Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

REVIEW ARTICLE

Quantifying Macroinvertebrate Responses to In-Stream Habitat Restoration: Applications of Meta-Analysis to River Restoration

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Abstract

The assumption that restoring physical habitat heterogeneity will increase biodiversity underlies many river restoration projects, despite few tests of the hypothesis. With over 6,000 in-stream habitat enhancement projects implemented in the last decade at a cost exceeding $1 billion, there is a clear need to assess the consistency of responses, as well as factors explaining project performance. We adopted an alternative approach to individual case-studies by applying meta-analysis to quantify macroinvertebrate responses to in-stream habitat restoration. Meta-analysis of 24 separate studies showed that increasing habitat heterogeneity had significant, positive effects on macroinvertebrate richness, although density increases were negligible. Large woody debris additions produced the largest and most consistent responses, whereas responses to boulder additions and channel reconfigurations were positive, yet highly variable. Among all strategies, the strength and consistency of macroinvertebrate responses were related to land use or watershed-scale conditions, but appeared independent of project size, stream size, or recovery time. Overall, the low quality and quantity of pre- and post-project monitoring data reduced the robustness of our meta-analysis. Specifically, the scope and strength of conclusions regarding the ubiquity of macroinvertebrate responses to restoration, as well as the identification of variables controlling project performance was limited. More robust applications of meta-analysis to advance the science and practice of river restoration will require implementing rigorous study designs, including pre- and post-project monitoring replicated at both restored and control sites, collection of abiotic and biotic variables at relevant spatiotemporal scales, and increased reporting of monitoring results in peer-reviewed journals and/or regional databases.

Key words: boulder additions, channel reconfiguration, effectiveness monitoring, in-stream habitat restoration, large woody debris, macroinvertebrates, meta-analysis.

Introduction

Habitat degradation is a serious threat to biodiversity (Dobson et al. 1997; Vitousek et al. 1997; Wilcove et al. 1998). Aquatic ecosystems are among the most heavily impacted (Allan & Flecker 1993; Sala et al. 2000), with only 2% of U.S. rivers being of "high natural quality" (Benke 1990), and freshwater organisms disproportionately threatened with extinction (Stein et al. 2000; Dudgeon et al. 2005). Consequently, the number of river restoration projects has increased exponentially in recent decades (Bernhardt et al. 2005). Restoration of in-stream habitat has been a primary focus of these efforts, making it one of the most common river restoration practices (Purcell et al. 2002; Bernhardt et al. 2007).

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doi: 10.1111/j.1526-100X.2009.00605.x

Typically, the goal of in-stream habitat restoration is to increase the diversity, density, and/or biomass of aquatic organisms through enhanced hydraulic and substrate heterogeneity and increased food availability (e.g., Laasonen et al. 1998; Lepori et al. 2005; Roni et al. 2006). In physically homogenized systems, habitat restoration is most commonly achieved at the reach-scale (<60× bankfull width) through boulder additions, large woody debris (LWD) additions, or channel reconfiguration (i.e., changes in planform). Such practices assume local species richness and density is controlled by physical habitat heterogeneity (Dean & Connell 1978; Minshall 1984; Kerr & Packer 1997; Taniguchi & Tokeshi 2004; Scealy et al. 2007). In restoration ecology, the assumption that habitat improvement increases species richness and density is sometimes called the "field of dreams" hypothesis (Palmer et al. 1997) (i.e., if you build it, they will come). This assumption is an underlying ecological tenant of many river restoration projects, despite few tests of whether species richness and density increase following habitat improvements (Lepori et al. 2005; Roni et al. 2006).

Effectiveness monitoring of restoration projects is rare, with only 15–30% of projects including post-project monitoring

(Bernhardt et al. 2005, 2007). To date, riverine fishes have not only been the predominant focus of in-stream habitat restoration, but also the primary end point used to measure ecological responses (Larson et al. 2001; Muotka et al. 2002; Rosi-Marshall et al. 2006). Although responses of riverine fishes to restoration have been the subject of several qualitative reviews (Larson et al. 2001; Pretty et al. 2003; Thompson 2006), macroinvertebrate responses have only recently been investigated, despite their critical role in maintaining stream ecosystem functions through the transformation and translocation of nutrients and energy (reviewed in Wallace & Webster 1996; Baxter et al. 2005). The few studies conducted to date have mirrored fish density and richness responses by producing equivocal results. For example, Nakano and Nakamura (2006) and Pederson et al. (2007) observed increased macroinvertebrate richness and density following channel reconfigurations, whereas post-project richness and density estimates of Biggs et al. (1998), Friberg et al. (1998), and Purcell et al. (2002) did not exceed pre-restoration levels. Consequently, despite widespread implementation, the effectiveness of in-stream habitat restoration to enhance richness and density of macroinvertebrates and higher trophic levels remains unclear.

The literature is filled with admonitions for the need to conduct post-project effectiveness monitoring (Kondolf 1995; Bash & Ryan 2002; Bernhardt et al. 2007; Katz et al. 2007). The predominant strategy to date has assessed responses on a case-by-case basis; an alternative approach is to learn from the collection of post-project assessments through quantitative meta-analysis (Arnqvist & Wooster 1995; Osenberg et al. 1999). Although meta-analysis has informed the restoration and management of coral reefs (Gardner et al. 2003), marine reserves (Halpern 2003), and terrestrial vegetation (Pywell et al. 2003), this approach has not been applied to river restoration. Using research synthesis methodologies, such as meta-analysis, we might more effectively integrate the multitude of small-scale, single-study evaluations, characterized by naturally high variability and low statistical power, to provide a more robust assessment of habitat restoration effectiveness.

In this study, we conducted a meta-analysis to synthesize macroinvertebrate density and richness responses to habitat restoration aimed at increasing reach-scale habitat heterogeneity. Specifically, we asked (1) whether habitat restoration increases macroinvertebrate density and richness and (2) whether different ecological (e.g., land use, watershed size, recovery time) and methodological (e.g., restoration strategy, project size) variables influence the magnitude and direction of macroinvertebrate responses. To our knowledge this is the first application of meta-analysis to assess the effectiveness of river restoration practices.

Methods

Selection Criteria

We identified studies by searching for the keywords: "restoration AND macroinvertebrates," "stream restoration," "river restoration," "heterogeneity AND macroinvertebrates," "habitat AND macroinvertebrates," "LWD AND macroinvertebrates," "boulder additions AND macroinvertebrates," and "channel reconfiguration AND macroinvertebrates" in BIOSIS, Web of Science, Science Citation Index and Digital Dissertations, as well as references within. Once identified, five criteria determined study inclusion: (1) published in a peer-reviewed journal; (2) published quantitative macroinvertebrate density and/or richness estimates; (3) active restoration involving channel reconfiguration or the addition of boulders, weirs, artificial riffles, or LWD; (4) macroinvertebrate responses quantified at the reach and not microhabitat-scale (macroinvertebrates sampled within individual microhabitats [e.g., edge, macrophyte, thalweg] were pooled for analysis when possible); and (5) study design included a before-after (BA), before-after-control-impact (BACI), or control-impact (CI) design. We attempted to contact authors of all studies not meeting our selection criteria in an effort to obtain all required information.

Does Increasing Physical Habitat Heterogeneity Enhance Macroinvertebrate Richness and Density?

Quantitative meta-analysis compares results among studies through computation of a common effect size, which is traditionally scaled by unit variance and weighted by sample size (Arnqvist & Wooster 1995; Osenberg et al. 1999). In our analysis, different study designs (e.g., CI vs. BACI), sampling intervals, and degrees of replication among studies constrained effect size choice and computation; therefore, we ran two separate analyses to maximize the number of included studies. The first analysis included only replicated studies (i.e., analysis of multiple independent systems) and quantified the magnitude and direction of macroinvertebrate responses (i.e., density and richness) using the effect size d (Gurevitch & Hedges 1993), computed as:

$$d = \frac{\overline{X}_{\mathrm{E}} - \overline{X}_{\mathrm{C}}}{SD_{\mathrm{pooled}}} J$$

where $\overline{X}_{\mathrm{E}}$ and $\overline{X}_{\mathrm{C}}$ are the means for the experimental (E) (i.e., restored or post-restoration conditions) and control (C) (i.e., unrestored or pre-restoration conditions) groups, respectively; the pooled standard deviation, SD_{pooled} is computed as:

$$SD_{\mathrm{pooled}} = \sqrt{\frac{(N_{\mathrm{E}} - 1)(SD_{\mathrm{E}})^2 + (N_{\mathrm{C}} - 1)(SD_{\mathrm{C}})^2}{N_{\mathrm{E}} + N_{\mathrm{C}} - 1}}$$

where SD_{E} and SD_{C} are the standard deviations of the experimental (E) and control (C) groups, respectively; N_{E} and N_{C} are respective sample sizes; and J corrects for bias due to small or different sample sizes by weighting studies according to:

$$J = 1 - \frac{3}{4(N_{\mathrm{E}} + N_{\mathrm{C}} - 2) - 1}$$

Effect sizes (d) and associated variance estimates were adjusted to unconditional variance estimates for use in a mixed effects model according to Gurevitch and Hedges (1993). We used a mixed effects model because of assumed random variation among studies due to differences in restoration design and implementation, environmental conditions, and community composition as well as other factors. In the context of this study, d represents the difference in density or richness between restored and unrestored reaches or between pre- and post-restoration conditions, scaled by the pooled standard deviation; studies exhibiting large differences and low variability result in the greatest effect sizes. A 90% confidence interval was used to test whether d was statistically significant from zero, with significance corresponding to a confidence interval that does not contain zero. An alpha level of 0.10 was chosen due to the inconsistent nature (see Section "Nuances and Necessary Caveats") of available data and low sample sizes.

For a majority of studies, the focus on a single, unreplicated restoration project precluded computation of a variance-weighted effect size; therefore, for the second analysis, we used all studies (both replicated and unreplicated) to compare macroinvertebrate density and richness between restored and unrestored reaches (CI design) or between pre- and post-restoration conditions (BA design) using the response ratio (Osenberg et al. 1997):

$$\textit{Response ratio} = \ln\left(\frac{\overline{X}_{\mathrm{E}}}{\overline{X}_{\mathrm{C}}}\right)$$

where $\overline{X}_{\mathrm{E}}$ is the mean of the experimental group and $\overline{X}_{\mathrm{C}}$ is the mean of the control group. Response ratios greater than zero indicate higher density or richness levels for the restored versus unrestored reaches or for post-restoration versus pre-restoration conditions. We used a two-tailed, one-sample Student t test to quantify whether response ratios significantly differed from zero; replication was achieved by combining results from all studies. p Values equal to or less than 0.10 were interpreted as statistically significant.

To standardize data extraction and computation of effect sizes (d) and response ratios, we took the following steps and precautions. First, to avoid comparing results from disparate study designs (e.g., BA vs. CI), mean and variance estimates were extracted from studies having both impact and control reaches using a CI study design, where the "impact" was the restored reach and the "control" was an unrestored reach. For the two studies lacking an unrestored control reach (8 and 20), results were extracted according to a BA study design; all analyses were subsequently run with and without these two studies to determine the influence of combining CI and BA study designs. Second, to further investigate how different study designs or control types influenced our results, we compared response ratios computed from data extracted using both BA and CI study designs (studies 11, 14, 17, 20, 21), and studies that sampled both unrestored and minimally impacted control reaches (studies: 3, 5, 8, 13, 22) (i.e., target or reference conditions) with a two-tailed, two-sample Student t test.

Finally, for studies quantifying macroinvertebrate responses repeatedly through time, we computed d and the response ratio for a single time per study corresponding to the timescale common to the greatest number of studies (i.e., 1 year). Thus, if a project was sampled annually for 4 years post-project, we utilized the results measured after 1 year only. In a review of macroinvertebrate recovery rates to a myriad of disturbances, Yount and Niemi (1990) found that richness and density recovered to predisturbance levels within 1 year. However, given all studies did not sample exactly 1 year post-restoration, we assessed the influence of disparate recovery periods among studies by regressing response ratios against recovery period. In addition, we visually examined how response ratios for richness and density changed through time (i.e., recovery trajectories) for the five studies (3, 11, 14, 18, 24) sampled repeatedly post-project. We defined recovery as the persistent return to or surpassing of control or pre-restoration conditions.

Methodological and Ecological Determinants of Macroinvertebrate Responses

For replicated studies only, density and richness effect sizes (d) were compared between LWD and boulder additions using the Q statistic in a mixed effects model, which is analogous to an F statistic in analysis of variance (ANOVA) (Gurevitch & Hedges 1993); the small number of published studies precluded the use of channel reconfiguration studies. Using all studies, both replicated and unreplicated, density and richness response ratios were compared among LWD additions, boulder additions, and channel reconfigurations using a one-way ANOVA. One-way ANOVA also was used to compare macroinvertebrate density and richness response ratios among land uses (forested, urban, and agricultural). We examined the influence of project size (ratio of restored stream length to bankfull width) and stream size (bankfull width) on density and richness response ratios with simple linear regression; all relationships were visually inspected to check for non-linear relationships.

Assessment of Publication Bias

To examine the robustness of our study against publication bias (i.e., the "file drawer problem" or the failure to publish null results), we computed "fail-safe" numbers (Orwin 1983; Gates 2002) for effect size (d) estimates using MetaWin version 2.0 (Rosenberg et al. 2000). A fail-safe number estimates the number of additional null-result studies needed to produce statistically insignificant results. We used an effect size of 0.2 as a threshold for determining statistical/ecological significance (Cohen 1969). The reliance of this technique on variance estimates limited fail-safe number estimation to the 10 replicated studies only.

Results

Overview of Studies

We identified 53 peer-reviewed publications describing the effects of habitat restoration on macroinvertebrate assemblages. Of the 53 publications, 31 were eliminated because of failure to meet selection criteria such as using a control or reporting density or richness estimates. The remaining 22 publications contained 24 individual studies with 18 reporting both density and richness estimates and 6 reporting only richness or density estimates (Table 1). Ten of the studies analyzed replicated restoration projects within a similar physiographic

Table 1. Description of replicated and unreplicated studies included in the meta-analysis.

Reference	*Location (No. of Restored Systems)*	*Primary Cause of Degradation*	*Restoration Action*	*Sample Period (months)*	*Study Design*	*Response Variable*
Replicated						
1. Harrison et al. (2004)	England (7)	Channelization	BA	Average: 150	CI	D, R
2. Harrison et al. (2004)	England (6)	Channelization	BA	Average: 150	CI	D, R
3. Laasonen et al. (1998)	Finland (9)	Channelization	BA	1, 12, 36	CI[a,b]	D, R
4. Larson et al. (2001)	Washington, U.S.A. (4)	Urbanization	LWD	Average: 60	CI	D, R
5. Lepori et al. (2005)	Sweden (7)	Channelization	BA	Average: 66	CI[a]	D, R
6. Lester et al. (2007)	Australia (8)	Cattle grazing	LWD	12	BACI[c]	D, R
7. Lester et al. (2007)	Australia (8)	Cattle grazing	LWD	12	BACI[c]	D, R
8. Muotka & Laasonen (2002)	Finland (4)	Channelization	BA	36	BACI[a,c,d]	D
9. Roni et al. (2006)	Oregon, U.S.A. (13)	Silviculture	BA	Average: 96	CI	D, R
10. Tullos et al. (2009)	North Carolina, U.S.A. (9)	Urbanization	CR	Average: 24	CI	R
Unreplicated						
11. Biggs et al. (1998)	Denmark (1)	Channelization	CR	1, 6, 12	BACI[c]	D, R
12. Ebrahimnezhad & Harper (1997)	England (1)	Channelization	BA	36	CI	D, R
13. Edwards et al. (1984)	Ohio, U.S.A. (1)	Channelization	BA	Unknown	CI[a]	D, R
14. Friberg et al. (1998)	Denmark (1)	Channelization	CR	12, 24, 48, 72	BACI[c]	D, R
15. Gerhard & Reich (2000)	Germany (1)	Channelization	LWD	48	CI	D, R
16. Gortz (1998)	Denmark (1)	Channelization	BA	48	CI	D, R
17. Lemly & Hilderbrand (2000)	Virginia, U.S.A. (1)	Silviculture	LWD	12	BACI[c]	D
18. Moerke et al. (2004)	Indiana, U.S.A. (1)	Mitigation	CR	0.5, 4, 12, 24, 36, 48, 60	CI	D
19. Nakano & Nakamura (2006)	Japan (1)	Channelization	CR	12	CI	D, R
20. Negishi & Richardson (2003)	British Columbia (1)	Channelization	BA	12	BACI[c,d]	D, R
21. Pederson et al. (2007)	Denmark (1)	Channelization	CR	12	BACI[c]	R
22. Purcell et al. (2002)	California, U.S.A. (1)	Channelization	CR	36	CI[a]	D, R
23. Rosi-Marshall et al. (2006)	Michigan, U.S.A. (1)	Silviculture	LWD	48	CI	D
24. Sarriquet et al. (2007)	Brittany, France (1)	Channelization	BA	36, 48, 60	CI	D, R

Restoration actions indicated by boulder additions (BA), LWD additions (LWD), and channel reconfiguration (CR); study design by control-impact (CI) or before-after-control-impact (BACI); and utilized data by density (D) and richness (R). [a]Study included external reference representing target conditions of restoration. [b]Unrestored control located on separate system. [c]All BACI designs first analyzed as CI study design. [d]Study analyzed as BA design because the upstream control represented minimally impacted conditions.

region (i.e., LWD introduced to multiple neighboring streams), with seven (70%) utilizing a CI study design and only one (10%) repeatedly sampling through time. The 14 unreplicated studies showed similar study design trends, with 9 studies (64%) using a CI study design; however, a greater number of studies (4 or 29%) repeatedly sampled through time. Among all studies, control reaches were commonly located upstream of the restoration project (19 studies or 80%) and overwhelmingly represented degraded or unrestored conditions; only 5 studies (21%), also sampled minimally, impacted control reaches (i.e., target conditions of restoration).

The majority of restoration efforts sought to reverse or mitigate the effects of channelization (68%), whereas silvicultural (12%), urbanization (8%), and agricultural (8%) impacts were less commonly addressed (Table 1); however, several disturbances frequently interacted to warrant restoration. Boulder additions or artificial riffles (47%) were the most common strategies, followed by channel reconfigurations (29%) and LWD additions (25%). Restoration projects were conducted over relatively small spatial scales, with over half encompassing less than 300 m of stream (~58× bankfull width). Channel reconfigurations constituted the majority of large-scale (>1 km or 200 × bankfull width) projects. Common habitat goals of all restoration strategies were to create more heterogeneous flow and substrate conditions; increase sinuosity, and pool and riffle formation; and enhance spawning, feeding, and refugia habitats for resident fishes.

Does Increasing Physical Habitat Heterogeneity Enhance Macroinvertebrate Richness and Density?

Across all restoration strategies for the 10 replicated studies, we found significant, positive effects of habitat restoration on macroinvertebrate richness relative to unrestored control reaches or pre-restoration conditions (Fig. 1a). In contrast, variability in the direction and magnitude of density responses precluded detection of statistical significance (Fig. 1b). On average, richness estimates in restored reaches were 14.2% greater than unrestored control reaches, and density estimates were 28% greater.

For replicated and unreplicated studies combined, richness levels were 1.1 times greater (back-transformed response ratios), equivalent to 2.3 genera on average, for restored versus unrestored reaches; the response ratio was statistically greater than zero ($t = 1.79$, $p = 0.08$, $df = 21$; Fig. 2a). For density, the average magnitude of change (1.23 times greater or an additional 660 individuals on average) was greater than richness increases; however, variable responses among studies precluded detection of a significant difference ($t = 1.22$, $p = 0.24$, $df = 22$; Fig. 2b).

The use of different study designs or control types did not significantly influence response ratios. Response ratios for richness ($t = -0.07$, $p = 0.95$, $df = 4$) and density ($t = -1.91$, $p = 0.12$, $df = 4$) did not differ significantly between the use of BA or CI study designs or the use of unrestored or minimally impacted control reaches (density: $t = 0.93$, $p = 0.41$, $df = 4$; richness: $t = 0.79$, $p = 0.47$, $df = 4$; Fig. 3).

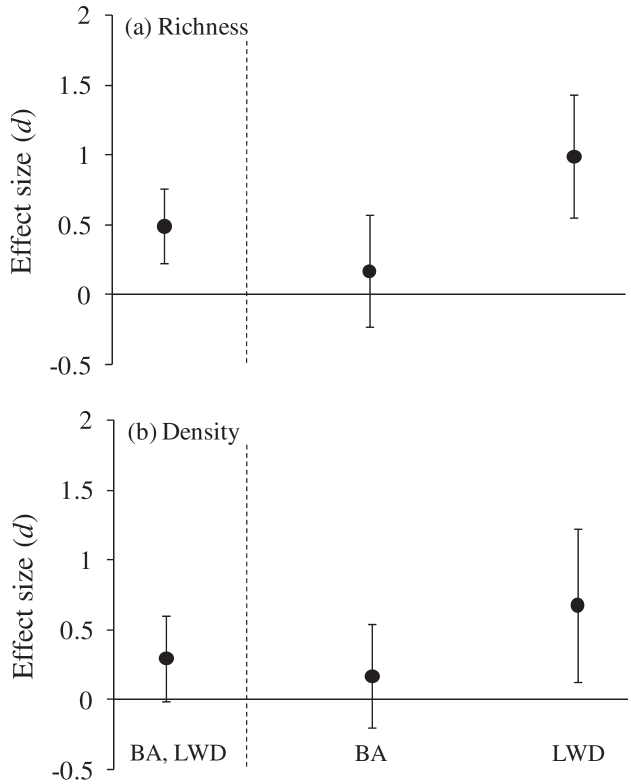

Figure 1. Average effect sizes (d) with 90% confidence intervals for richness (a) and density (b) compared among all restoration strategies combined (BA and LWD), as well as for individual restoration strategies. Responses to individual restoration strategies are separated from combined responses by a dashed vertical line. Effect sizes represent the difference between restored and unrestored reaches or pre- and post-restoration conditions scaled by unit variance and weighted by sample size. Figure represents 10 studies with true replication only (studies no. 1–10).

Methodological and Ecological Determinants of Macroinvertebrate Responses

For the 10 replicated studies, LWD additions significantly increased both richness and density ($d = 0.99$ and 0.68, respectively), whereas boulder additions resulted in non-significant increases ($d = 0.17$ and 0.16, respectively; Fig. 1a & 1b). LWD additions resulted in significantly greater increases in macroinvertebrate richness than boulder additions ($Q = 4.7$, $p = 0.03$, $df = 1$), whereas density effect sizes did not significantly differ between strategies ($Q = 1.6$, $p = 0.66$, $df = 3$). On average, richness and density increases were, respectively, 83 and 75% greater for LWD than boulder additions.

Inclusion of all studies allowed comparisons of density and richness responses among LWD additions, boulder additions, and channel reconfigurations. Both boulder ($t = 1.8$, $p = 0.10$, $df = 9$) and LWD additions ($t = 4.1$, $p = 0.01$, $df = 4$) significantly increased richness, whereas channel reconfigurations resulted in non-significant increases ($t = 0.54$, $p = 0.61$, $df = 5$; Fig. 2a). Response ratios for density were positive

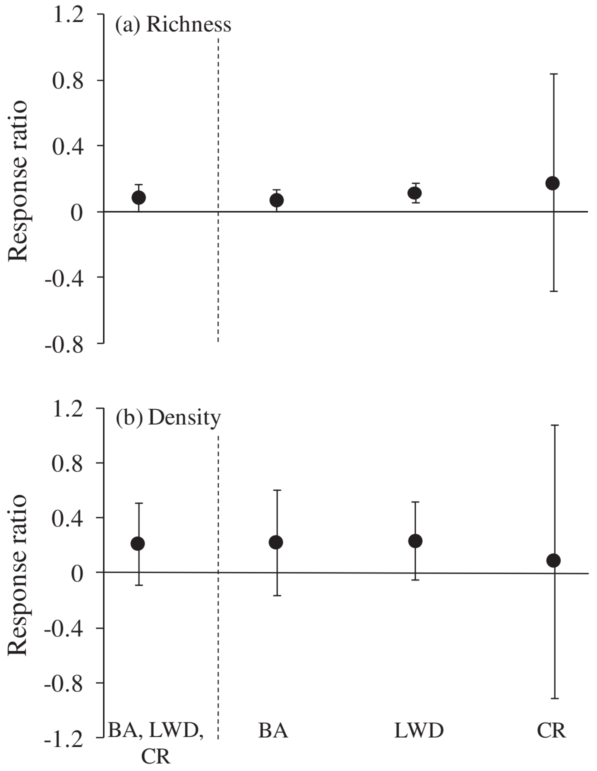

Figure 2. Average response ratios with 90% confidence intervals for richness (a) and density (b) compared among all restoration strategies combined (BA, LWD, and CR), as well as individual restoration strategies. Responses to individual restoration strategies are separated from combined responses by a dashed vertical line. Response ratios represent the ratio of treatment to control reaches or post- to pre-restoration conditions. Figure includes all 24 studies, replicated and unreplicated.

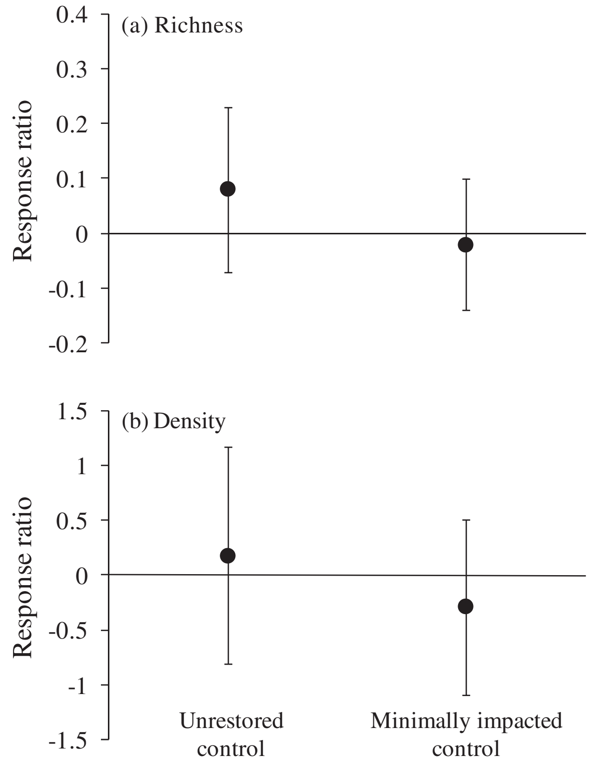

Figure 3. Average response ratios with 90% confidence intervals for richness (a) and density (b) compared among the five studies (3, 5, 8, 13, 22) using both unrestored or degraded control reach and a minimally impacted control reach.

but highly variable, and thus insignificant for LWD additions ($t = 0.47$, $p = 0.66$, $df = 5$), boulder additions ($t = 1.05$, $p = 0.32$, $df = 10$), and channel reconfigurations ($t = 0.60$, $p = 0.57$, $df = 6$; Fig. 2b). In contrast to results from the 10 replicated studies, inclusion of all studies did not result in significantly different richness or density responses among restoration strategies (density: $F_{2,20} = 0.01$, $p = 0.99$; richness: $F_{2,19} = 0.06$, $p = 0.94$).

Response ratios did not differ significantly among land uses (density: $F_{2,20} = 1.49$, $p = 0.25$; richness: $F_{2,19} = 1.01$, $p = 0.38$); however, projects conducted in forested regions resulted in significant, positive response ratios (density: $t = 1.98$, $p = 0.08$, $df = 9$; richness: $t = 1.81$, $p = 0.10$, $df = 9$) and exhibited the lowest variability among land uses (Fig. 4), whereas effect sizes for agricultural and urban projects were insignificant. Response ratios were not related to stream size (density: $r^2 = 0.04$; richness: $r^2 = 0.02$), project size (density: $r^2 = 0.01$; richness: $r^2 = 0.03$), or recovery period (density: $r^2 = 0.0$; richness $r^2 = 0.01$). For the five studies sampled at multiple times post-project, richness levels equaled or exceeded those of the unrestored control reach within 1 year (Fig. 5a), whereas density recovery trajectories were highly variable (Fig. 5b).

Assessment of Publication Bias

Given the number of available replicated studies, fail-safe numbers were relatively low for density (4.5) indicating that density results for the replicated studies would likely change with the addition of unpublished studies. In contrast, fail-safe numbers were relatively high for richness (12.9).

Discussion

With the completion of over 6,000 in-stream habitat restoration projects over the last decade at a cost exceeding $1 billion (Bernhardt et al. 2005), there is a clear need for post-project effectiveness monitoring. We adopted an alternative approach to individual studies by applying quantitative meta-analysis to a collection of in-stream habitat restoration projects. We found (1) in-stream habitat restoration 1 year post-restoration had significant, positive effects on macroinvertebrate richness and inconclusive effects on density across all strategies; (2) among strategies, LWD additions resulted in the greatest richness increases; (3) forested reaches exhibited the most consistent, positive richness and density responses, although response ratios did not differ among land uses; and (4) richness

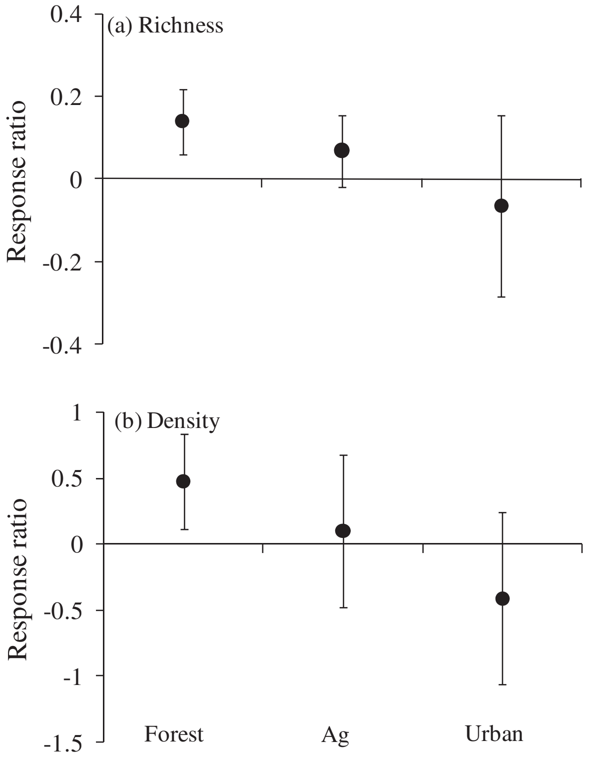

Figure 4. Average response ratios with 90% confidence intervals for richness (a) and density (b) compared among forested, agricultural, and urban reaches.

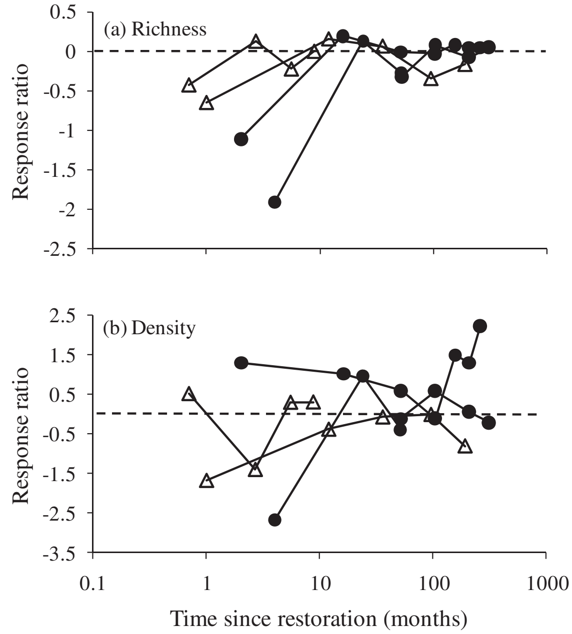

Figure 5. Richness (a) and density (b) response ratios as a function of time since restoration for the five studies (3, 11, 14, 18, 24) sampling at multiple times post-restoration. Solid black circles indicate channel reconfiguration projects and hollow triangles indicate boulder additions. The dashed horizontal line represents the return to pre-restoration conditions.

levels returned to or exceeded pre-restoration conditions within 1 year (but see Section "Nuances and Necessary Caveats").

Does Increasing Physical Habitat Heterogeneity Enhance Macroinvertebrate Richness and Density?

We observed significant richness increases across a diversity of impairments, in-stream restoration strategies, and physiographic conditions 1 year post-restoration, whereas density responses were largely inconclusive.Increases observed in richness (2.3 genera on average or 10%) and density (660 individuals on average or 23%) quantify the magnitude of potential ecological gains for restoration practitioners; however, highly variable results among studies underscore that average increases cannot accurately predict macroinvertebrate responses to future projects. Using currently available data, our results support the hypothesis that increasing the physical heterogeneity of homogenized stream reaches has the potential to enhance macroinvertebrate richness, but not density (see section "Discussion").

Methodological and Ecological Determinants of Macroinvertebrate Responses

Modest effect sizes resulted from variability in both the magnitude and direction of change among studies. Inconsistent responses to restoration are commonly attributed to both reach-scale (e.g., degree of degradation, restoration strategy, and project size), and watershed-scale (e.g., connectivity to and quality of the regional species pool, watershed-scale perturbations) factors (Frissell & Ralph 1998; Bond & Lake 2003; Lake et al. 2007). In this study, macroinvertebrate responses depended on the restoration strategy and, to a lesser extent, on land use, which was used as a surrogate for watershed-scale conditions. Project size, stream size, and recovery period were not shown to be related to response ratios. Furthermore, differential responses among restoration strategies were not observed consistently among all studies: significant differences were found solely for replicated studies, which may reflect increased statistical power or a higher standard of restoration design, implementation, and monitoring, or both.

Observed richness increases for LWD additions suggest that these improvements more effectively restored the processes leading to increased habitat heterogeneity and subsequent biological diversity than boulder additions. Boulder additions frequently failed to create new habitats, such as deep pools, back waters, or vegetated margins (Harrison et al. 2004; Lepori et al. 2005), which limited macroinvertebrate responses to increased proportions of rheophilic taxa, while reach-scale diversity remained unchanged (Hilderbrand et al. 1997; Larson et al. 2001; Lepori et al. 2005; Roni et al. 2006). In contrast, LWD additions consistently increased reach-scale habitat heterogeneity by adding pool–riffle morphologies to channelized reaches or reducing pool–riffle spacing (Hilderbrand et al. 1997; Larson et al. 2001). The addition of pools to channelized reaches increased the proportion of low velocity, depositional habitats characterized by finer particle sizes, and greater organic matter retention (Wallace et al. 1995; Lemly & Hilderbrand 2000; Lepori et al. 2005). Such conditions promoted recruitment of shredder, collector-gatherer, and/or predatory macroinvertebrates, which are typically absent or in low abundance within channelized reaches (Laasonen et al. 1998). LWD also represents novel surfaces compared to mineral substrates, providing food sources for xylophilic species and housing unique algal assemblages (Sabater et al. 1998; Hoffman & Herring 2000), both of which can contribute to increased invertebrate taxonomic and functional diversity.

While the implemented restoration strategy explained some variability in the direction and magnitude of responses among studies, macroinvertebrate responses also varied among studies using the same restoration strategy. Variability was generally greatest for channel reconfiguration projects and density responses and lowest for LWD addition projects and richness responses. We considered three ecological and one statistical explanation for the variability of responses among studies implementing the same restoration strategy: (1) differential recovery rates among studies; (2) the initial state of the ecosystem; (3) discordance between the scale at which restoration was conducted and the scale of degradation processes; and (4) disparate sample sizes, variance estimates, and degree of replication among studies.

Macroinvertebrate assemblages have been found to exhibit rapid recovery rates (<1 year) to a myriad of disturbances (Yount & Niemi 1990). High macroinvertebrate resilience is frequently attributed to their life history strategies (e.g., short generation times, aerial dispersal, high drift propensity) and the frequent availability of up or downstream source colonists (reviewed in Mackay 1992). However, macroinvertebrate recovery rates post-restoration have been highly variable, with some studies observing recovery within 1 year (Biggs et al. 1998; Laasonen 1998; Brooks et al. 2002; Moerke et al. 2004) and others failing to detect recovery even after several years (Fuchs & Statzner 1990; Friberg et al. 1998). Such variability is frequently attributed to biological hysteresis, a paucity of local refugia, poor connectivity to the regional species pool, or persistent watershed-scale degradation (Fuchs & Statzner 1990; Frissell & Ralph 1998; Lake 2007). Nevertheless, variable response ratios were not consistently explained by different recovery periods among studies; we found no relationship between recovery period and response ratios. Furthermore, richness recovery trajectories consistently plateaued after approximately 12 months, whereas density recovery trajectories were highly variable.

Differences in the initial ecosystem state (i.e., extent of degradation) could confound responses among systems. Provided connectivity to an intact regional species pool, we would expect restoration implemented in the most degraded ecosystems to elicit the greatest responses. In contrast, considerable efforts would be required to elicit similar responses in less degraded systems. Based on this theory, we would predict urban restoration efforts to provide the greatest return on our restoration investment. However, observed responses for urban versus forested ecosystem, in our review, suggest larger landscape-scale processes limit recovery potential.

Discordance between the scale of restoration relative to the scales of degradation processes provides a more plausible explanation for variability in the magnitude and direction of responses among studies (Larson et al. 2001; Bond & Lake 2003; Harrison et al. 2004). For example, reach-scale habitat manipulations often enhance fish or macroinvertebrate populations when perturbations are local in nature, whereas ecological benefits are generally low when larger, watershed-scale degradation persists (Yount & Niemi 1990; Frissell & Ralph 1998; Lake 2007). For example, Larson et al. (2001) found watershed-scale perturbations overwhelmed reach-scale LWD additions: high sediment loads buried log installations, and macroinvertebrate community composition was related to percent developed land and not to reach-scale physicochemical conditions. Using land use as a proxy for watershed-scale conditions, we found restoration projects implemented in forested upland environments exhibited more consistent, positive density and richness responses than projects located in agricultural or urban areas, which were constrained to lowland regions. The decreased likelihood of watershed-scale perturbations and increased probability for connectivity to an intact regional species pool for forested uplands likely explain differences in the magnitude and consistency of responses among land uses (Fuchs & Statzner 1990; Lepori et al. 2005; Lake 2007). Despite only anecdotal evidence from our study, position in the watershed (Fuchs & Statzner 1990; Harrison et al. 2004), land use within which a project is nested (Larson et al. 2001; Lester et al. 2007), and overall watershed conditions (Yount & Niemi 1990; Kauffman et al. 1997; Frissell & Ralph 1998) have all been found to constrain reach-scale restoration responses .

Variable responses among studies could also result from disparate sample sizes and variance estimates among studies (Gurevitch & Hedges 1999). High within-study variability and low statistical power, common to macroinvertebrate studies, have caused some to question their use to detect reach-scale restoration responses (Bunn & Davies 2000; Brooks et al. 2002; Negishi & Richardson 2003). However, for the 10 replicated studies the median retrospective power for detecting a 20% change in density and richness post-restoration was 11 and 81%, respectively. Disparate power estimates are due to the larger within-study variance estimates for density. Thus, samples sizes were adequate to detect meaningful richness, but not density responses. Macroinvertebrate abundance metrics are notoriously variable at small spatial scales due to both abiotic (e.g., microhabitat variability in velocity, depth, substrate) and biotic (e.g., oviposition, phenology, predation) variables (Resh & McElravy 1992; Bunn & Davies 2000; Heino et al. 2004), limiting their usefulness as tractable response variables. This is problematic given that one of the primary goals of habitat restoration is to increase fish biomass through enhanced food resource availability. Assessment of restoration responses using abundance metrics must therefore be done with a high level of replication and rigorous study design.

Nuances and Necessary Caveats

In this study, we present the first known application of quantitative meta-analysis to assess river restoration effectiveness. Our results should be interpreted with caution and viewed as a first attempt to identify emergent patterns from the myriad of weakly replicated, inconclusive, and even conflicting published studies. Specifically, our efforts to identify ubiquitous macroinvertebrate response patterns, as well as variables controlling project performance were impeded by several obstacles. The primary problems included: (1) low quantity and poor quality of published biotic and abiotic data; (2) lack of rigorous study designs; (3) a dearth of replicated restoration efforts within physiographically similar areas; and (4) probable publication bias, which limited the inference of our study.

The low number of published macroinvertebrate studies, as well as data of inconsistent quality highlights the current state of stream restoration science and reaffirms the need to implement more rigorous study designs and improve data reporting (Bernhardt et al. 2005, 2007). Specifically, the failure to sample a control reach or to collect and/or report quantitative density and richness estimates excluded the majority of published studies. The paucity of published restoration assessments combined with our high exclusion rate to produce low fail-safe numbers for density (4.5) and richness (12.9); however, given the small number of available studies and the limitation of using only replicated studies when computing fail-safe numbers, our richness findings appear quite robust to publication bias. In contrast, the inclusion of additional studies would likely have a strong bearing on our density estimates.

For studies meeting the selection criteria, the dearth of pre-restoration data required a CI study design, pairing restored and degraded reference sites on the same stream to quantify macroinvertebrate responses to restoration. CI study designs lack the pre-restoration data needed to assess inherent differences between control and treatment reaches that might confound responses to restoration treatments (Laasonen et al. 1998; Halpern 2003; Negishi & Richardson 2003). Space-for-time substitution is of particular concern with macroinvertebrate communities, which are known to vary naturally at small spatial scales (Resh & McElravy 1992; Heino et al. 2004). Furthermore, the exclusive use of degraded or unrestored control sites to quantify post-restoration responses can be misleading. For example, we found macroinvertebrate richness significantly increased post-restoration relative to unrestored stream reaches, but richness levels did not return to target or minimally impacted conditions for the subset of studies utilizing both unrestored and minimally impacted control reaches. Consequently, the current studies allowed us to quantify changes in macroinvertebrate richness or density relative to if restoration did not occur, but not the extent to which sites returned to minimally impacted conditions. More informative studies would include pre-restoration data to account for confounding variables, collect data over longer time frames to further understand both short-term and long-term responses, and use target or reference conditions to assess the magnitude of change. Such improvements in study design are required to understand how the structure and function of systems have changed due to restoration and to what extent restoration can return systems to minimally impacted states.

In addition to publication bias, the estimated fail-safe numbers also likely resulted from the variability introduced by the aforementioned methodological, abiotic, or biotic differences among studies, which appeared greater for density than richness metrics. To explore such issues, we tried partitioning variance among different methodological or ecological variables; however, the paucity of such information constrained potential analyses. For example, changes in habitat heterogeneity were rarely quantified, despite being the primary target of restoration actions. Consequently, we were unable to quantify how ecological outcomes depend on the degree of degradation, as well as the quality and extent of restoration efforts. Improved integration of biotic and abiotic effectiveness monitoring is needed to develop a mechanistic understanding between alterations to the physical template (e.g., temperature, habitat area, and connectivity) and desired biotic responses (e.g., increased invertebrate biomass or diversity and reduction in whirling disease occurrence).

Conclusions

River restoration is more commonly attempted at the reach-scale than watershed-scale because of financial constraints, land availability, and sociopolitical boundaries. Despite growing criticism and problems identified herein, reach-scale restoration efforts will likely play an integral part in restoring degraded freshwater ecosystems (Lake 2007). Consequently, future research should aim to develop a mechanistic understanding of when, where, and which methods are most effective.

Although we were able to use meta-analytical techniques to assess the viability of reach-scale restoration strategies, data quality and quantity limited our ability to elucidate methodological or ecological determinants of macroinvertebrate responses. Relating restorations efforts to observed outcomes and understanding under what conditions this relationship changes represent the core strength of meta-analytical techniques. Advancing the science and practice of river restoration with this analytical tool will require the development of larger datasets populated by studies with improved study designs and data reporting.

Our results support the hypothesis that increased physical habitat heterogeneity can enhance macroinvertebrate richness. In contrast, responses of macroinvertebrate density remain less certain and more difficult to detect given the inherent variability of density metrics. Consequently, habitat restoration may represent a viable management strategy for increasing biodiversity and subsequent ecosystem resistance and resilience, whereas the goal of supporting higher trophic levels through increased biomass of basal resources (e.g., macroinvertebrates) remains less certain. Regardless of the specific restoration goal, macroinvertebrates play integral roles in lotic ecosystems and cannot continue to be ignored in the design and monitoring of restoration projects. However, given that macroinvertebrate metrics can exhibit considerable variability at small spatial scales for reasons unrelated to restoration actions, their use to assess restoration effectiveness needs to be done with caution and rigorous study designs.

Implications for Practice

- Prioritize restoration efforts by assessing the scale of degradation processes and the condition of the regional species pool, and by identifying viable colonization pathways.
- When reporting on post-project assessments, specify how restoration was conducted, the extent of restoration efforts (e.g., number and size of logs per 100 m), project cost, watershed-scale conditions, mean and variance estimates, and other pertinent information.
- Use a rigorous study design that includes pre- and post-project monitoring replicated at both restored and external control sites to account for spatial and temporal variability.
- Collect both abiotic and biotic variables at concordant and relevant spatiotemporal scales to quantify links between restoration actions and desired ecological responses.

Acknowledgments

Funding for this research was provided by the Intermountain Center for River Rehabilitation and Restoration. We thank S. Durham, R. Al-Chokhachy, and two anonymous reviewers for their insightful comments, which greatly improved the quality of the manuscript.

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