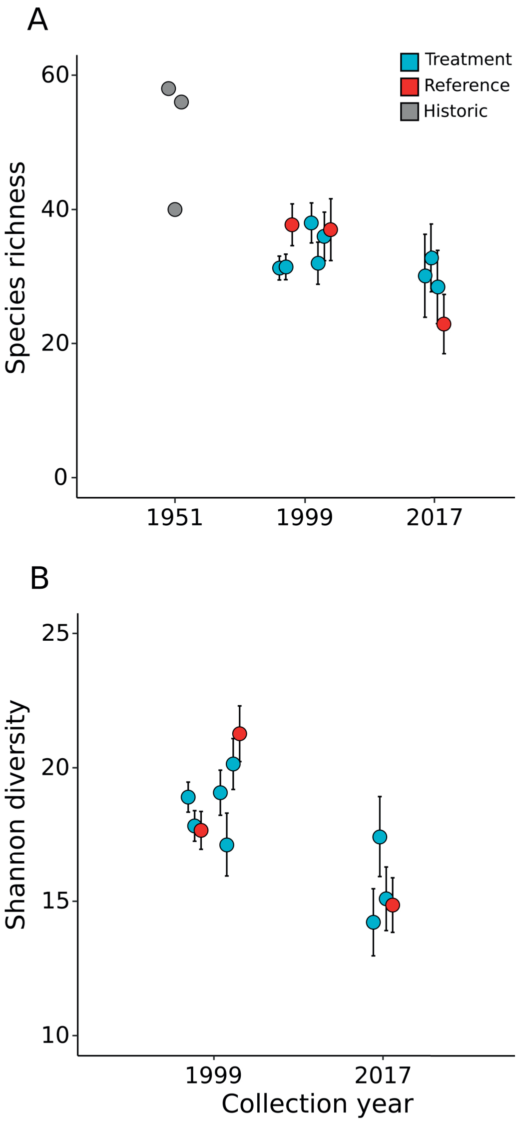

Fig. 2. Plot of species richness (*A*) and Shannon diversity (*B*) from 1999, 2002, and 2017 for treatment (blue) and reference (red) sites. Colored circles are mean estimated richness values from iNEXT accumulation curves. Error bars are unconditional 95% confidence intervals. For historical comparison in (*A*), we included richness values from collections made by Gaufin (1951), represented by gray circles, from 3 sites along the Middle Provo River. Note that the historic site with a richness of 40 was calculated based on only 11 kick-screen samples; richness values from other historic sites were calculated based on 25 samples. We could not include historical Shannon diversity values because Gaufin (1951) did not report the information required to calculate them.

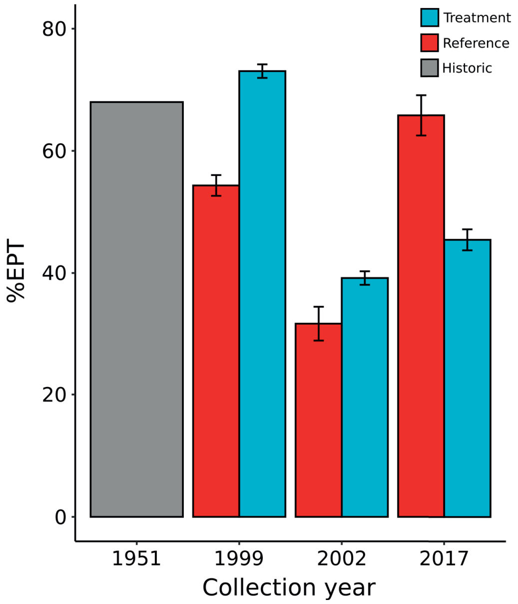

Fig. 3. Bar plots of the percent of individuals belonging to Ephemeroptera, Plecoptera, and Trichoptera (%EPT) from 1999, 2002, and 2017 for treatment and reference sites. Error bars represent mean standard error. For historical comparison, we included %EPT data from Gaufin (1951). An error bar was not included for the historical reference because Gaufin (1951) does not provide sufficient information to calculate mean standard error.

species in 2017. A significant decrease in Shannon diversity occurred at sites 1, 3, and 4 (Supplementary Material 3). Comparisons with historical data from the Middle Provo River (Gaufin 1951) suggest that sharp declines in species richness have occurred since 1951 (Fig. 2A). For a list of taxa collected in 1951, 1999, 2002, and 2017 and a comparison of the most dominant taxa collected in 1999 and 2017, see Supplementary Material 4.

Overall, a significant reduction in %EPT occurred over time when accounting for all sampling sites ($P < 0.0001$, Table 2). However, a significant interaction between year and treatment was also found ($P < 0.0001$), reflecting the decrease and subsequent rise in %EPT in the reference site but a decrease and less extreme rise in %EPT in the treatment sites. %EPT in 2017 at treatment sites appears to be ~33% lower than the historical levels observed in 1951 (Gaufin 1951) (Fig. 3). At the scale of individual sites, a significant reduction in %EPT was found in sites 1 and 3 (Supplementary Material 5).

Within both treatment and reference sites, the insect community experienced significant changes in the proportion of individuals belonging to different FFGs (Fig. 4, Table 3). We found that year

TABLE 2. Linear mixed effects model for the effect of treatment and year on %EPT (Ephemeroptera, Plecoptera, Trichoptera). Site was included as a random effect. %EPT was significantly affected by year and by an interaction between year and treatment.

Response variable and fixed effect	Numerator df	Denominator df	*F*	*P*
%EPT				
Treatment	1	2	0.238	0.674
Year	1	1178	22.672	<0.001
Treatment * Year	1	1178	45.415	<0.001

TABLE 3. Zero-inflated negative binomial mixed models for the effect of treatment and year on the proportion of individuals belonging to each functional feeding group (FFG). Site was included as a random effect. Year had a significant effect on the proportion of individuals belonging to all FFGs besides scrapers. Interactions between treatment and year were also present in some models.

Functional feeding group and fixed effect	Numerator df	Denominator df	*F*	*P*
Shredders				
Treatment	1	2	7.024	0.118
Year	1	1178	18.984	<0.001
Treatment * Year	1	1178	1.682	0.195
Collector-filterers				
Treatment	1	2	0.128	0.755
Year	1	1178	61.932	<0.001
Treatment * Year	1	1178	10.469	0.001
Collector-gatherers				
Treatment	1	2	0.026	0.886
Year	1	1178	347.389	<0.001
Treatment * Year	1	1178	32.653	<0.001
Scrapers				
Treatment	1	2	6.891	0.12
Year	1	1178	0.451	0.502
Treatment * Year	1	1178	0.015	0.903
Predators				
Treatment	1	2	30.195	0.032
Year	1	1178	762.442	<0.001
Treatment * Year	1	1178	51.362	<0.001

had a significant effect on the proportion of shredders ($P < 0.0001$), collector-filterers ($P < 0.0001$), collector-gatherers ($P < 0.0001$), and predators ($P < 0.0001$) within the community but not on scrapers. Treatment had no effect in any of our models, but year-by-treatment interactions were common. Most notably, the proportion of shredders, although already low in 1999, decreased by nearly sixfold from 1999 to 2017. In addition, the proportion of predators increased from ~2% to >10% in the reference site and to >15% in the treatment area, while the proportion of collector-gatherers decreased by ~28% and collector-filterers increased by ~24% in both reference and treatment sites. The proportion of scrapers remained relatively stable across our study period. Comparisons with Gaufin (1951) suggest that the FFG structure of the community has changed remarkably over the past century, with a relatively balanced community—each FFG representing ~8% to 40% of the community—being replaced by one dominated by collector-gatherers (Fig. 4).

The proportion of individuals belonging to different HGs also changed over time (Supplementary Material 6). We found that year had a significant effect on the proportion of clingers ($P < 0.0001$), swimmers ($P < 0.0001$), and sprawlers ($P < 0.0001$) but not on burrowers. Treatment type had no effect, but significant interactions were again common between year and treatment.

Sampling year had a significant effect on all abiotic factors we measured (Supplementary Material 2). However, effect sizes differed greatly. Surface silt cover was low at all sites in 1999 but increased in 2002 and 2017 (year had moderate effect; $\varepsilon^2 = 0.237$). Compactness was relatively high at all sites and years, changing little over time (small effect; $\varepsilon^2 =$

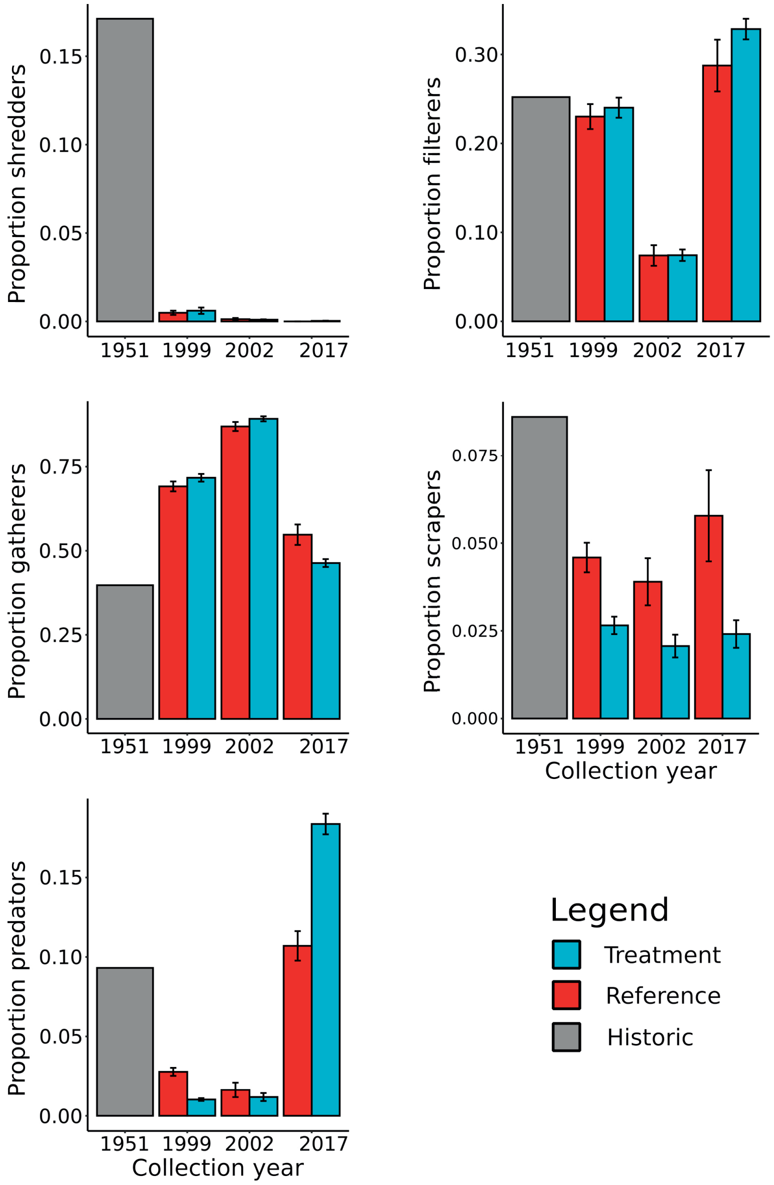

Fig. 4. Bar plots of the proportion of individuals belonging to various functional feeding groups (FFGs) from 1999, 2002, and 2017 for treatment and reference sites. Error bars represent mean standard error. For historical comparison, we included FFG data from Gaufin (1951). Error bars were not included for the historical references because Gaufin (1951) does not provide sufficient information to calculate mean standard errors.

0.015). Levels of detritus also increased over time (moderate effect; $\varepsilon^2 = 0.081$), but detritus size decreased (moderate effect; $\varepsilon^2 = 0.096$). Vegetation cover declined over time with a high effect ($\varepsilon^2 = 0.280$). Vegetation type remained similar through time (low effect; $\varepsilon^2 = 0.061$). Effect sizes differed when analyzing the effect of year on each abiotic factor separately for each site (see Supplementary Material 2 for details).

DISCUSSION

In the mid-20th century, the Middle Provo River supported a highly diverse macroinvertebrate community. Gaufin (1951) found an average of 53 macroinvertebrate species per site in 1951, ~70% of which were sensitive EPT taxa. The Middle Provo also appeared to be functionally balanced, with ~8% to 40% of individuals coming from each FFG (Gaufin 1951). Our comparative sampling results indicate that the macroinvertebrate community of the Middle Provo has not been fully restored by the PRRP. In fact, species richness, Shannon diversity, and %EPT have significantly *decreased* since 1999 at the treatment sites where the restoration took place (Sites 1–3). Despite significant changes to the FFG structure of the stream since 1999, the Middle Provo continues to be dominated by collectors. Shredding insects, which appear to have declined drastically from 1951 to 1999, have continued to decrease in abundance (Fig. 4). Importantly, we also observed a significant decrease in macroinvertebrate richness and diversity at the reference site (Site 4), suggesting that ongoing anthropogenic disturbances beyond the scope of the PRRP are preventing full recovery.

Nevertheless, the PRRP had at least some short-term benefits for aquatic communities of the Middle Provo River. For example, in our study, richness and diversity appears to have increased marginally from 1999 to 2002 in at least some sites (Supplementary Material 3). Similarly, both Shiozawa and Weibell (2006) and Olsen (2009), who conducted macroinvertebrate assessments closer to the PRRP completion in 2008, found that macroinvertebrate richness was higher postrestoration at downstream sites, though the upper sites had fewer species, perhaps due to their proximity to Jordanelle Dam and Reservoir. In addition, 2 geomorphologic assessments of the Provo River restoration concluded that, while some PRRP objectives were met (such as reduced water flow and increased sinuosity), an extensive hyporheic zone was not established and much of the stream was still sediment starved (Goetz 2008, Erwin et al. 2016), which may have limited the long-term reestablishment of macroinvertebrates. However, in a similar restoration assessment involving fish communities in the Middle Provo, fish diversity was higher postrestoration than prerestoration (Belk et al. 2016), demonstrating the success of the restoration project for a different taxonomic group.

We suggest that the apparent lack of long-term recovery of macroinvertebrates in the Middle Provo is not due to a failure of the PRRP, but instead due to the continued degradation of other hydrological, chemical, and geomorphologic factors on the Middle Provo. Indeed, although %EPT has increased at the reference site since 1999, the simultaneous decline in macroinvertebrate richness, diversity, and shredders at this site suggest that ongoing impacts on the Middle Provo may be preventing more substantial recovery. For example, large dams, which continue to affect the Provo River, rob sediments from downstream reaches (Ward and Stanford 1983), causing sediment transport rates to rise above deposition rates (Chin et al. 1994, Whiting and King 2003). Over time, this can cause substrates to cement (i.e., armor), resulting in the loss of habitat for benthic species (Hauer et al. 2018). For this reason, both Olsen (2009) and Erwin et al. (2016) recommended the manual addition of gravel immediately below Jordanelle Dam, but it is unclear whether these recommendations were acted upon. Our results show that although fine sediment cover increased from 1999 to 2017, substrate embeddedness remained high at all sites even after the restoration (Supplementary Material 2). This substrate issue could partially explain why the PRRP had limited success in restoring the macroinvertebrate community of the Middle Provo.

Beyond altering sedimentation, retention dams also alter natural flow regimes, change water temperatures, and destroy habitat for aquatic taxa (Ward and Stanford 1995, Poff and Schmidt 2016). These changes threaten aquatic insects because species rely on specific temperature and flow requirements for respiratory homeostasis, phenological cues, and reproductive success (Kennedy et al. 2016, Verberk et al. 2016, Perkin and Wilson 2021). Dams also stop allochthonous inputs from flowing downstream and restrict flows for water retention and flood mitigation, preventing water from entering the floodplain and replenishing the stream with detritus (Ward and Stanford 1983). Such impacts, along with impaired riparian plant communities (Olsen 2009), may limit food availability for detritivores and could explain the sharp decline in shredders we report here, as well as the extirpation of a once-abundant stonefly, *Pteronarcys californica*, throughout the Middle Provo River (Birrell et al. 2019). Since dam construction and river channelization had impacted this river decades before the PRRP, it is also possible that other insect species were in severe decline or completely extirpated before the restoration project began and thus beyond its help without intentional reintroduction.

An additional factor that may be preventing the Provo River from recovering is nutrient pollution from agricultural land use, which can degrade aquatic communities via eutrophication (Davies et al. 2008, He et al. 2011, Withers et al. 2014, Mateo-Sagasta et al. 2018). Although our study was not equipped to quantify the severity of eutrophication in the Middle Provo, we did observe high densities of thick periphyton mats throughout our study sites (Supplementary Material 2). The presence of such periphyton is indicative of eutrophication and may prevent some species from establishing, such as those that prefer the tops of rocks like most scrapers and sprawlers (Mattila and Räisänen 1998, Schneider and Lindstrøm 2011), the latter of which had been reduced between 1951 and 1999 before the PRRP began (Fig. 4, Supplementary Material 6). High levels of primary production can also lead to reductions in oxygen at night, though this does not appear to be common in the Middle Provo (iUTAH 2017). Although current levels of agricultural intensity are likely similar to prerestoration levels, it is possible that the Middle Provo's proximity to agricultural production limited the success of the restoration project (Goodsell et al. 2017).

Overall, our results indicate that large-scale stream restorations that rely primarily on physically restructuring habitat may be insufficient to restore stream macroinvertebrate communities (Palmer et al. 2010) when other underlying causes of river degradation remain unresolved. The PRRP may have led to short-term improvements in insect species richness (Olsen 2009), but as other abiotic factors of the Middle Provo remain impaired, the insect community has continued to decline in diversity. This does not negate the need for the restoration of physical habitat, which is to be commended, but instead clarifies the importance of long-term, holistic approaches that also consider the hydrological, chemical, and biological integrity of rivers (Palmer et al. 2010, Erwin et al. 2016). Bernhardt et al. (2005) also point out that there is little accountability or data accessibility for the outcomes of river restoration projects. The benefits of long-term monitoring reach beyond local management applications to inform ecological theory and future research (Likens et al. 1970). Thus, a protocol for making data from river restoration projects widely available would be extremely beneficial to restoration practitioners, especially as climate change and human development continue to impact these vulnerable ecosystems (Tonkin et al. 2019).

We recommend that the restructured sites along the Provo River Restoration Project be continually monitored using multiple methods—including our easily implemented macroinvertebrate sampling technique—that address species diversity, water quality (Carling et al. 2015), riparian plant community assemblage, geomorphology, and hydrological patterns. Such monitoring will provide a clearer understanding of what is happening to this ecosystem through general indicators of watershed health and has the potential of informing water managers and restoration ecologists of practices that maintain and improve species diversity. By re-evaluating current restoration methods with a more holistic approach, it may be possible to achieve a sustainable increase in macroinvertebrate biodiversity in the Middle Provo River.

VOUCHER SPECIMENS

All samples collected in 2017 were deposited in the Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, as aggregate samples according to collection date and locality.

SUPPLEMENTARY MATERIAL

Six online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol83/iss2/6).

SUPPLEMENTARY MATERIAL 1. Macroinvertebrate sampling protocol and site details.

SUPPLEMENTARY MATERIAL 2. Abiotic measurements and statistical analysis.

SUPPLEMENTARY MATERIAL 3. Species richness and Shannon diversity measurements for all sites.

SUPPLEMENTARY MATERIAL 4. List of taxa found in all sampling years.

SUPPLEMENTARY MATERIAL 5. Boxplots of %EPT measurements for all sites.

SUPPLEMENTARY MATERIAL 6. Habit group measurements and statistical analysis.

ACKNOWLEDGMENTS

We would like to thank the Brigham Young University Research Administration Office for funding this research (ORCA-2017), as well as the Biology Department and Monte L. Bean Life Science Museum of Brigham Young University for providing lab space for sample storage and insect identification. We also thank Jeff Andrus for insect identification, and all student researchers who participated in sample collection: Hannah Pardoe, Alex Birrell, Jeremy Birrell, Desert Mulford, Samantha Standring, Rebecca Clement Maldonado, Anne Thomas, Zachary Jaramillo, Sara Jaramillo, Max Richmond, Madeleine Burt, Amanda Collyer, Mitch Young, Robert Erickson, and Ben Burt. In addition, we thank Art Woods for assisting in editing the manuscript and Jon Graham and David Patterson for helping with the statistical analysis.

LITERATURE CITED

ASHLEY, J., AND R.L. JONES. 2002. The Central Utah Project. Journal of Land, Resources, and Environmental Law 22:273–308.

BARBOUR, M.T., J. GERRITSEN, B.D. SNYDER, AND J.B. STRIBLING. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. 2nd edition. EPA 841-B-99-002, U.S. Environmental Protection Agency, Office of Water, Washington, DC. 337 pp.

BELK, M.C., E.J. BILLMAN, C. ELLSWORTH, AND B.R. MCMILLAN. 2016. Does habitat restoration increase coexistence of native stream fishes with introduced brown trout: a case study on the Middle Provo River, Utah, USA. Water 8:1–9.

BERNHARDT, E.S., M.A. PALMER, J.D. ALLAN, G. ALEXANDER, K. BARNAS, S. BROOKS, J. CARR, S. CLAYTON, C. DAHM, J. FOLLSTAD-SHAH, ET AL. 2005. Synthesizing U.S. river restoration efforts. Science 308:636–637.

BIRRELL, J.H., J.B. MEEK, AND C.R. NELSON. 2019. Decline of the giant salmonfly *Pteronarcys californica* Newport, 1848 (Plecoptera: Pteronarcyidae) in the Provo River, Utah, USA. Illiesia 15:83–97.

CARDOSO, P., AND S.R. LEATHER. 2019. Predicting a global insect apocalypse. Insect Conservation and Diversity 12:263–267.

CARLING, G.T., D.G. TINGEY, D.P. FERNANDEZ, S.T. NELSON, Z.T. AANDERUD, T.H. GOODSELL, AND T.R. CHAPMAN. 2015. Evaluating natural and anthropogenic trace element inputs along an alpine to urban gradient in the Provo River, Utah, USA. Applied Geochemistry 63:398–412.

CARPENTER, S.R., E.H. STANLEY, AND M.J. VANDER ZANDEN. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annual Review of Environment and Resources 36:75–99.

CHAO, A., N.J. GOTELLI, T.C. HSIEH, E.L. SANDER, K.H. MA, R.K. COLWELL, AND A.M. ELLISON. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45–67.

CHIN, C.O., B.W. MELVILLE, AND A.J. RAUDKIVI. 1994. Streambed armoring. Journal of Hydraulic Engineering 120:899–918.

DAVIES, B.R., A.J. BIGGS, A.P.J. WILLIAMS, A.J.T. LEE, AND A.S. THOMPSON. 2008. A comparison of the catchment sizes of rivers, streams, ponds, ditches and lakes: implications for protecting aquatic biodiversity in an agricultural landscape. Hydrobiologia 597:7–17.

DEWALT, R.E., C. FAVRET, AND D.W. WEBB. 2005. Just how imperiled are aquatic insects? A case study of stoneflies (Plecoptera) in Illinois. Annals of the Entomological Society of America 98:941–950.

DIJKSTRA, K.D.B., M.T. MONAGHAN, AND S.U. PAULS. 2014. Freshwater biodiversity and aquatic insect diversification. Annual Review of Entomology 59:143–163.

ELOSEGI, A., AND S. SABATER. 2012. Effects of hydromorphological impacts on river ecosystem functioning: a review and suggestions for assessing ecological impacts. Hydrobiologia 712:129–143.

ERWIN, S.O., J.C. SCHMIDT, AND T.M. ALLRED. 2016. Post-project geomorphic assessment of a large process-based river restoration project. Geomorphology 270:145–158.

GAUFIN, A.R. 1951. Production of bottom fauna in the Provo River, Utah. Doctoral dissertation, Iowa State College, Ames, IA. ProQuest Dissertations Publishing. DP11893. https://www.proquest.com/docview/302028353?pq-origsite=gscholar&fromopenview=true

GOETZ, R.R. 2008. A post-project assessment of the Provo River Restoration Project: channel design, reconfiguration, and the re-establishment of critical physical processes. Master's thesis, Utah State University, Logan, UT. ProQuest Dissertations Publishing. 1454540. https://www.proquest.com/docview/89250888?pq-origsite=gscholar&fromopenview=true

GOODSELL, T.H., G.T. CARLING, Z.T. AANDERUD, S.T. NELSON, D.P. FERNANDEZ, AND D.G. TINGEY. 2017. Thermal groundwater contributions of arsenic and other trace elements to the Middle Provo River, Utah, USA. Environmental Earth Sciences 76:1–12.

GOTELLI, N.J., AND R.K. COLWELL. 2011. Estimating species richness. Pages 39–54 *in* A.E. Magurran and B.J. McGill, editors, Biological diversity: frontiers in measurement and assessment. 1st edition. Oxford University Press, New York, NY.

HALLMANN, C.A., M. SORG, E. JONGEJANS, H. SIEPEL, N. HOFLAND, H. SCHWAN, W. STENMANS, A. MÜLLER, H. SUMSER, T. HÖRREN, ET AL. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLOS ONE 12:e0185809.

HARRISON, S.S.C., J.L. PRETTY, D. SHEPHERD, A.G. HILDREW, C. SMITH, AND R.D. HEY. 2004. The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. Journal of applied Ecology 41:1140–1154.

HARVEY, J.A., R. HEINEN, I. ARMBRECHT, Y. BASSET, J.H. BAXTER-GILBERT, T.M. BEZEMER, M. BÖHM, R. BOMMARCO, P.A.V. BORGES, P. CARDOSO, ET AL. 2020. International scientists formulate a roadmap for insect conservation and recovery. Nature Ecology and Evolution 4:174–176.

HAUER, C., P. LEITNER, G. UNFER, U. PULG, H. HABERSACK, AND W. GRAF. 2018. The role of sediment and sediment dynamics in the aquatic environment. Pages 151–169 *in* S. Schmutz and J. Sendzimir, editors, Riverine Ecosystem Management, Springer, Cham.

HE, B., S. KANAE, T. OKI, Y. HIRABAYASHI, Y. YAMASHIKI, AND K. TAKARA. 2011. Assessment of global nitrogen pollution in rivers using an integrated biogeochemical modeling framework. Water Research 45:2573–2586.

HSIEH, T.C., K.H. MA, AND A. CHAO. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456.

[IUTAH] IUTAH GAMUT WORKING GROUP. 2017. iUTAH GAMUT Network Raw Data. iUTAH Modeling and Data Federation. http://data.iutahepscor.org/mdf/

JOHNSON, M.F., C.R. THORNE, J.M. CASTRO, G.M. KONDOLF, C.S. MAZZACANO, S.B. ROOD, AND C. WESTBROOK. 2020. Biomic river restoration: a new focus for river management. River Research and Applications 36:3–12.

KENNEDY, T.A., J.D. MUEHLBAUER, C.B. YACKULIC, D.A. LYTLE, S.W. MILLER, K.L. DIBBLE, E.W. KORTENHOEVEN, A.N. METCALFE, AND C.V. BAXTER. 2016. Flow management for hydropower extirpates aquatic insects, undermining river food webs. BioScience 66:561–575.

KLEIN, L.R., S.R. CLAYTON, J.R. ALLDREDGE, AND P. GOODWIN. 2007. Long-term monitoring and evaluation of the Lower Red River Meadow restoration project, Idaho, U.S.A. Restoration Ecology 15:223–239.

LEPORI, F., D. PALM, E. BRÄNNÄS, AND B. MALMQVIST. 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? Ecological Applications 15:2060–2071.

LIKENS, G.E., F.H. BORMANN, N.M. JOHNSON, D.W. FISHER, AND R.S. PIERCE. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed-ecosystem. Ecological Monographs 40:23–47.

MACADAM, C.R., AND J.A. STOCKAN. 2015. More than just fish food: ecosystem services provided by freshwater insects. Ecological Entomology 40:113–123.

MACDONALD, M.J., L.K. ALBERTSON, AND G.C. POOLE. 2021. Ecosystem engineering in the streambed: net-spinning caddisflies influence hydraulic properties. Ecohydrology 14:e2266.

MANGIAFICO, S.S. 2016. Summary and analysis of extension program evaluation in R, version 1.20.01. Rutgers Cooperative Extension, New Brunswick, NJ. https://rcompanion.org/documents/RHandbookProgramEvaluation.pdf

MATEO-SAGASTA, J., S.M. ZADEH, AND H. TURRAL, EDITORS. 2018. More people, more food, worse water? A global review of water pollution from agriculture. Food and Agriculture Organization of the United Nations, Rome, Italy. https://www.fao.org/3/ca0146en/ca0146en.pdf

MATTILA, J., AND R. RÄISÄNEN. 1998. Periphyton growth as an indicator of eutrophication; an experimental approach. Hydrobiologia 377:15–23.

MERRITT, R.W., K.W. CUMMINS, AND M.B. BERG, EDITORS. 2008. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co., Dubuque, IA. 1158 pp.

MILLER, S.W., P. BUDY, AND J.C. SCHMIDT. 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river-restoration. Restoration Ecology 18:8–19.

NILSSON, C., L.E. POLVI, J. GARDESTRÖM, E.M. HASSELQUIST, L. LIND, AND J.M. SARNEEL. 2015. Riparian and in-stream restoration of boreal streams and rivers: success or failure? Ecohydrology 8:753–764.

OLSEN, D. 2009. Middle Provo River 2006 Monitoring Report. BIO-WEST Inc. https://www.mitigationcommission.gov/prrp/pdf/2006_monitoring_report.pdf

PALMER, M., J.D. ALLAN, J. MEYER, AND E.S. BERNHARDT. 2007. River restoration in the twenty-first century: data and experiential knowledge to inform future efforts. Restoration Ecology 15:472–481.

PALMER, M.A., H.L. MENNINGER, AND E. BERNHARDT. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 55:205–222.

PALMER, M., AND A. RUHI. 2019. Linkages between flow regime, biota, and ecosystem processes: implications for river restoration. Science 365:1–13.

PAYTON, M.E., M.H. GREENSTONE, AND N. SCHENKER. 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? Journal of Insect Science 3:1–6.

PERKIN, E.K., AND M.J. WILSON. 2021. Anthropogenic alteration of flow, temperature, and light as life-history cues in stream ecosystems. Integrative and Comparative Biology 61:1134–1146.

PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, EISPACK AUTHORS, S. HEISTERKAMP, B. VAN WILLIGEN, J. RANKE, AND R CORE TEAM. 2021. Package ‘*nlme*’. Linear and nonlinear mixed effects models. R-core. http://cran.rapporter.net/web/packages/nlme/nlme.pdf

POFF, N.L.R., AND J.C. SCHMIDT. 2016. How dams can go with the flow. Science 353:1099–1100.

R CORE TEAM. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

SÁNCHEZ-BAYO, F., AND K.A.G. WYCKHUYS. 2019. Worldwide decline of the entomofauna: a review of its drivers. Biological Conservation 232:8–27.

SCHNEIDER, S.C., AND E.A. LINDSTRØM. 2011. The periphyton index of trophic status PIT: a new eutrophication metric based on non-diatomaceous benthic algae in nordic rivers. Hydrobiologia 665:143–155.

SHIOZAWA, D.K., AND B.J. WEIBELL. 2006. The investigation of the macrobenthos of the Provo River between Jordanelle and Deer Creek Reservoirs, Part II. A report to the Utah Reclamation Mitigation and Conservation Commission, Provo, UT.

SHIOZAWA, D.K., B.J. WEIBELL, AND E. MCLAUGHLIN. 2002. The investigation of the macrobenthos of the Provo River between Jordanelle and Deer Creek Reservoirs, Part I. A report to the Utah Reclamation Mitigation and Conservation Commission, Provo, UT.

STEWART, G.B., H.R. BAYLISS, D.A. SHOWLER, W.J. SUTHERLAND, AND A.S. PULLIN. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. Ecological applications 19:931–941.

STRAYER, D.L., AND D. DUDGEON. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29:344–358.

SUTER, G.W., AND S.M. CORMIER. 2015. Why care about aquatic insects: uses, benefits, and services. Integrated Environmental Assessment and Management 11:188–194.

TONKIN, J.D., N.L.R. POFF, N.R. BOND, A. HORNE, D.M. MERRITT, L.V. REYNOLDS, J.D. OLDEN, A. RUHI, AND D.A. LYTLE. 2019. Prepare river ecosystems for an uncertain future. Nature 570:301–303.

[UDNR] UTAH DEPARTMENT OF NATURAL RESOURCES. 2021. Blue Ribbon fisheries. https://wildlife.utah.gov/blue-ribbon-fisheries.html

[URMCC] UTAH RECLAMATION MITIGATION AND CONSERVATION COMMISSION. 1997. Provo River Restoration Project, final environmental impact statement summary. U.S. Department of the Interior. https://www.mitigationcommission.gov/prrp/pdf/prrp_eis.pdf

[URMCC] UTAH RECLAMATION MITIGATION AND CONSERVATION COMMISSION. 2002. Provo River Restoration

Project aquatic invertebrate sampling 1999–2002. https://www.mitigationcommission.gov/prrp/pdf/prrp_macro_sampling.pdf

VERBERK, W.C.E.P., J. OVERGAARD, R. ERN, M. BAYLEY, T. WANG, L. BOARDMAN, AND J.S. TERBLANCHE. 2016. Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. Comparative Biochemistry and Physiology Part A 192:64–78.

WAGNER, D.L., E.M. GRAMES, M.L. FORISTER, M.R. BERENBAUM, AND D. STOPAK. 2021. Insect decline in the Anthropocene: death by a thousand cuts. Proceedings of the National Academy of Sciences 118:e2023989118.

WALTERS, D.M., J.S. WESNER, R.E. ZUELLIG, D.A. KOWALSKI, AND M.C. KONDRATIEFF. 2018. Holy flux: spatial and temporal variation in massive pulses of emerging insect biomass from western U.S. rivers. Ecology 99:238–240.

WARD, J.V., AND J.A. STANFORD. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T.D.I. Fontaine and S.M. Bartell, editors, Dynamics of lotic ecosystems, Ann Arbor Science, Ann Arbor, MI.

WARD, J.V., AND J.A. STANFORD. 1995. The serial discontinuity concept: extending the model to floodplain rivers. Regulated Rivers: Research and Management 10:159–168.

WHITEWAY, S. L., P.M. BIRON, A. ZIMMERMANN, O. VENTER, AND J.W. GRANT. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. Canadian Journal of Fisheries and Aquatic Sciences 67:831–841.

WHITING, P.J., AND J.G. KING. 2003. Surface particle sizes on armoured gravel streambeds: effects of supply and hydraulics. Earth Surface Processes and Landforms 28:1459–1471.

WITHERS, P.J.A., C. NEAL, H.P. JARVIE, AND D.G. DOODY. 2014. Agriculture and eutrophication: where do we go from here? Sustainability 6:5853–5875.

WOHL, E., S.N. LANE, AND A.C. WILCOX. 2015. The science and practice of river restoration. Water Resources Research 51:5974–5997.

ZHANG, X., AND N. YI. 2020. NBZIMM: negative binomial and zero-inflated mixed models, with application to microbiome/metagenomics data analysis. BMC Bioinformatics 21:1–19.

Received 14 January 2022
Revised 19 January 2023
Accepted 1 February 2023
Published online 10 August 2023