


RESEARCH ARTICLE

Primarily neutral effects of river restoration on macroinvertebrates, macrophytes, and fishes after a decade of monitoring

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Restoring river habitat heterogeneity is expensive and time consuming, yet often has little effect on aquatic biota. Such poor restoration outcomes could be partly caused by the predominance of short-term studies, which do not account for natural temporal fluctuations nor changes in the effects of restoration through time. Consequently, research that examines the longer-term dynamics of river restoration is crucial for providing a temporal perspective of restoration outcomes and for informing the effectiveness of restoration methods. We used the Nidda River in Germany as a case study of the temporal effects of river hydro-morphological restoration on different aquatic taxa. We surveyed macroinvertebrate, macrophyte, and fish communities across three sites prerestoration (2008) and then monitored changes in one control versus two restored sites across 10 years (2010–2019). Overall, we found few effects of restoration on the macroinvertebrate and macrophyte communities, with no effects whatsoever on fishes. Restoration improved some components of the macroinvertebrate and macrophyte communities; however, these positive effects were temporally inconsistent and did not translate to improvements in river ecosystem health (based on an index of ecological quality). Our findings illustrate how allowing for more time for community development will not necessarily alter the fact that local-scale river habitat restoration can elicit little to no change in aquatic communities. Combining local- with broad-scale restoration efforts that address the primary drivers of hydroecological decline, in addition to long-term monitoring, may therefore be required to ensure that river restorations successfully meet their ecological goals.

Key words: aquatic, biodiversity, ecological quality, freshwater, long-term monitoring, temporal

Implications for Practice

- Local-scale habitat restoration can positively influence river communities, but we also recommend combining these efforts with mitigation of watershed-scale stressors.
- The effects of restoration can differ through time and across taxa. We therefore suggest that restoration efforts include some temporal monitoring of multiple taxa groups, with samples collected across several years before restoration and 10 or more years afterwards.

Introduction

Aquatic ecosystems worldwide, and particularly rivers, have been degraded by a variety of anthropogenic stressors, including habitat destruction and hydromorphological alteration (Strayer & Dudgeon 2010; Best 2019). Habitat restoration is a potentially valuable tool for counteracting this degradation and associated biodiversity loss, yet a great deal of uncertainty exists in the benefits it provides. River restoration is frequently accomplished through hydromorphological remodeling, including creating new channels to produce regions of faster and slower flowing water (Lorenz et al. 2009) and introducing new substrates (White & Walsh 2020; Roberts et al. 2021). These efforts aim to improve river habitat heterogeneity, thus aiding community recovery when species fill the newly created niches (Palmer

et al. 2010). But, at least in the short term, studies of the effects of river habitat restoration on aquatic biota have reported a range of positive, neutral, and even negative effects (Louhi et al. 2011; Haase et al. 2013; Nilsson et al. 2015). This variability in outcomes presents a critical problem for restoration projects that

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invest a great deal of time and money to often achieve little to no effect.

No observable effects of river habitat restoration on aquatic biota can occur because poor habitat is not the only factor limiting recovery. For example, communities may fail to recover as habitat heterogeneity improves because of the continued presence of broader-scale stressors that are not necessarily addressed through local-scale restoration efforts, such as land use changes, pollution, or climate warming (Bernhardt & Palmer 2011; Wahl et al. 2013). Limited dispersal opportunities can also constrain the effects of restoration if, for instance, there are no nearby sources of new colonists or if dispersal barriers (e.g. dams) continue restricting the arrival of new species (Sundermann et al. 2011; Tonkin et al. 2014; Tummers et al. 2016). These example limitations highlight that efforts to restore the ecological quality of flowing freshwaters, which is a common legislative goal (WFD 2000), require considering and addressing an array of factors that can act in concert with habitat restoration to affect aquatic communities.

One often mentioned, but frequently unaddressed, factor that can determine the effects of restoration is the time frame of study (Feld et al. 2011; Hasselquist et al. 2015; Kail et al. 2015). A majority of projects perform no postrestoration monitoring (e.g. 90% in the United States and 70–80% in the United Kingdom and Europe; Bernhardt et al. 2005; Thompson 2015; England et al. 2021), and of the projects that do, a majority do not collect time series data. Instead, they may compare different sites that have been restored at different times (“space-for-time” approaches; Lorenz et al. 2012) or compare snapshots of a time before to a time after restoration (“before-after” approaches; Schmutz et al. 2014). As an example of this general lack of longer-term monitoring, a review of 379 macroinvertebrate restoration projects by Al-Zankana et al. (2020) determined that only a few collected postrestoration data across multiple years. This temporal knowledge gap has been frequently highlighted by a variety of studies and meta-analyses because it limits our ability to delineate the true effects of restoration on aquatic communities (Kondolf & Micheli 1995; Schmutz et al. 2014; Kail et al. 2015). For instance, river environments are naturally variable, including interannual fluctuations in flow and sediment transport (Thoms 2006). Thus, any differences between preres-toration and postrestoration communities (or a lack thereof) could be simply caused by natural environmental variability, which can require a decade or more of consistent monitoring to measure and control for (Kondolf & Micheli 1995; Didham et al. 2020). In addition, restoration could initially benefit aquatic biota in the short term, but these effects may fade through time if the improved habitat conditions do not persist (Palmer et al. 2010; Marttila et al. 2016). Alternatively, no effects may be observed for several years or even decades owing to the often-slow pace of the processes involved, such as colonization, succession, and recovery of biochemical conditions (Kondolf & Micheli 1995; Feld et al. 2011; Hasselquist et al. 2015). Restoration can even have initial negative effects owing to habitat disturbance, which may be gradually overwritten by positive effects as habitats stabilize through time (Leps et al. 2016; England et al. 2021). Research that examines the

longer-term dynamics of restored ecosystems is therefore sorely needed to provide a temporal perspective of restoration outcomes and to inform the effectiveness of restoration methods.

To this end, we used the hydromorphological restoration of the Nidda River in Germany as a case study of the temporal dynamics of river restoration across different aquatic taxa. We surveyed the preres-toration (2008) macroinvertebrate, macrophyte, and fish communities at three sites in the river, and then monitored community changes across 10 years (2010–2019) in one control site (i.e. unrestored) versus two sites that underwent hydromorphological restoration. We monitored these three taxa groups to provide a comprehensive perspective of the effects of restoration on key aquatic biota. In addition, all three groups are equally important bioindicators used to assess the health of freshwater ecosystems across the European Union (WFD 2000), thus allowing us to assess changes in ecosystem health at the restored river sites. Our objectives were to: (1) quantify postrestoration temporal changes in abundance, biodiversity, community composition, and ecosystem health (via metrics of ecological quality); and (2) compare these temporal dynamics to control and preres-toration conditions. Our study provides a long-term perspective of the effects of river restoration through time and across different taxa. In addition, we offer insights for other restoration projects about the methods and time frames required to assess whether improvements in aquatic communities have been successfully achieved.

Methods

Study System

The Nidda River catchment encompasses an area of ~2000 km² near Frankfurt, Hesse, Germany (Fig. 1). The Nidda River itself is a permanent waterbody comprised of six major tributaries, with low and high flow periods typical of temperate regions. Precipitation averages 750 mm annually, most of which is evenly distributed across seasons. The river is located in a region dominated by agricultural land use (Schweizer et al. 2018). Consequently, the river was straightened (“channelized”), and levees were constructed, over several tens of kilometers during the early- and mid-20th century to increase the amount of agricultural land and reduce flooding. This channelization process tends to homogenize a river’s width, depth, substrate composition, and bank inclination (Hohensinner et al. 2018). Municipal and industrial wastewater treatment plants were also built to manage point-source pollutants from urban centers along the river’s course. These anthropogenic stressors of agricultural land use, hydrological alteration, and wastewater have been consistently present in the region for the last several decades. The ecological quality of the river therefore tends to be generally poor, particularly below the headwaters (see Schweizer et al. 2018; Brettschneider et al. 2019a for further details).

In 2009, a restoration project was initialized across a 3 km section of the river. The project was initiated owing to concerns from local residents, water managers, policymakers, and nongovernmental organizations that river channelization compromises the ecological quality, aesthetics, and accessibility of the

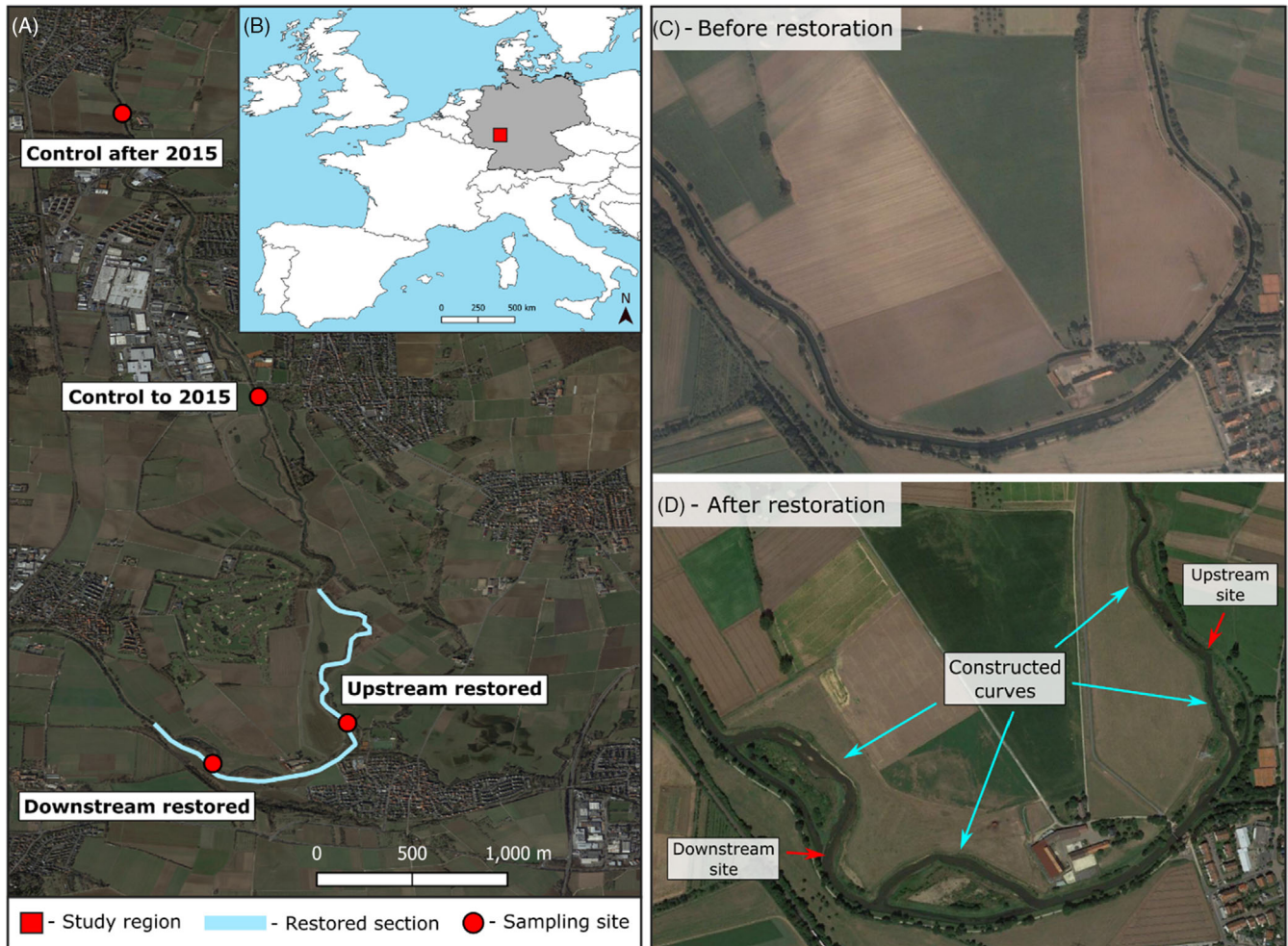


Figure 1. Aquatic community samples were collected from (A) two restored and two control sampling sites (filled circles) in the Nidda River in (B) the Frankfurt, Hessen region of Germany during 2008–2019. In 2009, 3 km of the river was restored (compare C vs. D) by (D) constructing river curves (blue arrows), adding earth and stone barriers, and removing the levee from the eastern/northern bank. The (D) upstream and downstream sampling sites, located within the newly constructed curves, are also indicated with red arrows. After 2015, the (A) control site was moved further upstream owing to the implementation of a new restoration project. Map data was obtained from Google Earth (©2021) and sampling site coordinates are provided in Table S1.

ecosystem (Deffner & Haase 2018). These concerns were supported by early (2007–2008) assessments of macroinvertebrates, macrophytes, and fishes in several parts of the river that found these communities were generally degraded (Haase et al. 2013). The primary objectives of the Nidda restoration project were to return the channelized river to a more natural sinuosity, to hydrologically reconnect the river to its floodplain, and to improve the aesthetics and accessibility of the river for local residents (visualized in Figs. 1 & 2). The restoration was accomplished by: (1) cutting new curves for the river from the surrounding agricultural land (compare Fig. 1C vs. 1D); (2) removing bank stabilization (large stones) to allow for free meandering of the river; (3) removed stones were consolidated into barriers used to redirect the river's flow into the newly constructed curves (Fig. 2B & 2C); (4) the 2 m levee (Fig. 2A) on the eastern/northern bank was removed and repositioned further into the floodplain, which reduced the height of the river bank to

~0.5 m (Fig. 2B); finally, (5) the islands between the old and new river courses were further built-up to better control flow and erosion (Fig. 2B & 2C). These changes were expected to benefit the diversity of aquatic habitats and thus species via the creation of zones of both faster and slower water flow, by providing new substrate via the barrier and island structures, and by improving connectivity to the floodplain (also see Figs. S1 & S2 for further details on how restoration has influenced substrate heterogeneity). In addition to improving aquatic habitat, the restoration project was also intended to augment human-related services by improving aesthetics and recreational access to the river.

Study Design

To determine the temporal effects of the above restoration efforts on aquatic biota, we conducted surveys at two sites



Figure 2. Photographs that illustrate the physical and ecological conditions of the Nidda River sites (A) prerestoration, (B) 6 months postrestoration (summer 2010), (C) 9 years postrestoration (summer 2018), and (D) in response to some postrestoration erosion. (A) The channelization of the river is evident from its straightened course as are the levees (red lines) on both banks. (B) The early, postrestoration conditions after the levee was removed from the eastern/northern bank (compare the upper red line to the lower red line). Constructed barriers and built-up islands (red arrows) were also used to redirect flow into the newly constructed curves. (C) The conditions of the river, banks, barriers, and islands several years after restoration at the downstream sampling site (sampling zone indicated with a red arrow; coordinates in Table S1). (D) Erosion is evident after several years in some sections of the constructed curves as the river cuts a more natural path following the removal of the levee. The photograph in (A) was provided by Robert Marc Lehmann, whereas photographs in (B, C, D) were provided by Nathalie Kaffenberger.

representative of the restored river sections (one “upstream” and one “downstream” site) and at one unrestored site further upriver (the “control”; see Fig. 1A). The control site was selected to be upstream of the restored sections to ensure it would be unaffected by any changes in the river environment caused by restoration. In addition, the control site was selected to be within 2 km of the restored sections to ensure there were no differences among sites in river inputs (e.g. intermediate tributaries or treatment plants; Fig. 1A) or surrounding human disturbances (e.g. land use; Fig. 1A), and little change in hydromorphological or substrate characteristics (given the homogenous structure of a channelized river; also see Figs. S1 & S2). However, the control site had to be moved further upstream after 2015 owing to the initiation of a new restoration project. Although this

undoubtedly introduced some unexpected variability into our control comparisons, both sites are geographically close and have straight channels with similar habitat types, thus we expect few differences in their biota. All sites were initially sampled during summer (June–August) in 2008, prior to restoration, and then again postrestoration in 2010, 2012, 2013, 2015, 2017 (2018 fish only), and 2019.

Sampling Protocol

We assessed the abundance of aquatic macroinvertebrates, macrophytes, and fishes at all sites following standardized methods (WFD 2000). Macroinvertebrates were sampled in June at each site in each year from downstream to upstream across the entire

width of a 100 m transect. Sampling followed a multi-habitat procedure (Haase et al. 2004) in which we first assessed the cover of microhabitats at each site then collected kick net samples (0.0625 m²) for every 5% cover of each microhabitat (20 total subsamples covering a total area of 1.25 m²). All subsamples were then pooled for each site and identified to the lowest taxonomic level possible, which was generally the genus or species level, although some macroinvertebrate taxa were classified to higher levels (e.g. Oligochaeta). Reported abundances approximate individuals m⁻².

Macrophytes were sampled in August of each year across the same area as the macroinvertebrate samples. Surveys were conducted by wading against the river flow or using rakes to collect macrophytes from unwadeable sections. All submerged and emergent higher plants and mosses were identified to the genus or species level. Abundance of each taxon was estimated as its total cover across the transect using Kohler's (1978) ordinal cover classes of: (1) rare, (2) occasional, (3) frequent, (4) abundant, and (5) very abundant.

Fishes were sampled in August of each year, except in 2017. Flood conditions during 2017 meant that sampling had to be delayed until October 2018. Samples were collected from a boat by electrofishing (Electric Fishing Device EFGI 650, Bretschneider, Chemnitz, Germany) against the river flow along a 300–500 m transect that overlapped the transect used for the macroinvertebrates and macrophytes. Longer transects were employed for the fishes because transect length is proportional to river width for this taxa group (following methods in Diekmann et al. 2005). All individuals were identified alive to species-level and then released. Reported abundances approximate individuals m⁻¹.

Changes in Abundance and Biodiversity

To compare temporal abundance and biodiversity changes between the restored and control sites, we analyzed temporal shifts in total community abundance, the number of taxa ("richness"), and diversity (measured as the Shannon index) during the postrestoration years (2010–2019) using generalized linear models. The abundances of macroinvertebrates and fishes were calculated as the total number of individuals, whereas for macrophytes we first converted the ordinal cover measurements to the mean values of Braun–Blanquet's cover classes and then summed all cover values across all taxa (following Engloner 2012). The continuous response variables of abundance, richness, and Shannon diversity in each year were then each modeled against a categorical predictor representing each site, a continuous predictor for each sampling year, and the interaction between site and year. All models assumed a Gaussian distribution (log link for abundance and an identity link for richness and Shannon diversity), except for some models of richness which required a Poisson distribution (log link). Assumptions of Gaussian-distributed models were evaluated using plots of residual versus fitted values, normal quantile–quantile, and constant leverage. Poisson-distributed models were evaluated using plots of Pearson residuals versus fitted values and by calculating

dispersion (indicated by Φ in "Results" section). We assessed the significance ($p < 0.05$) of model terms using a model reduction approach in which we successively removed higher-order terms and compared models with and without those terms using log-likelihood ratio tests (LRTs; Zuur et al. 2009). Model reduction concluded when only significant terms or the null model remained.

Changes in Community Composition

We also quantified temporal community "turnover" between consecutive sampling years at each site (i.e. temporal β -diversity) and temporal shifts in taxa community composition. These analyses determined whether restoration drove any compositional changes through time, regardless of changes in overall community abundance or biodiversity. Temporal turnover was calculated for each site as community dissimilarity between consecutive years based on Simpson's index, which ranges from 0 (complete compositional turnover) to 1 (no change). Turnover was modeled using a beta distribution following the same modeling methods described for abundance and biodiversity. Composition was calculated as the Hellinger (Legendre & Gallagher 2001) transformed abundance of each taxon in the macroinvertebrate, macrophyte, and fish communities. We then assessed the significance ($p < 0.05$) of compositional differences among sites and changes through time using nonparametric, permutational multivariate analyses of variance (PERMANOVA; Anderson 2001). The response variables for these models were the distance matrices of among-site community similarities for each taxa group (based on their Hellinger-transformed abundances), which were modeled against a categorical predictor for site, a continuous predictor for sampling year, and the interaction between site and year. Permutational multivariate analyses of variances were conducted using Euclidean distance with 1,000 permutations. The results of these models were visually represented by first decomposing the Hellinger-transformed taxa abundances into their primary axes of variation using principal components analysis (PCA) and plotting the first two PCA axes.

Changes in Ecosystem Health

To determine whether any community changes translated to shifts in ecosystem health, we quantified temporal changes in the ecological quality class (EQC) of the macroinvertebrate, macrophyte, and fish communities. In the European Union, the "Water Framework Directive" (WFD) is the principal piece of protective water legislation that guides efforts to improve the health of freshwater ecosystems (WFD 2000). The WFD assesses ecosystem health using the EQC index to categorize macroinvertebrate, macrophyte, and fish communities into five classes—1 (high), 2 (good), 3 (moderate), 4 (poor), or 5 (bad)—with the goal that each community is at high or good ecological quality. The EQC index is calculated based on the compositional similarity of sampled versus reference (i.e. less-anthropogenically disturbed) communities. Lower EQC values

indicate better quality communities comprised of taxa and traits that are more similar to those from reference ecosystems.

In Germany, EQCs are calculated from a combination of multiple metrics using specific software for each taxa group because each group uses different metrics reflecting changes in different bioindicator taxa (e.g. Ephemeroptera, Plecoptera, and Trichoptera for macroinvertebrates; Böhmer et al. 2004). These calculations were performed for each sampling year using the German Perlodes software (v5.0.8) for macroinvertebrates, Phylib (v5.3) for macrophytes, and fiBS (v8.1) for fishes. We analyzed temporal changes in EQCs, and differences among sites, using the same model procedures detailed above for other Gaussian-distributed univariate response variables.

All of the above statistical analyses were performed in R 4.1.0 (R Core Team 2021). Generalized linear models were conducted via the “glmmADMB” package (v0.8.3.3; Fournier et al. 2012; Skaug et al. 2016) and all multivariate analyses were performed using the “vegan” package (v2.5–7; Oksanen et al. 2020).

Results

Macroinvertebrates

We observed no effects of restoration on macroinvertebrate abundance (Fig. 3A), but there were temporal differences between the restored and control sites in richness and Shannon diversity (evidenced by significant site * year interactions; Richness: LRT, $n = 18$, $L = 8.84$, $df = 2$, $p = 0.012$, $\Phi = 2.01$; Shannon diversity: LRT, $n = 18$, $L = 8.40$, $df = 2$, $p = 0.015$; Fig. 3D & 3G). In the first year after restoration, both richness and Shannon diversity exhibited larger declines in the restored sites compared to the controls. For example, between 2008 and 2010, the upstream and downstream restored sites, respectively, declined from 35 to 21 taxa (−40%) and from 57 to 32 taxa (−44%), whereas the control site only declined from 39 to 30 taxa (−23%). However, during the years that followed, both richness and Shannon diversity tended to increase in the restored sites while conversely declining in the controls, eventually resulting in higher values for both metrics in the restored sites after

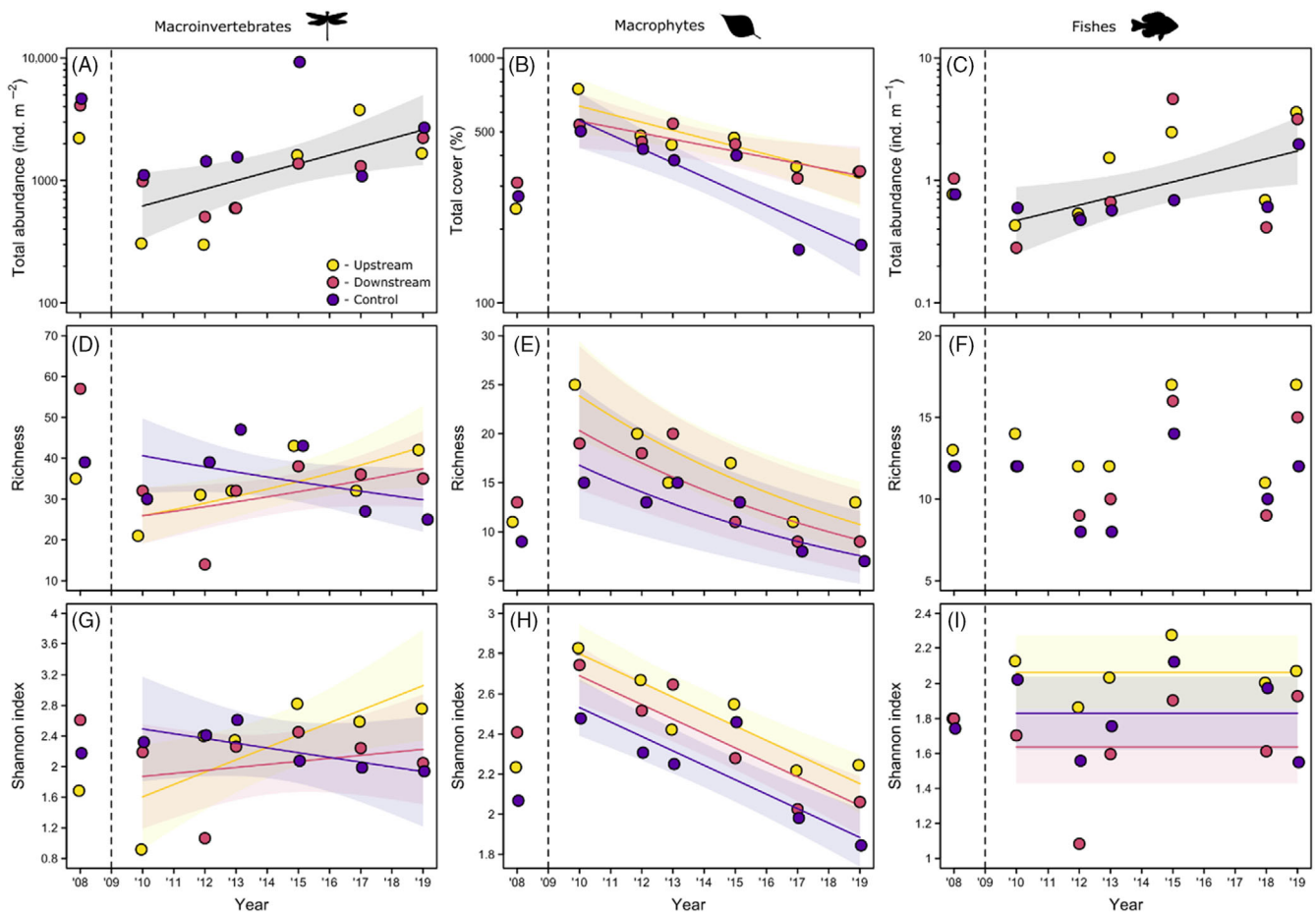


Figure 3. Abundance, richness, and Shannon diversity of (A, D, G) macroinvertebrates, (B, E, H) macrophytes, and (C, F, I) fishes in the upstream (yellow circles), downstream (red circles), and control sites (purple circles) of the Nidda River (2008–2019). A dashed line indicates the year of restoration. Best-fit lines and 95% CIs (shaded areas) are included for all models with significant terms ($p < 0.05$), with color schemes matching that of the points. A single black line and gray shaded area indicates a model in which year was the only significant term (i.e. no difference among sites) and the absence of a line indicates models with no significant terms.

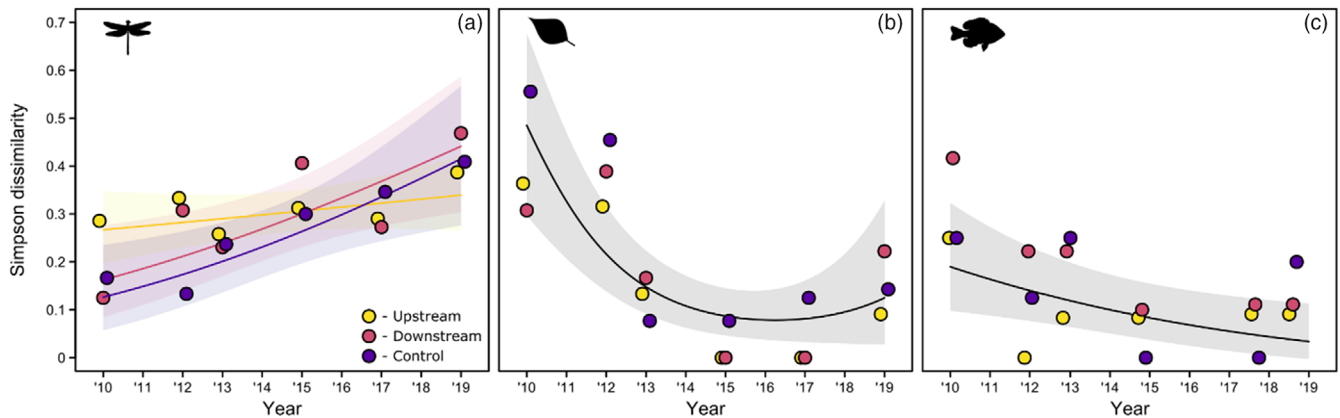


Figure 4. Temporal turnover of (A) macroinvertebrates, (B) macrophytes, and (C) fishes in the upstream (yellow circles), downstream (red circles), and control sites (purple circles) of the Nidda River (2008–2019). Temporal turnover is calculated as community dissimilarity between successive years. For example, turnover in 2010 represents the degree of community change from 2008 to 2010. Best-fit lines and 95% CIs (shaded areas) are included for all models with significant terms ($p < 0.05$), with color schemes matching that of the points. A single black line and gray shaded area indicates a model in which year was the only significant term (i.e. no difference among sites).

10 years (42 and 35 taxa in the respective restored sites during 2019 vs. 25 taxa in the control).

We found no differences between the restored and control sites in macroinvertebrate community turnover (Fig. 4A), composition (Fig. 5A & 5B), or EQCs (Fig. 6A), and no evidence of changes in the effects of restoration through time. Turnover did tend to decline more through time in the controls compared to the upstream restored site (significant site * year interaction; LRT, $n = 18$, $L = 6.93$, $df = 2$, $p = 0.031$, $\Phi = 2.37$), but temporal changes in the downstream restored site matched those of the controls (Fig. 4A), indicating no consistent effect of restoration.

Macrophytes

Macrophyte abundance tended to decline through time across all sites, but these declines were less severe in the restored sites (evidenced by a significant site * year interaction; LRT, $n = 18$, $L = 7.57$, $df = 2$, $p = 0.023$; Fig. 3B). Percent macrophyte cover decreased by 35% per year in the upstream restored site, 25% per year in the downstream restored site, and 43% per year in the control site (note that total cover can be well above 100% because it is the summed values for all taxa). Regarding richness and Shannon diversity, both metrics were higher in the restored versus the control sites (Fig. 3E & 3H), but these same differences also existed prior to restoration in 2008.

We observed no differences in community turnover among sites (Fig. 4B), however macrophyte community composition diverged between the restored and control sites (evidenced by a significant site effect; PERMANOVA, $n = 21$, $F\text{-model}_{2,15} = 2.64$, $p = 0.0010$). During 2012 and consistently thereafter, composition in the restored sites was generally associated with the upper left of the ordination, whereas the control sites were associated with the lower right (Fig. 5C). Compositional differences among sites were driven by the greater dominance of primarily *Sparganium emersum* in the restored

sites, with secondary contributions from other species such as *Persicaria hydropiper* and *Potamogeton crispus*. Conversely, the control sites were dominated primarily by *Sparganium erectum*, in addition to other species such as *Fontinalis antipyretica*, *Leptodictyum riparium*, and *Potamogeton nodosus* (Fig. 5D).

Macrophyte EQCs were consistently worse (i.e. higher values) in the restored compared to the control sites (evidenced by a significant site effect; LRT, $n = 18$, $L = 8.86$, $df = 2$, $p = 0.012$; Fig. 6B). The EQC of all sites ranged between 3 (moderate) to 5 (bad), with an average value of 4.50 ± 0.55 (mean \pm SD) in the upstream restored site, 3.83 ± 0.41 in the downstream restored site, and 3.67 ± 0.52 in the controls.

Fishes

We found no differences in fish abundance (Fig. 3C) or richness (Fig. 3F) among sites. Shannon diversity was higher in the upstream restored site compared to the controls (evidenced by a significant site effect; LRT, $n = 18$, $L = 8.78$, $df = 2$, $p = 0.012$; Fig. 3I). However, Shannon diversity was also comparatively lower in the downstream restored site, indicating no consistent effect of restoration. We also found no evidence of any differences in fish community turnover (Fig. 4C), composition (Fig. 5E & 5F), or EQCs (Fig. 6C) among sites.

Discussion

Generally Neutral Effects of Restoration

We observed few effects of restoration on the macroinvertebrate, macrophyte, and fish communities, even after 10 years of monitoring. Restoration did positively influence some components of the macroinvertebrate and macrophyte communities (discussed further below), but most metrics exhibited no post-restoration changes. We also observed no changes whatsoever in the fish community (similar to Lepori et al. 2005 and Jähnig et al. 2011, but see Höckendorff et al. 2017 for a contrasting

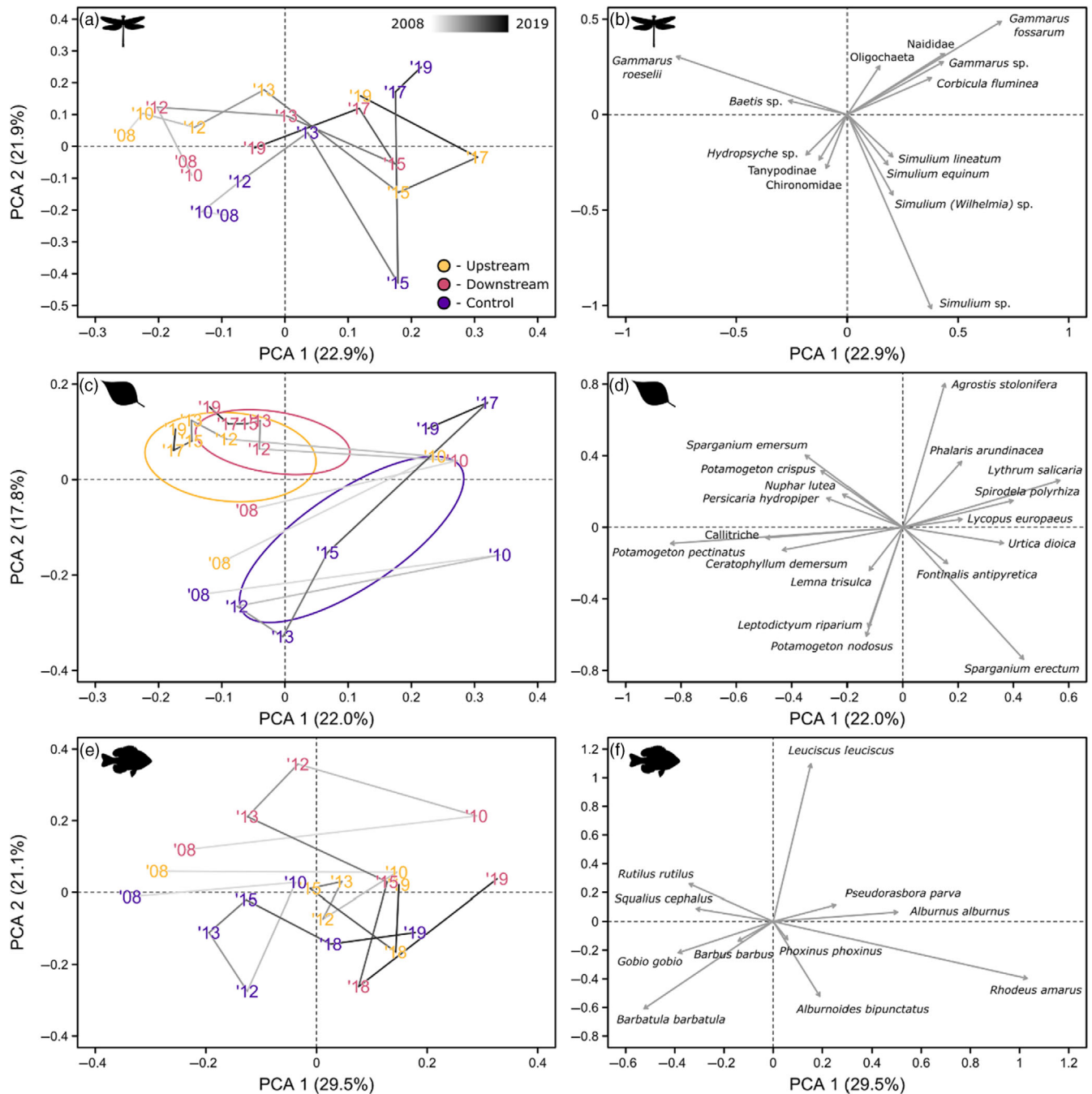


Figure 5. Composition of (A, B) macroinvertebrates, (C, D) macrophytes, and (E, F) fishes in the upstream (yellow), downstream (red), and control (purple) sites of the Nidda River (2008–2019) as determined by PCA. Overall community similarities are indicated by the points in each panel, which are illustrated as years (closer points have more similar communities), and year-to-year composition trajectories are illustrated using lines that progress across a greyscale color gradient through time (from light gray to black during 2008–2010). Colored ellipses indicate significant ($p < 0.05$) differences among sites and show the central tendency of composition for each site across years.

example). These results match conclusions from previous studies that local-scale hydromorphological restoration can have little effect on aquatic biota (Palmer et al. 2010; Nilsson et al. 2015; Leps et al. 2016). There are two common explanations for why this may occur. First, the capacity for communities to change in response to restoration can be limited if new

colonists cannot arrive. A lack of colonists can occur if habitat connectivity remains unchanged (e.g. physical barriers are not removed; Tummers et al. 2016), if there are no new species available to disperse from other parts of the watershed (Sundermann et al. 2011; Roni et al. 2018), or if there are no purposeful introductions of new native species (Haase & Pilotto 2019).

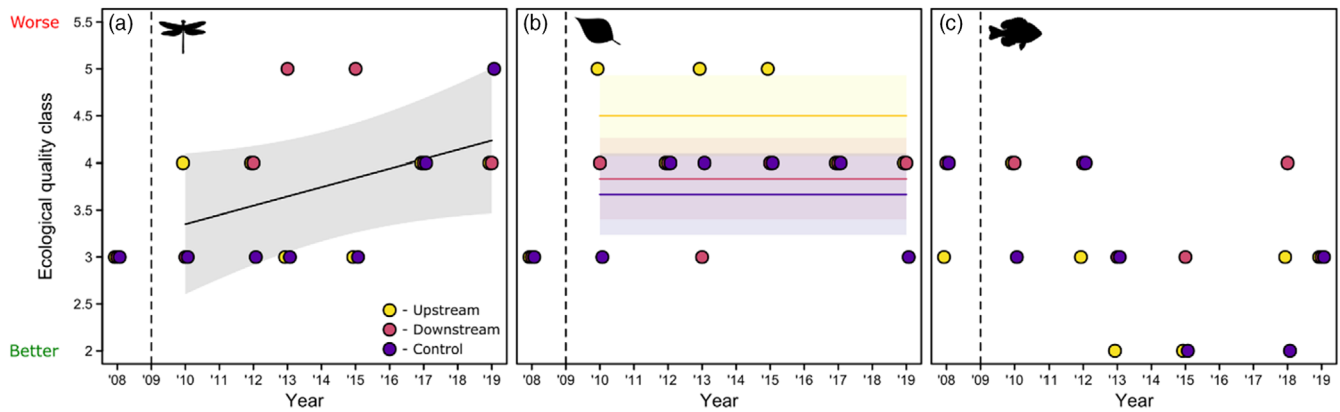


Figure 6. Ecological quality classes (EQCs) of (A) macroinvertebrates, (B) macrophytes, and (C) fishes in the upstream (yellow circles), downstream (red circles), and control sites (purple circles) of the Nidda River (2008–2019). A dashed line indicates the year of restoration. Prerestoration EQCs were in the moderate to poor classes (3–4) and we found little to no postrestoration improvement nor differences between the control and restored sites. Best-fit lines and 95% CIs (shaded areas) are included for all models with significant terms ($p < 0.05$), with color schemes matching that of the points. A single black line and gray shaded area indicates a model in which year was the only significant term (i.e. no difference among sites) and the absence of a line indicates models with no significant terms.

However, this explanation is unlikely given that we observed consistent postrestoration increases in macroinvertebrate richness and shifts in macrophyte composition, indicating that new species were establishing in later years. In addition, fish ecological quality occasionally reached the good to moderate range (i.e. EQCs of 2–3). These years with better quality scores indicate that new fish species representative of better environmental conditions were intermittently present and thus able to arrive at these sites, they just did not persist through time.

A second, and more probable, explanation is that more extensive and broader-scale efforts are required to address the generally poor ecological quality of our sites. Local-scale habitat restoration, like that conducted at the Nidda River, is necessary for aquatic communities to recover. However, while the restored 3 km section of the Nidda River is more extensive than most German restoration projects (the average length is ~ 1.5 km; Haase et al. 2013) and likely cost over €1,000,000 (average cost is \sim €400,000 per km; Haase et al. 2013), it is still a short section of the total length of the river. Colonists and pollutants from upstream, unrestored river sections may therefore be entering the restored sections and restricting community change (Bernhardt & Palmer 2011; Wohl et al. 2015; Roberts et al. 2021). Restoring a longer section of the river may have achieved better results, but conducting such extensive habitat restoration projects is generally not feasible owing to funding, administration, and land ownership limitations (Alexander & Allan 2007). Alternatively, local-scale restoration could be combined with efforts to address relevant, watershed-scale stressors. For example, the Nidda watershed is still contaminated by a variety of point-source (e.g. municipal and industrial wastewater) and non-point-source (e.g. nutrients and chemicals from agricultural runoff) pollutants that can adversely affect freshwater organisms (Schweizer et al. 2018; Brettschneider et al. 2019a). Restoration may even have worsened this contamination by disturbing polluted sediments and facilitating sediment–water exchange by

reducing flow velocity (Brettschneider et al. 2019b). Addressing these types of stressors is likely best accomplished through efforts to reduce chemical pollution throughout the watershed, such as by improving the effectiveness of wastewater treatment (e.g. via “end-of-pipe” technologies; Joss et al. 2008) or by adopting targeted agricultural management practices that reduce fertilizer use and runoff (Bosch et al. 2013). Improving broader-scale water management practices would in turn facilitate local-scale recovery efforts by better ensuring that upstream contaminants no longer flow through restored river sections.

Some Positive Effects of Restoration

We observed postrestoration increases in macroinvertebrate richness (similar to Lorenz et al. 2009; Miller et al. 2010) and less steep declines in macrophyte abundance, suggesting some positive effects of restoration. However, when viewed alongside associated shifts in community composition and ecosystem health, these changes were ultimately minor and did not necessarily reflect improvement. For example, the lack of any marked change in macroinvertebrate community composition and EQCs indicated, respectively, that increased richness was driven by increases in primarily rare taxa and that these gains had no influence on ecosystem health. Furthermore, macrophyte ecological quality declined in the restored sections and the dominant macrophyte species are good colonizers of disturbed environments (*Sparganium emersum*; Barrat-Segretain & Amoros 1996), suggesting that restoration ultimately had a negative influence on macrophytes. These findings illustrate how the benefits provided by river habitat restoration depend not only on how it affects the number of taxa, but also on which taxa are changing (i.e. composition) and how they relate to the goals of restoration. From a conservation perspective, any improvement in richness could be considered positive because even small gains can diversify the number of unique functional roles (Mouillot

et al. 2013; Dee et al. 2019) and stabilize communities against future disturbances (Grime 1998; Yachi & Loreau 1999). Conversely, restoration that promotes only rare macroinvertebrates, that somewhat reduces but does not alleviate macrophyte declines, and elicits no change (and even a worsening) of ecosystem health may represent a poor ecological return for the money, time, and effort invested.

Temporal Dynamics

Temporal changes in macroinvertebrate richness and macrophyte abundance revealed how some effects of restoration can depend upon the time frame of study. A frequent conclusion from meta-analyses is that river restoration often has highly variable effects, including positive, neutral, and even negative outcomes (Palmer et al. 2010; Haase et al. 2013; Kail et al. 2015). This variability has been theorized to be partly driven by the duration of monitoring (Palmer et al. 2010; Kail et al. 2015) and our results provide some support for this assertion. During the first few years following restoration, macroinvertebrate richness was generally lower in the restored compared to the control sites, with no clear differences in macrophyte abundance or composition. After 6–10 years, macroinvertebrate richness and macrophyte abundance were consistently higher in the restored sites, with clear differences in macrophyte composition. Therefore, if we had only implemented short-term monitoring (e.g. just the 2010 sampling), then we would have misinterpreted the effects of restoration by concluding it had negative effects on macroinvertebrates and no effect on macrophytes. However, by monitoring across longer time periods, we observed how the effects of restoration shifted as new taxa established in the restored sites. These findings illustrate that distinguishing between the consistent and transient effects of restoration requires monitoring that, at minimum, spans multiple timepoints both before and after restoration (e.g. multiple before-after control-impact sampling designs or “mBACI”; Roni et al. 2018). A decade or more of postrestoration data may also be required for projects to separate the effects of restoration from natural environmental fluctuations (echoing recommendations from Kondolf & Micheli 1995; Hasselquist et al. 2015; Didham et al. 2020). More extensive postrestoration monitoring would also help to identify any stressors that are still impacting restored communities, which can be integrated into adaptive management programs and future decision-making.

In conclusion, although our results show some temporal changes in the effects of local-scale habitat restoration, it ultimately elicited little to no ecological improvement regardless of the amount of time allowed for community development (at least up to a decade afterwards). Such a consistent lack of change is particularly concerning because river restoration is time consuming and expensive, yet our results show it may produce no evident community change and can even negatively affect ecosystem health. However, it is important to note that restoration projects generally have goals beyond ecological improvement. For example, the Nidda restoration project also aimed to improve human-related services, such as aesthetics

and recreation. Local-scale river restorations generally achieve these types of human-related goals (Jähnig et al. 2011; Deffner & Haase 2018; Kaiser et al. 2020), thus providing socioeconomic benefits that can compensate for, or even outweigh, a lack of change in aquatic biota. We are therefore not suggesting that local-scale efforts to restore river habitats are ineffective. Instead, we recommend that restoration efforts integrate multiple local- and broader-scale methods that address the primary drivers of hydrogeological decline, and multiple temporal perspectives, to ensure that both human-related and ecological goals are being successfully met.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Locations for the “upstream,” “downstream,” and two “control” sites sampled for macroinvertebrates, macrophytes, and fishes during 2008–2019.

Figure S1. Substrate diversity (measured using the Shannon index) in the upstream (yellow circles), downstream (red circles), and control sites (purple circles) of the Nidda River (2010–2019).

Figure S2. Composition of (a) substrate in the (b) control, (c) upstream, and (d) downstream sites of the Nidda River (2010–2019) as determined by Principal Components Analysis (PCA).

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