On the efficacy of restoration in stream networks: comment and critique

David Murray-Stoker\textsuperscript{1,2,3}

\textsuperscript{1}Odum School of Ecology, University of Georgia, Athens, GA 30602, U.S.A.
\textsuperscript{2}Present Address: Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada
\textsuperscript{3}Present Address: Department of Biology, University of Toronto Mississauga, Mississauga, ON L5L 1C6, Canada

ORCID: https://orcid.org/0000-0002-4774-6948

E-mail: dstoker92@gmail.com
Swan and Brown (2017) recently addressed the effects of restoration on stream communities under the meta-community framework. Using a combination of headwater and mainstem streams, Swan and Brown (2017) evaluated how position within a stream network affected the outcome of restoration on invertebrate communities. Ostensibly, their hypotheses were partially supported as restoration had stronger effects in headwater streams: invertebrate taxonomic richness was increased and temporal variability decreased in restored reaches; however, these results were not consistent upon closer scrutiny for both the original paper (Swan and Brown 2017) and the later erratum (Swan and Brown 2018). This is due to issues with experimental design, improper use of statistical analyses, and discrepancies between written methods and what was actually conducted. Here, I provide a secondary analysis of the data, with hypotheses and interpretations in the context of stream, restoration, and metacommunity ecology.

**Keywords:** community diversity, metacommunity theory, open science, questionable research practices, restoration ecology

### Introduction

In a recent study, Swan and Brown (2017) evaluated how restoration affected community diversity in streams through the use of metacommunity theory. Under this framework, local effects are associated with species’ niches while regional effects are more associated with dispersal (Leibold et al. 2004). In the context of stream networks, headwaters are isolated patches more likely to be impacted by niches and environmental characteristics and mainstems are well-connected more likely to be affected by dispersal (Heino et al. 2003, Leibold et al. 2004, Grant et al. 2007, Altermatt 2013, Heino 2013). Restoration of stream habitats was therefore
expected to have a greater impact on communities in headwaters relative to mainstems (Swan and Brown 2017).

Although Swan and Brown (2017, 2018) noted that restoration techniques can vary in intrusiveness on stream ecosystems, they did not account for this in their experimental design and statistical analyses. Restored streams in their study received various combinations of bank stabilization, in-channel manipulation, and riparian reforestation (i.e. tree planting) treatments, and these treatments were not applied in a consistent or systematic manner (Swan and Brown 2017: Table 2). Swan and Brown (2017) did not set a restoration criterion for site inclusion in their study, instead including all sites regardless of the combination of applied restoration treatments. I suggest that this oversight leads to unnecessary assumptions about the efficacy of restoration by assuming the effects of all treatments combinations are equivalent, and this issue could have been partially resolved a priori by hypothesizing how each restoration reach would affect headwater and mainstem streams and then setting requirements for site inclusion in the analyses.

I contend that the various restoration treatments differ not only in their overall effects but also if the treatment is applied in headwater or mainstem streams, and, for these reasons, criteria for site selection could be set. I suggest that bank stabilization and in-channel manipulation treatments are more likely to have consistent effects in both headwaters and mainstems, while riparian reforestation would likely have stronger effects in headwater compared to mainstem streams. A similar argument was made by Swan and Brown, though it was not explicitly noted until the erratum (Swan and Brown 2018). Bank stabilization and in-channel manipulation can increase bed stability and substrate availability and diversity in both headwater and mainstem streams; however, the effects of riparian reforestation could act on a gradient from headwaters to
mainstems. For example, leaf litter is an important source of habitat and nutrients in headwaters but less so in mainstems (Vannote et al. 1980, Rosi-Marshall and Wallace 2002). Additionally, the utility of riparian reforestation on reducing nutrient inputs notwithstanding (Collins et al. 2013), the effects of riparian reforestation could be stronger in headwater streams because they are isolated systems, whereas mainstem streams receive flows of water, nutrients, and organisms from many tributaries (Vannote et al. 1980). Effectively, mainstems are dependent on other tributaries and any local restoration effects via riparian reforestation could be overwhelmed by incoming flows from unrestored streams (Wahl et al. 2013).

Here, I present a re-analysis of the data provided by Swan and Brown (2017, 2018) because of the hypothesized differences in the consistency and effectiveness of the applied restoration treatments. I required sites in the re-analysis to have received both the bank stabilization and in-channel manipulations treatments (hereafter “revised” sites), although sites receiving riparian reforestation were also included if they received both the bank stabilization and in-channel manipulations treatments. I also re-analyzed the full data (hereafter “full” sites) to determine if any differences, or lack thereof, between the full and revised sites analyses could be attributed to increased variation in the revised sites due to decreased sample size. Finally, I compare the interpretation and conclusions from my re-analysis to those in Swan and Brown (2017) and the erratum (Swan and Brown 2018).

**Methods**

I generally followed the analyses as written by Swan and Brown (2017), with modifications made when necessary. The three community response variables were local diversity, spatial dissimilarity, and temporal variation. Local diversity was calculated as taxonomic richness (i.e. number of different taxa present) and taxonomic diversity (i.e.
Shannon’s diversity) and compared using an analysis of variance (ANOVA). The model was constructed to examine the individual effects of reach (restored or adjacent), order (headwater or mainstem), and season (spring, summer, fall, and winter) and all two- and three-way interactions, with individual ANOVAs for richness and diversity; I also fit the full and reduced taxonomic richness models proposed in the erratum (Swan and Brown 2018) as a separate set of ANOVAs. Spatial dissimilarity between communities in restored and adjacent reaches for each order-by-season combination was quantified using the modified Gower index (Anderson et al. 2006) with a logarithm with a base of 5 on an untransformed abundance matrix. Modified Gower dissimilarities were then compared using an ANOVA with the individual effects of season and order as well as their interaction. Temporal variability was measured as the multivariate dispersion (i.e. mean distance to the centroid) of repeated samples for each stream-by-reach-by-order combination (Anderson et al. 2006). Distances were calculated in principal coordinates space after Bray-Curtis dissimilarity was performed on the untransformed abundance matrix. Temporal variability was then compared using an ANOVA with the individual effects of order and reach and their interaction. All ANOVAs were performed for both the full and revised sites, with stream identity fitted as a random blocking factor in each ANOVA; all ANOVAs were fitted by restricted maximum likelihood.

Exploratory data analysis was conducted prior to any model fitting to determine if the data met test assumptions (Zuur et al. 2009). For the full sites analyses, numerical summaries demonstrated an unbalanced design, with equal representation of restored and unrestored reaches but a large disparity in the number of samples between headwaters and mainstems for each of the taxonomic richness and diversity (headwater n = 38, mainstem n = 62), spatial dissimilarity (headwater n = 19, mainstem = 31), and temporal variation (headwater n = 10, mainstem n = 16)
analyses. Additionally, the assumption of homogeneity of variance was violated for the
taxonomic richness and diversity and the spatial dissimilarity analyses. The unbalanced design
was greatly reduced for the revised sites analyses: taxonomic richness and diversity (headwater n
= 30, mainstem n = 40), spatial dissimilarity (headwater n = 15, mainstem = 20), and temporal
variation (headwater n = 8, mainstem n = 10); however, the assumption of homogeneity of
variance was still violated. To better meet the assumption of equal variance, taxonomic richness
was \( \ln \)-transformed, taxonomic diversity was square root-transformed, and spatial dissimilarity
was \( \ln \)-transformed for all analyses. Along with using transformations to response variables to
meet model assumptions, I used Type III sums of squares for evaluating main and interactive
effects of factors included in the ANOVA. Swan and Brown (2017, 2018) used Type I sums of
squares, which are inadequate for unbalanced and multi-factor designs with interactions between
or among factors (Shaw and Mitchell-Olds 1993, Quinn and Keough 2002).

Model assumptions were inspected graphically, and significance was considered at \( P < 0.050 \). I removed the spring sample from the restored reach of site 227 from analyses because
there was no corresponding sample from the adjacent reach, which would have precluded paired
comparisons of restored-adjacent sites; however, I did not remove any sites prior to fitting the
full and reduced model ANOVAs set by Swan and Brown (2018). All analyses were conducted
using R version 3.5.3 (R Core Team 2019) with the nlme (version 3.1-139, Pinheiro et al. 2019)
and vegan (version 2.5-4, Oksanen et al. 2019) packages; data and R code are deposited in the
figshare repository (10.6084/m9.figshare.6448010). Given I made necessary modifications to the
analyses written by Swan and Brown (2017, 2018), later comparisons between the re-analysis
presented here and the results presented by Swan and Brown (2017, 2018) will only be in terms
of statistical and ecological interpretation and not exact values of statistical tests.
Results and Discussion

There were no main or interactive effects of season, order, or reach on taxonomic richness for either the full or revised sites analyses (Table 1, Figure 1). The full model of taxonomic richness proposed in the erratum (Swan and Brown 2018) did not show any main or interactive effects of season, order, or reach (Table 2); however, the reduced model of taxonomic richness demonstrated an interaction between order and season ($F_{3,80} = 4.105, P = 0.009$) and significant main effects of season ($F_{3,80} = 4.358, P = 0.007$) and treatment ($F_{1,80} = 4.844, P = 0.031$). In contrast to taxonomic richness, taxonomic diversity varied by season for the full ($F_{3,80} = 12.267, P < 0.001$) and revised ($F_{3,80} = 10.999, P < 0.001$) sites (Table 1, Figure 2). There were no further main or interactive effects of season, order, or reach on taxonomic diversity for either the full or revised sites (Table 1, Figure 2). Spatial dissimilarity did not vary by any of the main or interactive effects of season and order for both the full and revised sites (Table 1, Figure 3). Additionally, temporal variation did not vary by the main effects of or interaction between reach and order for the full and revised sites (Table 1, Figure 4).

Differences in significant main effects or interactions within the full and revised sites in the re-analysis did not seem to be the result of increased variation in the revised sites. In fact, variance, as measured by 95% confidence intervals, was either similar or even reduced for each of local diversity, spatial dissimilarity, and temporal variability for the revised sites compared to the full sites (Figures 1-4). It is therefore unlikely that that revised sites analysis was unable to detect effects due to increased variation and more likely due to reduced statistical power associated with a smaller sample size or the true lack of an effect of restoration in this system.

Effectiveness of Local Restoration
I hypothesized that stream-channel manipulations would have a more consistent effect between headwaters and mainstems relative to the effects of riparian reforestation, with stronger effects of restoration in headwaters relative to mainstems. As there were no significant effects of restoration on any of the community metrics between headwaters and mainstems, this hypothesis could be invalid or, at a minimum, revised and re-tested. I should note that I was unable to directly test this hypothesis because I was re-analyzing data from a previous study and the experimental design precluded any robust test to isolate the effects; however, the hypothesis was intended to guide criteria for site selection and reduce variation in restoration treatments among sites and not to necessarily compare in-channel manipulations and riparian reforestation treatments. Regarding evidence for stream-channel manipulations and other treatments for effective restoration, previous research suggests local habitat manipulations are ineffective for structuring communities and increasing biodiversity (Palmer et al. 2010). An emerging hypothesis is that local factors, such as habitat complexity and water quality, are overwhelmed by regional factors, such as dispersal and position within the larger network (Heino 2013, Tonkin et al. 2014). Given restoration did not have an effect on any diversity measure of communities in either headwaters or mainstems, this could suggest either restoration was wholly inadequate for both headwaters and mainstems or that the larger network and regional species pool were already degraded (Sundermann et al. 2011), overwhelming any mitigating effects of restoration.

Restoration Ecology and Experimental Design

Restoration of the streams was done in isolation of the study design and prior to data collection, resulting in variation in the types of treatments applied to and the time since restoration of the streams (Swan and Brown 2017). Although Swan and Brown (2017) noted this limitation of their study, they failed to acknowledge they could have better controlled for this
variation by setting strict criteria for site selection and inclusion, which was the foundation for
my re-analysis. This concern was briefly acknowledged in the erratum (Swan and Brown 2018),
where the data quality control process removed sites if they only received riparian reforestation
treatments without at least one of either the bank stabilization or in-channel manipulation
treatments; however, Swan and Brown (2017, 2018) proceeded to analyze data from sites
receiving any combination of restoration treatments, despite suggesting that in-stream
modification treatments would have stronger effects on communities relative to riparian
reforestation (Swan and Brown 2018). Setting a more stringent criterion for site inclusion, as was
done in this re-analysis of the revised sites, would have reduced the variation in the applied
restoration treatments.

The inconsistent application of restoration treatments prohibited a robust evaluation that
could have been possible with a factorial experiment; therefore, the singular and interactive
effects of the restoration treatments in the study system remain untested. This further complicates
the indiscriminate usage of “restoration” by Swan and Brown (2017, 2018) and in the full sites
analysis presented here, as the underlying mechanism of restoration on the stream invertebrate
communities remains an unknown quantity. Identifying how individual and combinations of
restoration treatments affect stream communities would provide valuable insight for maximizing
the effectiveness of restoration efforts. In the absence of this knowledge, reducing the variation
in which restoration treatments were applied to the streams, as done with revised sites analysis,
arguably would have been a better avenue.

Contradicting Results and Questionable Research Practices

Restoration was not found to have a significant effect on local diversity, spatial
dissimilarity, or temporal variability of stream invertebrate communities between paired restored
and unrestored reaches in headwaters and mainstems. These results presented here, not exact values of test statistics but in terms of interpretation, directly contradict the results presented in the original paper (Swan and Brown 2017) and in the erratum (Swan and Brown 2018). This is concerning, as any data management and analytical errors in the original paper were supposedly resolved in the erratum (Swan and Brown 2018); however, the discrepancies can be partially explained by the erroneous reporting and implementation of statistical analyses. First, as was noted above, Swan and Brown (2017, 2018) analyzed an unbalanced design with unequal variance using an ANOVA with Type I sums of squares, when transformations to response variables were necessary to meet test assumptions and Type III sums of squares were more appropriate for investigating the main and interactive effects (Shaw and Mitchell-Olds 1993, Quinn and Keough 2002). This renders the results presented by Swan and Brown (2017, 2018) baseless, as violation of test assumptions make any results derived from that test invalid. Second, the fitting of the random effects in the ANOVAs was incorrect. Swan and Brown (2018) reported fitting stream identity as a random effect. With the R code provided with the erratum (Swan and Brown 2018: Supporting Information), each site-by-reach combination was fitted a random effect, despite adjacent and restored reaches being separated by < 10 m (Swan and Brown 2017). Fitting stream identity alone would have been a more appropriate fitting of a random effect that reflected the non-independence of the reaches at such small spatial scales, and, importantly, an accurate implementation of the written methods. Third, removal of the restored site without a paired observation is necessary for the fundamental goal of the study: comparing community diversity between paired restored and adjacent reaches across headwater and mainstem streams. Without removing the site, comparisons would be made to an unpaired reach, violating the experimental design and central goal of the study.
Finally, and of greatest concern, is the wholesale disagreement between the reported analytical procedure and what was actually conducted when analyzing temporal variability. Temporal variability was reportedly quantified as the mean distance to the group centroid (Anderson et al. 2006) after applying a Bray-Curtis dissimilarity index on an untransformed abundance matrix (Swan and Brown 2017). Results presented in the erratum were actually derived from the spatial median after a Jaccard index was applied to a presence-absence matrix (Swan and Brown 2018: Supporting Information). No random effect of stream identity was fitted for this ANOVA, although it would have been appropriate given the study design (Quinn and Keough 2002). Moreover, headwaters and mainstems were not parsed into separate groups; this resulted in the spatial median being calculated for a stream-by-reach combination rather than each stream-by-reach-by-order combination. As Swan and Brown (2017) intended to evaluate the difference in temporal variability between headwaters and mainstems in response to restoration, the analytical procedure was unable to detect or quantify this effect appropriately. None of the changes to the analytical procedure were reported in the erratum, and these alterations were only found upon scrupulous evaluation of the provided R code (Swan and Brown 2018: Supporting Information). Without consulting the supporting information or if no R code was provided, it would have been assumed the results presented in the erratum (Swan and Brown 2018) were derived from the analysis described in the original study (Swan and Brown 2017), just with the corrected dataset; this assumption would have been incorrect.

Concluding Remarks

I intended to re-analyze the data provided by Swan and Brown (2017, 2018) to determine if the same patterns were observed if only sites receiving at least both intensive, stream-channel restoration treatments were included. I then evaluated the same hypotheses as proposed by Swan.
and Brown (2017), as the hypothesized mechanisms were consistent with metacommunity theory. I did not find any effects of restoration on local diversity, spatial dissimilarity, and temporal variability, let alone differential effects between headwaters and mainstems. This is contrary to results presented by Swan and Brown (2017, 2018), who reported that restoration increased taxonomic richness and decreased temporal variability in restored headwater streams. I have demonstrated that the statistical tests from which those results were derived were invalid, and, therefore, recommend use of the results presented here. I also have some evidence demonstrating questionable research practices conducted by Swan and Brown (2017, 2018), whereby written methods were not properly followed when analyzing the data. I have concluded that, given restoration had no effect on any community diversity metric, local restoration of streams can be ineffective if (1) both dispersal and habitat quality are structuring biodiversity (Heino et al. 2015, Smith et al. 2015, Downes et al. 2017) and (2) the larger regional community is already degraded (Sundermann et al. 2011). It matters not that this conclusion is partially convergent with that of Swan and Brown (2017, 2018), because I arrived at my conclusion based on a thorough and robust re-analysis of the data, while Swan and Brown (2017, 2018) based their conclusions on the erroneous reporting and implementation of statistical analyses.
Literature Cited

Altermatt, F. 2013. Diversity in riverine metacommunities: A network perspective. Aquatic Ecology 47:365–377.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683-693.

Collins, K. E., C. Doscher, H. G. Rennie, and J. G. Ross. 2013. The effectiveness of riparian ‘restoration’ on water quality: A case study of lowland streams in Canterbury, New Zealand. Restoration Ecology 21:40-48.

Downes, B. J., J. Lancaster, A. Glaister, and W. D. Bovill. 2017. A fresh approach reveals how dispersal shapes metacommunity structure in a human-altered landscape. Journal of Applied Ecology 54:588–598.

Grant, E. H. C., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: Population dynamics and ecological processes in dendritic networks. Ecology Letters 10:165–175.

Heino, J. 2013. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? Oecologia 171:971–980.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshwater Biology 60:845–869.

Heino, J., T. Muotka, and R. Paavola. 2003. Determinants of macroinvertebrate diversity in headwater streams: Regional and local influences. Journal of Animal Ecology 72:425–434.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The
metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: Community Ecology Package. R package version 2.5-4. <https://CRAN.R-project.org/package=vegan>

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.

Pinheiro J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-139. <https://CRAN.R-project.org/package=nlme>

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://cran.r-project.org/>

Rosi-Marshall, E. J., and J. B. Wallace. 2002. Invertebrate food webs along a stream resource gradient. Freshwater Biology 47:129-141.

Shaw, R. G., and T. Mitchell-Olds. 1993. ANOVA for unbalanced data: An overview. Ecology 74:1638–1645.

Smith, R. F., P. D. Venugopal, M. E. Baker, and W. O. Lamp. 2015. Habitat filtering and adult dispersal determine the taxonomic composition of stream insects in an urbanizing landscape. Freshwater Biology 60:1740–1754.
Sundermann, A., S. Stoll, and P. Haase. 2011. River restoration success depends on the species pool of the immediate surroundings. Ecological Applications 21:1962-1971.

Swan, C. M., and B. L. Brown. 2017. Metacommunity theory meets restoration: isolation may mediate how ecological communities respond to stream restoration. Ecological Applications 27:2209-2219.

Swan, C. M., and B. L. Brown. 2018. Erratum for: Metacommunity theory meets restoration: isolation may mediate how ecological communities respond to stream restoration. Ecological Applications 28:1370–1371.

Tonkin, J. D., S. Stoll, A. Sundermann, and P. Haase. 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. Freshwater Biology 59:1843-1855.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Wahl, C. M., A. Neils, and D. Hooper. 2013. Impacts of land use at the catchment scale constrain the habitat benefits of stream riparian buffers. Freshwater Biology 58:2310–2324.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2009. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.
Table 1: ANOVA results for taxonomic richness, taxonomic diversity, spatial dissimilarity, and temporal variability. Models were fitted using restricted maximum likelihood and with Type III sums of squares for estimating main and interactive effects of factors.

| Source of Variation | Full Sites | | | Revised Sites | | |
|---------------------|-----------|------|--------|-----------|------|--------|
|                     | numDF    | denDF | F      | P        | numDF | denDF | F      | P        |
| Taxonomic Richness  |           |       |        |          |       |       |        |          |
| Season              | 3         | 73    | 1.991  | 0.123    | 3      | 47    | 1.411  | 0.251    |
| Order               | 1         | 11    | 1.419  | 0.259    | 1      | 7     | 0.004  | 0.951    |
| Reach               | 1         | 73    | 0.730  | 0.396    | 1      | 47    | 0.398  | 0.531    |
| Season x Order      | 3         | 73    | 1.641  | 0.187    | 3      | 47    | 0.553  | 0.649    |
| Season x Reach      | 3         | 73    | 0.045  | 0.987    | 3      | 47    | 0.143  | 0.934    |
| Order x Reach       | 1         | 73    | 0.308  | 0.581    | 1      | 47    | 1.375  | 0.247    |
| Season x Order x Reach | 3       | 73    | 0.083  | 0.969    | 3      | 47    | 0.149  | 0.930    |
| Taxonomic Diversity |           |       |        |          |       |       |        |          |
| Season              | 3         | 73    | 12.267 | < 0.001  | 3      | 47    | 10.999 | < 0.001  |
| Order               | 1         | 11    | 2.073  | 0.178    | 1      | 7     | 0.253  | 0.630    |
| Reach               | 1         | 73    | 0.088  | 0.768    | 1      | 47    | 0.085  | 0.772    |
| Season x Order      | 3         | 73    | 2.477  | 0.068    | 3      | 47    | 1.272  | 0.295    |
| Season x Reach      | 3         | 73    | 0.323  | 0.809    | 3      | 47    | 0.284  | 0.837    |
| Order x Reach       | 1         | 73    | 0.139  | 0.710    | 1      | 47    | 0.917  | 0.343    |
| Season x Order x Reach | 3       | 73    | 0.313  | 0.816    | 3      | 47    | 0.149  | 0.930    |
| Spatial Dissimilarity |           |       |        |          |       |       |        |          |
| Season              | 3         | 31    | 1.146  | 0.346    | 3      | 20    | 0.425  | 0.737    |
| Order               | 1         | 11    | 0.062  | 0.808    | 1      | 7     | 0.007  | 0.934    |
| Season x Order      | 3         | 31    | 1.356  | 0.275    | 3      | 20    | 0.306  | 0.821    |
| Temporal Variability |           |       |        |          |       |       |        |          |
| Order               | 1         | 11    | 0.030  | 0.866    | 1      | 7     | 0.957  | 0.361    |
| Reach               | 1         | 11    | 1.906  | 0.195    | 1      | 7     | 2.693  | 0.145    |
| Order x Reach       | 1         | 11    | 2.054  | 0.180    | 1      | 7     | 4.718  | 0.066    |

Tables
Table 2: ANOVA results for the full and reduced models of taxonomic richness proposed by Swan and Brown (2017, 2018). Models were fitted using restricted maximum likelihood and with Type III sums of squares for estimating main and interactive effects of factors. The unpaired sample was not removed from the data prior to fitting the full and reduced model ANOVAs.

| Source of Variation | Full Model | | | Reduced Model | | |
|---|---|---|---|---|---|---|---|
| | numDF | denDF | F | P | numDF | denDF | F | P |
| Season | 3 | 74 | 2.478 | 0.068 | 3 | 80 | 4.360 | 0.007 |
| Order | 1 | 11 | 0.925 | 0.357 | 1 | 11 | 1.579 | 0.235 |
| Reach | 1 | 74 | 1.409 | 0.239 | 1 | 80 | 4.844 | 0.031 |
| Season x Order | 3 | 74 | 2.359 | 0.078 | 3 | 80 | 4.105 | 0.009 |
| Season x Reach | 3 | 74 | 0.152 | 0.928 | N/A | N/A | N/A | N/A |
| Order x Reach | 1 | 74 | 0.979 | 0.326 | 1 | 80 | 3.530 | 0.064 |
| Season x Order x Reach | 3 | 74 | 0.071 | 0.976 | N/A | N/A | N/A | N/A |

Note: N/A indicates a factor or interaction that was removed in the reduced model.
Figures

Figure 1: Plots of taxonomic richness in headwaters (A and C) and mainstems (B and D).

Taxonomic richness is reported for restored (triangles) and adjacent (circles) sites; values from the full sites are reported in black (A and B), while those from the revised sites are reported in grey (C and D). Points represent mean ± 95% CI.
Figure 2: Plots of taxonomic diversity, calculated as Shannon’s diversity, in headwaters (A and C) and mainstems (B and D). Taxonomic diversity is reported for restored (triangles) and adjacent (circles) sites; values from the full sites are reported in black (A and B), while those from the revised sites are reported in grey (C and D). Points represent mean ± 95% CI.
Figure 3: Plots of spatial dissimilarity. Estimates are reported for headwaters (HW, circles) and mainstems (MS, triangles); values from the full sites are reported in black (A), while those from the revised sites are reported in grey (B). Points represent mean ± 95% CI.
Figure 4: Plots of temporal variability. Estimates are reported for headwaters (HW, circles) and mainstems (MS, triangles); values from the full sites are reported in black (A), while those from the revised sites are reported in grey (B). Points represent mean ± 95% CI.