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Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration

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Abstract. Channel reconfiguration is a popular but controversial approach to river restoration, and ecological responses to channel reconfiguration have not been rigorously assessed. We compared physical-habitat variables, taxonomic and functional-trait diversities, taxonomic composition, and functional-trait abundances between 24 pairs of upstream (control) and downstream reconfigured (restored) reaches in 3 catchment land uses (urban, agricultural, rural) across the North Carolina Piedmont. We asked how environmental filters and functional species traits might provide insight to biological responses to restoration. Taxonomic and functional-trait differences between control and restored reaches suggest that restoration affected aquatic assemblages only in agricultural and rural catchments. Our results highlight 2 important aspects of channel reconfiguration as a restoration practice. First, responses to restoration differ between agricultural/rural and urban catchments, possibly because of modified hydrological regimes caused by urbanization. Second, we find evidence that channel reconfiguration disturbs food and habitat resources in stream ecosystems. Taxa sensitive to disturbance were characteristic of control reaches, whereas insensitive taxa were characteristic of restored reaches. Abundances of traits related to reproduction (voltinism, development, synchronization of emergence, adult life span), mobility (occurrence in drift, maximum crawling rate, swimming ability), and use of resources (trophic and habitat preferences) differed significantly between control and recently restored reaches. Our results suggest that taxa in restored habitats are environmentally selected for traits favored in disturbed environments. Our work suggests how functional-trait approaches could benefit the practice of river restoration when used to target restoration activities and to develop informed expectations regarding recovery following restoration activities.

Key words: benthic macroinvertebrate, functional traits, channel reconfiguration, disturbance, bioassessment, river restoration.

River restoration often is undertaken to repair degradation caused by development of water and natural resources. It encompasses many objectives and

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outcomes (e.g., enhance water quality, manage riparian zones, improve instream habitat, fish passage, bank stabilization; Bernhardt et al. 2005). A common goal of river restoration is to recreate geomorphically stable reaches with high habitat availability and diversity (FISRWG 1998). This approach is based on an implicit positive correlation between habitat diversity and taxonomic and functional diversity of stream assemblages, as described by the habitat templet theory (Southwood 1977, 1988).

Channel reconfiguration is a widely practiced restoration activity based on *natural channel design* (Skidmore et al. 2001), intended to restore channel geomorphology (Shields et al. 2003) and habitat complexity (FISRWG 1998) in systems simplified by development. The objectives of channel reconfiguration projects are often to increase instream habitat quality and biological diversity, but how well projects achieve these objectives is rarely evaluated (Palmer et al. 2005), in part because of poorly defined objectives and a lack of comprehensive monitoring (Bernhardt et al. 2005). Lack of assessment leads to uncertainty about outcomes of river restorations because it maintains the currently inadequate understanding of short- and long-term ecosystem consequences of channel reconfiguration and the currently limited knowledge of the processes and mechanisms that control those consequences.

An effort to improve understanding of the processes and consequences of river restoration is underway as practitioners move toward more ecologically based restoration designs. Analysis of functional traits offers one approach toward this effort to better understand ecosystem functions, processes, and health (Loreau 1998, Chapin et al. 2000, Diaz and Cabido 2001, Loreau et al. 2001, Mouillot et al. 2006). Analysis of functional traits has already been applied to characterize various disturbances in stream ecosystems (Statzner et al. 1997), including wastewater treatment facilities (Charvet et al. 1998) and catchment urbanization (Dolédec et al. 1999, Gayraud et al. 2003).

Channel configurations often restructure habitat stability, food resources, and the thermal regime (Poff et al. 2006), creating conditions that favor only those species possessing functional traits suited to the constructed environment. In this sense, restoration activities that modify local environmental filters could determine which species from the regional pool would occur locally (Tonn et al. 1990, Weiher and Keddy 1995, Diaz et al. 1999). For example, removal of riparian vegetation and exposure of the streambed during channel reconfiguration could influence food resources and thermal regime (Sweeney et al. 2004), and increase dominance of grazing, warm eurythermal taxa in restored relative to control reaches. Creation of an entirely new channel could influence habitat stability and select for mobile taxa that reproduce rapidly. Beneficial outcomes of restoration, including reduced erosion of streambeds and banks, creation of scour pools, and construction of habitat structures, might increase habitat diversity and stability and generate conditions favorable for taxa that prefer stable substrates. These examples suggest that functional traits and environmental filters could benefit the field of river restoration by identifying activities and design strategies (e.g., passive vs active approaches, building habitats vs building habitat processes) that actively encourage or discourage specific species or ecological functions in the restored habitat.

Also relevant to understanding restoration consequences is the concept of ecological disturbance (sensu Townsend and Hildrew 1994), a discrete event that leads to replacement of individuals by members of the same or different taxa. Whether channel reconfiguration is a disturbance that filters taxa suited to modified and disturbed environments in the first years of post-construction recovery is unclear. Furthermore, prevailing environmental conditions, including variability and stability of habitats, can influence ecological responses to disturbances (Poff and Ward 1990). Catchment land uses influence stream hydrology and water quality and filter organisms on the basis of habitat stability (Temperton et. al 2004), but whether ecological responses to restoration differ among land uses is currently unclear.

These concepts of restoration as filters and disturbances are important for effective assessment of stream restorations. Few projects are monitored for longer than 5 y, so short-term effects of disturbance and recovery associated with construction of new channels and subsequent adjustments of the river might unduly influence evaluation of the success of the project. To begin investigating these concepts in the context of channel reconfiguration, we evaluated differences between paired upstream (control) and downstream reconfigured (restored) channels across 3 catchment landuse types. We assessed effects of restoration based on differences in physical habitat, taxonomic and functional diversity, community composition, and functional-trait abundances between control and restored reaches. We asked: 1) Do taxa in newly reconfigured reaches reflect a disturbance effect of the restoration practice? 2) Does catchment land use influence the presence and type of response observed? 3) Does the bioassessment approach used influence the presence and type of response observed? We use results from these analyses to discuss progress necessary for effective monitoring of stream restorations.

Methods

Study sites

We first identified all stream restoration projects under the regulation of state, federal, and regional permitting agencies in the North Carolina Piedmont. We filtered sites by limiting catchment areas to ≤13 km^2 to minimize environmental and community variation associated with increasing catchment size. We restricted sites to those at which comprehensive reconfiguration of the channel was performed. Restoration consisted of reconstructing channel pattern, profile, and dimension by cutting an entirely new channel or floodplain. Designs often included replanting of native vegetation and inclusion of various habitat structures (e.g., root wads, pool-scouring cross-vanes). Time since completion of construction ranged from 1 to 4 y prior to sampling. We anticipated that recovery at the study reaches might be incomplete when we sampled (<4 y after project completion) because time to recovery after restoration is not well understood (Fuchs and Statzner 1990). Thus, we use *restored* simply in reference to reaches where reconfiguration activities had occurred.

We used ArcGIS 9.1 (ESRI, Redlands, California) to delineate catchments of each site and analyzed dominant land use in each catchment based on the 1996 EarthSat Land Use Land Cover from BasinPro 8 (California Geographic Information Association, Raleigh, North Carolina). We adopted the US Geological Survey landuse categories developed by Anderson et al. (1976) and classified landuse polygons into 1 of 5 relevant categories (urban and built-up, agriculture, brush or transitional between open and forest, forest, barren). We classified each site as urban, agricultural, or rural based on the greatest percentage of areal coverage at the site. We defined rural polygons as brush or transitional between open and forest, forest, and barren lands. We used 8 urban (71–94% urban land use in catchment), 8 agricultural (53–99% agricultural), and 8 rural (57–99% rural) sites in our study.

All sites are in the Piedmont ecoregion of North Carolina, bounded by the Appalachian Mountains to the west and the low-elevation coastal plains to the east. Streams in the Piedmont are characterized by moderate slopes (0.07–2.67%) and igneous to metamorphic geology. Condition of the riparian area varies from mature to immature deciduous forest, herbaceous cover, lawn grass, and urban–suburban development. Minimal irrigation is required in the humid, warm-temperate climate of the North Carolina Piedmont. Thus, the effect of agriculture on the hydrologic regime is less than in areas in the western US, where irrigated agriculture accounts for ⅓ of the water withdrawn and ~90% of water use (Gollehon and Quinby 2000).

Study design

At each site, we paired the restored reach with a control reach immediately upstream of the restoration project. This upstream–downstream balanced, blocked (8 reach pairs/landuse type) study design assumes that catchment conditions of control and restored reaches are similar. Several control reaches did not fit the definition of reference or least-disturbed condition (Whittier et al. 2007) because of current or historical activities in the catchment. The control reach represented either: 1) the initial degraded condition from which the restored reach was expected to improve (urban catchments) or 2) a less disturbed and more desirable condition toward which restored reaches were expected to improve (rural and agricultural catchments). In urban control reaches, both local- and catchment-scale processes drive channel simplification (e.g., channelization, straightening, armoring, loss of floodplain access, removal of riparian vegetation, loss of instream habitat complexity, increased frequency, timing, and magnitude of runoff). Thus, we expected indicators of habitat quality and biodiversity to be better at restored than at control reaches for the urban sites. Rural and agricultural control reaches are largely unmodified and restoration activities in restored reaches address reach-scale simplification caused by local impacts (e.g., cattle access, realignment). Thus, we expected indicators of habitat quality and biodiversity to be similar between restored and control reaches for the rural and agricultural sites if restoration activities established the degree of habitat complexity found in the control reaches.

Site assessment and sampling

We visited each pair of reaches, in random order, once during the summer (June–August) in either 2003 or 2004. During the site visit, we assessed channel conditions and sampled benthic macroinvertebrates.

Channel features and habitat.—We defined 60-m-long restored and control study reaches at each site. In each reach, we surveyed 2 riffle cross-sections and a longitudinal profile and measured 24 variables to characterize channel form and features. We calculated average bankfull width, depth, and area to describe the form of the channels. We characterized the habitat based on the fine (sand or finer) and coarse (D90, the grain size for which 90% of the bed material grains are finer) fractions of the sediment matrix from pebble counts (Harrelson et al. 1994). We defined channel complexity within the active channel by the number of pools, defined as 1.5× riffle depth, and the volume of large woody debris (LWD) occurring along the longitudinal profile (volume of LWD/60 m). We used the Bank Erosion Hazard Index (Rosgen 2001) to characterize bank stability. We dried and weighed organic material trapped in the kick net (see *Benthic macroinvertebrates* below) as a surrogate for coarse particulate organic matter availability and storage. We also estimated Rapid Bioassessment Protocol (RBP) scores for each of the reaches with the protocol for high-gradient streams (Lazorchak et al. 1998, Barbour et al. 1999). This set of 11 RBP variables characterizes habitat features structured by channel substrates and morphology, streambed and bank characteristics, and riparian vegetation.

Benthic macroinvertebrates.—We collected benthic macroinvertebrates using the North Carolina Division of Water Quality Qual 5 method (NCDENR 2006). This protocol prescribes sampling insects from 1 riffle (kick net, 107 cm × 114 cm, 500-μm mesh), margin habitats (D-frame dip net, 900-μm mesh), rock/log habitat (fine-mesh wash), and 1 leaf pack, with a ~15-min visual search of larger habitats. We sampled control and restored reaches once on the same day at each site and moved from downstream (restored) to upstream (control). We picked insects by hand from samples, composited samples within each reach, and preserved them in 95% ethanol in the field. We identified insects in the laboratory to species when possible.

We used a majority rule approach and best professional judgment to assign primary functional traits (Merritt and Cummins 1996, Poff et al. 2006) to each genus based on the most abundant and common species in the genus. We analyzed all traits listed in Poff et al. (2006), including those identified as phylogenetically constrained (Poff et al. 2006). We did not assign fuzzy traits (Chevenet et al. 1994, Dolédec et al. 2006) because we lacked sufficient information on secondary taxon traits.

Statistical analyses

Diversity and habitat characteristics of control and restored reaches.—We calculated Shannon diversity (Shannon and Weaver 1949) based on number of genera and on number of trait states (e.g., rare, common, or abundant in drift) in each reach. We used paired *t*-tests (Excel 2003; Microsoft, Seattle, Washington) to evaluate whether habitat variables and Shannon genus and functional-trait diversities differed between paired reaches within each landuse group. We evaluated significance at $\alpha = 0.05$.

Taxonomic composition of control and restored reaches.—We evaluated differences in assemblage composition between control and restored reaches within each landuse group with blocked Multi-Response Permutation Procedures (MRBP; Mielke 1984) (PC-ORD, version 5/β; MjM Software, Gleneden Beach, Oregon). We $\log_{10}(x+1)$-transformed taxon relative abundances and used median alignment within blocks (control vs restored) and squared Euclidean distance (Mielke and Berry 2001, McCune and Grace 2002). We applied indicator taxon analysis (PC-ORD) when MRBP returned a significant difference between blocks. Indicator taxon analysis (Dufrêne and Legendre 1997) combines abundance and frequency-of-occurrence information for each taxon in each group (control or restored) into a single indicator value (IV), for which 100 is the highest possible value. We evaluated statistical significance of each indicator value with a Monte Carlo randomization method (1000 permutations).

Functional traits of control and restored reaches.—We used the same functional traits as for analysis of functional-trait diversity and calculated relative abundances of all functional-trait states at each site by multiplying the *site × relative abundance of each genus* matrix by the *presence of each functional-trait state × genus* matrix. We used the relative abundances of each functional-trait state (e.g., semivoltine, univoltine, multivoltine) at a reach to examine the functional composition of benthic communities in control and restored reaches.

We used a hierarchical agglomerative cluster analysis (Sørenson distance, flexible $\beta = -0.25$; PC-ORD) by land use to cluster sites on the basis of dissimilarities in trait relative abundances. We used the resultant dendrograms as a visual tool to determine whether clusters reflected control and restored reach classifications, a result that would indicate a functional-trait response to restoration activities within landuse groups. Last, we used paired *t*-tests to evaluate whether relative abundances of individual traits differed between control and restored reaches within landuse groups.

Results

Diversity and habitat characteristics of control and restored reaches

Habitat characteristics.—Many variables describing habitat complexity and stability, biodiversity, and functional traits did not differ between control and restored reaches. Percent vegetation cover was signif-

TABLE 1. Mean values of physical-habitat and diversity (genus and functional-trait states) variables at paired upstream (control) and downstream (restored) reaches of 8 channel reconfiguration sites in rural, agricultural, and urban catchments in North Carolina (24 sites total). *p*-values are from paired *t*-tests comparing control and restored reaches within landuse types. Bold font indicates significant ($\alpha = 0.05$) differences. LWD = large woody debris, BEHI = Bank Erosion Hazard Index, CPOM = coarse particulate organic matter, D90 = grain size for which 90% of sampled material is finer, RBP = Rapid Bioassessment Protocol.

	Rural			Agricultural			Urban		
Variables	Control	Restored	*p*	Control	Restored	*p*	Control	Restored	*p*
Environmental									
No. pools/60 m	**0.021**	**0.011**	**0.000**	0.015	0.011	0.176	**0.023**	**0.013**	**0.008**
Bankfull width (m)	6.1	6.3	0.86	**4.1**	**5.7**	**0.05**	6.0	5.8	0.80
Bankfull depth (m)	0.6	0.4	0.17	0.5	0.5	0.87	0.5	0.6	0.38
Bankfull area (m^2)	12.9	8.4	0.28	7.0	9.9	0.30	10.1	12.1	0.53
Slope (%)	0.006	0.007	0.19	0.012	0.008	0.44	0.006	0.006	0.95
Bank:height ratio	1.6	1.7	0.29	1.2	1.6	0.33	1.6	1.4	0.35
Width:depth ratio	11.3	20.9	0.10	10.6	12.9	0.53	13.6	10.8	0.33
Volume of LWD (m^3/60 m)	0.11	0.01	0.24	0.01	0.00	0.09	0.01	0.00	0.23
BEHI	11.73	17.11	0.10	17.24	21.47	0.65	15.82	24.11	0.09
CPOM (g/kick-net sample)	2.80	4.55	0.32	3.54	6.48	0.23	1.43	5.59	0.15
D90 (mm)	46.56	64.33	0.20	57.50	251.52	0.17	66.68	64.89	0.95
% sand and fines	60	54	0.25	55	52	1.00	55	56	0.99
% vegetation cover	**53**	**21**	**0.03**	**66**	**11**	**0.00**	**52**	**23**	**0.03**
Epifaunal substrate/available cover[a]	**13**	**5**	**0.01**	**16**	**5**	**0.00**	7	4	0.18
Embeddedness	14	13	0.44	13	12	0.21	12	12	0.52
Variability in velocity/depth regime[b]	12	13	0.59	12	11	0.46	9	11	0.09
Sediment deposition[c]	12	11	0.43	10	9	0.49	11	13	0.14
Channel flow status[d]	14	14	0.68	14	13	0.53	**12**	**14**	**0.01**
Channel alteration[e]	14	14	1.00	15	12	0.21	11	13	0.21
Frequency of riffles (or bends)	16	16	0.66	18	17	0.43	14	16	0.18
Left bank stability[f]	7	8	0.53	6	7	0.28	6	7	0.33
Right bank stability[f]	7	7	0.86	5	7	0.16	6	7	0.41
Vegetative protection[g]	13	12	0.71	14	13	0.68	10	12	0.41
Riparian vegetation width (m)	17	15	0.27	14	11	0.25	9	9	0.85
Diversity									
RBP score	134	123	0.30	**137**	**118**	**0.03**	102	112	0.25
Shannon genus diversity	2.34	2.28	0.69	1.98	1.74	0.28	**1.36**	**1.77**	**0.01**
Shannon functional-trait state diversity	49.11	50.00	0.45	52.56	50.67	0.74	38.33	41.44	0.09

[a] sensu Lazorchak et al. 1998; area and variety of hard surfaces, including rocks and snags

[b] sensu Lazorchak et al. 1998; availability of 4 velocity–depth conditions: 1) slow–deep, 2) slow–shallow, 3) fast–deep, and 4) fast–shallow

[c] sensu Lazorchak et al. 1998; presence of depositional features that indicate sediment accumulation in an unstable channel

[d] sensu Lazorchak et al. 1998; the amount of useable substrate as defined by the degree to which the channel is filled with water

[e] sensu Lazorchak et al. 1998; presence of large-scale anthropogenic changes (e.g., riprap, channelization) that simplify and reduce availability of habitat

[f] sensu Lazorchak et al. 1998; presence of or potential for bank failure, as evidenced by crumbling, unvegetated banks, exposed tree roots, and exposed soil

[g] sensu Lazorchak et al. 1998; extent to which bank is covered by vegetation

icantly higher at control than at restored reaches, but no other habitat characteristic differed significantly between control and restored reaches across landuse groups (Table 1). In rural catchments, variables associated with habitat complexity (number of pools/60 m, % vegetation cover, and epifaunal substrate/available cover) were significantly lower in restored than in control reaches, but no other significant differences in habitat characteristics were detected between control and restored reaches (Table 1). In urban catchments, one variable associated with area of habitat (channel flow status) was significantly greater in restored than control reaches, but other variables associated with habitat complexity (number of pools/60 m, % vegetation cover) were significantly lower in restored than in control reaches (Table 1). In agricultural catchments, variables associated with habitat complexity (% vegetation cover, epifaunal substrate/available cover, RBP score) were significantly higher in control than in restored reaches, whereas habitat area (bankfull width) was significantly lower in control than in restored reaches (Table 1).

TABLE 2. Results from multi-response permutation procedures analysis of taxonomic composition differences between paired upstream (control) and downstream (restored) reaches of 8 channel reconfiguration sites in rural, agricultural, and urban catchments in North Carolina (24 sites total). The *A*-statistic describes the strength of taxonomic composition differences between control and restored sites. Bold font indicates significant ($\alpha = 0.05$) differences.

Result	Rural	Agricultural	Urban
A-statistic	**0.070**	**0.090**	0.049
p	**0.050**	**0.022**	0.155

Taxonomic diversity.—Shannon genus diversity was significantly higher at restored than at control reaches in urban catchments (Table 1). Shannon genus diversity did not differ significantly between control and restored reaches in rural or agricultural catchments. Mean values of taxonomic diversity were lower at the restored sites than at the upstream sites in the rural (upstream = 2.34, restored = 2.28) and agricultural (upstream = 1.98, restored = 1.74) settings, but these differences were not statistically significant. Shannon functional-trait diversity did not differ significantly between control and restored reaches in urban, rural, or agricultural catchments.

Taxonomic composition of control and restored reaches

Taxonomic composition of assemblages differed between control and restored reaches in rural and agricultural catchments, but not in urban catchments (Table 2). Effect size, indicated by the *A*-statistic, was higher in agricultural than in rural catchments, indicating a greater difference in taxonomic composition between control and restored communities in the agricultural catchment than in the rural catchments. In rural catchments, relative abundances of Chironomidae and Baetidae were greater in restored than in control reaches, whereas relative abundance of Hydropsychidae was lower in restored than in control reaches (Fig. 1A). In agricultural catchments, relative abundance of Chironomidae did not differ between control and restored reaches, but relative abundances of Baetidae and Hydropsychidae were higher in restored than in control reaches (Fig. 1B). These taxa appear to have replaced Philopotamidae and Heptageniidae at restored reaches in agricultural catchments. The relative abundances of opportunistic taxa, such as

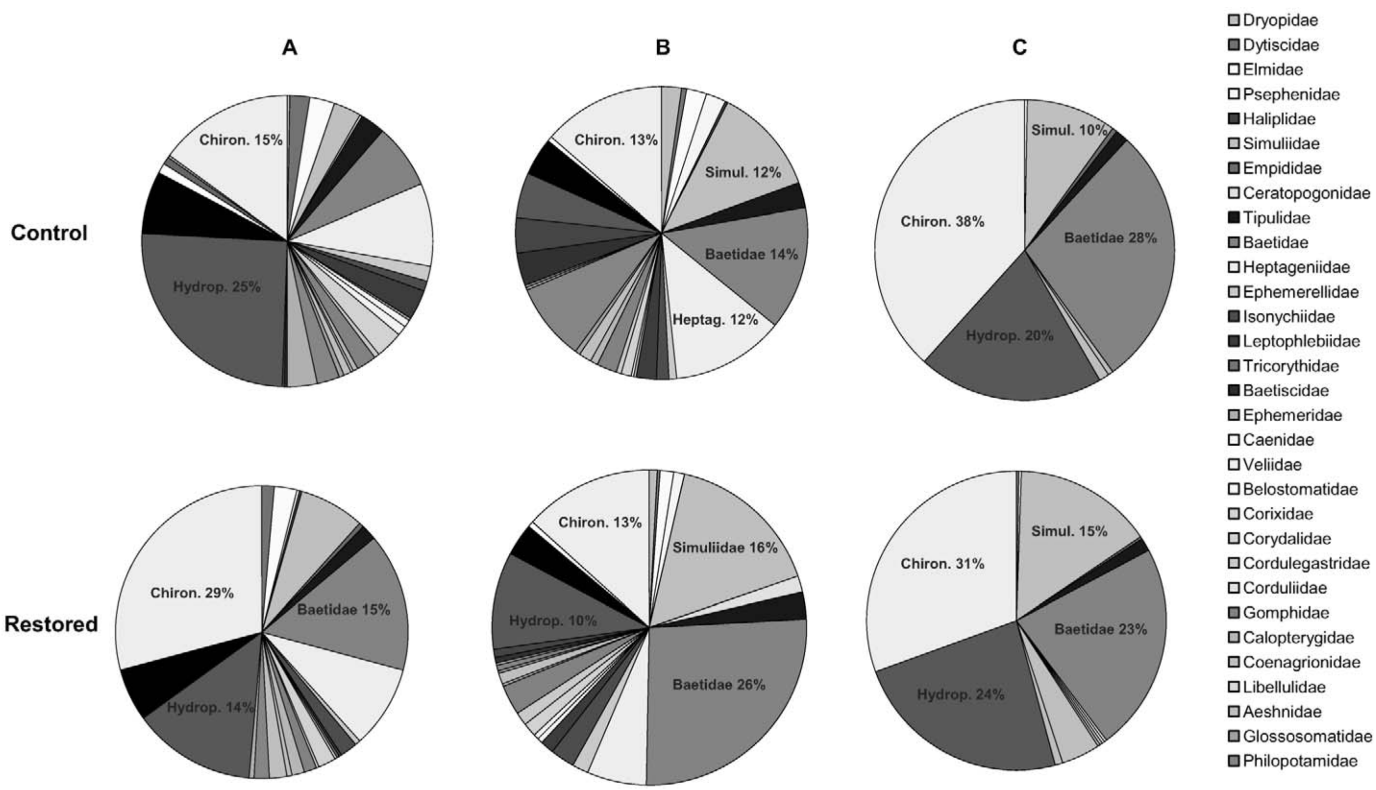

FIG. 1. Relative abundances of benthic macroinvertebrate families in paired upstream (control) and downstream (restored) reaches of 8 channel reconfiguration sites in rural (A), agricultural (B), and urban (C) catchments in North Carolina (24 sites total). Chiron. = Chironomidae, Hydropt. = Hydroptilidae, Simul. = Simuliidae.

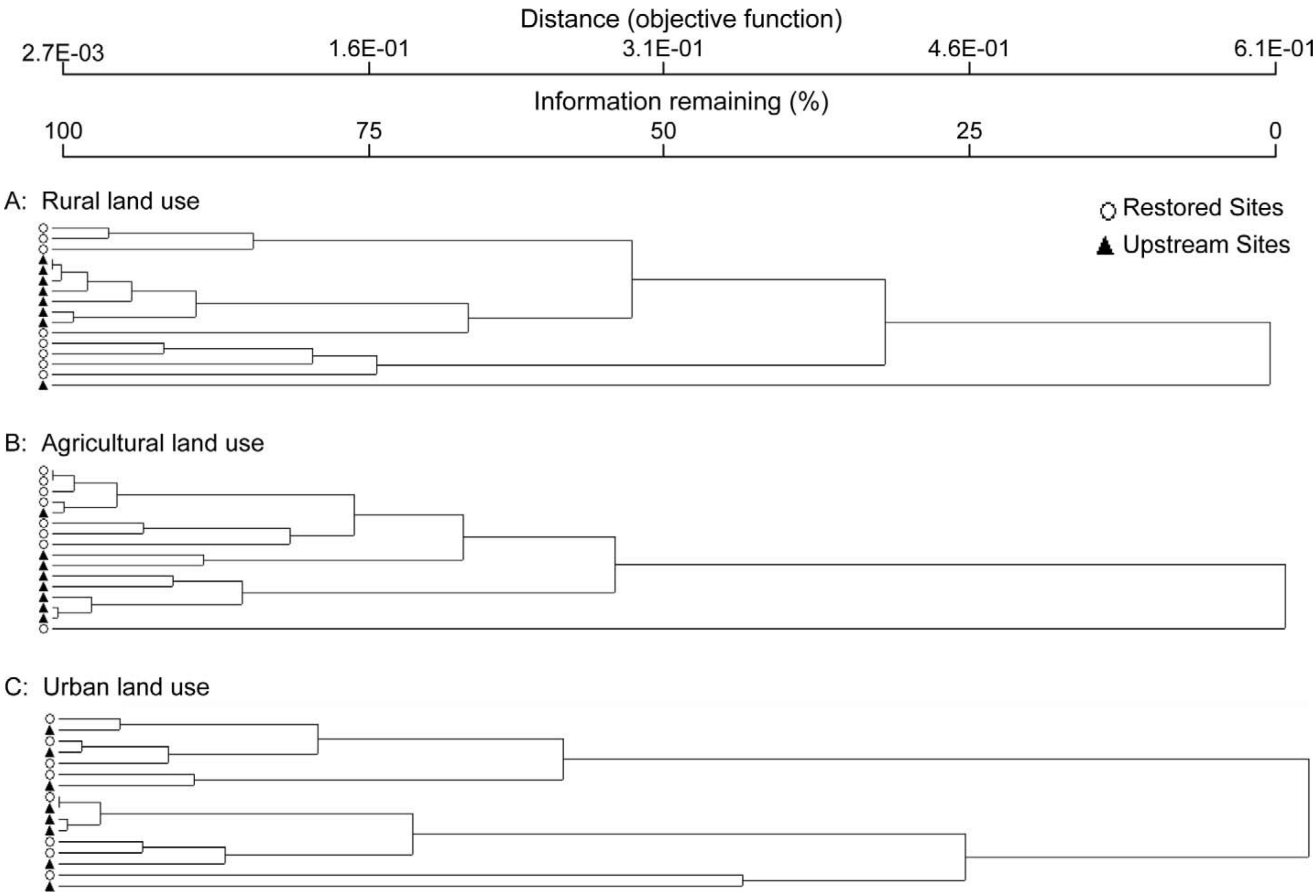

FIG. 2. Dendrograms (Sørenson distance) for functional-trait relative abundances of macroinvertebrate assemblages in paired upstream (control) and downstream (restored) reaches of 8 channel reconfiguration sites in rural (A), agricultural (B), and urban (C) catchments in North Carolina (24 sites total).

Chironomidae, Baetidae, Hydroptilidae, and Simuliidae, were high in both control and restored reaches in urban catchments compared to in rural and agricultural catchments, and illustrate the loss of taxonomic diversity within urban catchments (Fig. 1C). In urban catchments, relative abundances of these 4 families differed by <5 percentage points between control and restored reaches, and suggest that restoration activities had little effect on taxonomic composition at reaches in urban catchments.

Some of these patterns in family composition also were reflected in the indicator species analysis. For example, *Chironomus* was a good indicator (IV = 72, α = 0.04) for restored reaches in rural catchments, whereas *Baetis* was a relatively good indicator (IV = 57, α = 0.04) for restored reaches in agricultural catchments. In contrast, *Helichus* (IV = 63, α = 0.02) was a reliable indicator for control reaches in rural catchments, and *Dixa* was a reliable indicator of control reaches in agricultural (IV = 60, α = 0.03) and rural (IV = 67, α = 0.009) catchments.

Functional traits of control and restored reaches

Control and restored reaches tended to group separately in cluster dendrograms in rural (Fig. 2A) and agricultural (Fig. 2B) catchments, but not in urban (Fig. 2C) catchments. This suggests that functional traits of macroinvertebrates differed between control and restored reaches in agricultural and rural catchments, but not in urban catchments.

Relative abundances of functional traits differed between control and restored reaches within rural and agricultural catchments, but not within urban catchments (Table 3). In rural catchments, relative abundances of fast seasonal development, very short adult life spans, abundant occurrence in drift, very low maximum crawling rate, medium size at maturity, and collector-gatherer trophic habit were significantly

TABLE 3. Functional-trait relative abundances at paired upstream (control) and downstream (restored) reaches of 8 channel reconfiguration sites in rural and agricultural catchments in North Carolina (16 sites total). Only significant (α = 0.05) differences between the upstream and restored sites are shown. Trait assignments are based on Poff et al. (2006). Δ indicates direction of change in relative abundance at restored reaches relative to control reaches. + indicates higher relative abundance at restored reaches, − indicates lower relative abundance at restored reaches.

		Rural				Agricultural			
Functional trait	Trait state	Control	Restored	*p*	Δ	Control	Restored	*p*	Δ
Life history									
Voltinism	Univoltine					0.64	0.48	0.02	−
	Multivoltine					0.26	0.43	0.01	+
Development	Fast seasonal	0.40	0.62	0.03	+				
	Slow seasonal	0.58	0.36	0.03	−				
Synchronization of emergence	Poor					0.29	0.40	0.00	+
	Well					0.71	0.59	0.00	−
Adult life span	Very short	0.43	0.65	0.01	+				
Mobility									
Occurrence in drift	Rare	0.29	0.19	0.03	−	0.36	0.21	0.05	−
	Abundant	0.23	0.47	0.02	+	0.28	0.42	0.03	+
Maximum crawling rate	Very low	0.26	0.46	0.04	+				
	Low	0.53	0.371	0.05	−				
Swimming ability	Strong					0.17	0.30	0.00	+
	Weak					0.34	0.21	0.01	−
Morphology									
Size at maturity	Small	0.51	0.32	0.04	−				
	Medium	0.34	0.57	0.02	+				
Ecology									
Habit	Sprawl	0.08	0.04	0.01	−				
	Cling					0.58	0.44	0.02	−
	Swim					0.18	0.30	0.00	+
Trophic	Collector-gatherer	0.31	0.48	0.05	+	0.33	0.45	0.05	+
	Shredder	0.07	0.02	0.00	−				
	Herbivore					0.19	0.08	0.05	−

greater in restored than in control reaches, whereas relative abundances of slow seasonal development, rare occurrence in drift, low crawling rate, small size at maturity, sprawling habit, and shredder trophic habit were significantly greater in control than in restored reaches. In agricultural catchments, relative abundances of multivoltinism, poorly synchronized emergence, abundant occurrence in drift, strong swimming ability, swimming habit, and collector-gatherer trophic habit were significantly greater in restored than in control reaches, whereas univoltinism, well-synchronized emergence, rare occurrence in drift, weak swimming ability, clinging habit, and herbivore trophic habit were significantly greater in control than in restored reaches (Table 3). These differences in trait abundances in the agricultural and rural catchments generally suggest that an effect of restoration is to favor organisms with rapid population turnover, a tendency to drift, and habitat preferences that require greater swimming than crawling and clinging abilities. Collector-gatherers were abundant in restored reaches in both rural and agricultural catchments and appear to have replaced shredders in agricultural catchments and herbivores in rural catchments.

In rural and agricultural catchments, differences in relative abundances of functional traits between control and restored reaches were generally consistent with the results of the indicator taxon analysis. In rural catchments, *Helichus* and *Dixa* were reliable indicators of control reaches. These taxa, characterized by slower development, longer adult life spans, and rarer drift occurrence, generally are not found in heavily disturbed and impaired habitats. In contrast, *Chironomus* was a reliable indicator of restored reaches. This taxon is a common colonizer of recently disturbed habitats, and its presence suggests that restored reaches favor taxa associated with a disturbed environment. In agricultural catchments, *Dixa* was a good indicator of control reaches, whereas *Baetis* was a characteristic taxon in restored reaches. *Baetis* has a short adult life span, multivoltine reproduction, and abundant occurrence in drift, and tends to be an early recolonizer following disturbance (Vieira et al. 2006).

Discussion

Channel reconfiguration as a disturbance filter

We used functional traits to interpret how restoration modified local filters on community assembly during channel recovery. In general, both indicator species analysis and functional-trait differences indicated that channel reconfiguration in rural and agricultural catchments produced conditions favorable for organisms characterized by traits, such as multivoltinism, short adult life span, and rapid reproduction, that confer resistance or resilience to disturbance (Townsend et al. 1997b, Diaz et al. 2008). These results suggest that channel reconfiguration acts as a filter against organisms that require stable habitats in which to complete their life cycles in systems (nonurban) where disturbance regimes have not already been modified greatly.

Poff et al. (2006) showed that some functional-trait states are correlated and might be constrained such that the state of one trait influences the state of another. Such traits are poor indicators of environmental change, emphasizing the value of phylogenetically unconstrained (labile) traits for understanding mechanisms behind community responses to a changing environment. Subsequent work showed that phylogenetically unconstrained traits are more reliable than constrained traits for evaluating the effects of environmental filters (Cavender-Bares et al. 2004). Several of the functional traits that differed between control and restored sites in our study were identified by Poff et al. (2006) as phylogenetically unconstrained (e.g., trophic habit, habitat preference, occurrence in drift, maximum crawling rate, and voltinism). Thus, we are confident that the differences we detected in functional traits reflect differences in environmental filters between control and restored reaches.

Broad environmental change in aquatic habitats can impose 3 primary selective filters: thermal regime, food resources, and habitat stability (Poff et al. 2006). We do not know whether channel reconfiguration changed thermal regimes at our sites because we did not measure temperature. Further, we observed no differences in functional traits related to thermal preferences between control and restored reaches in any landuse group. The absence of such differences in rural and agricultural catchments could be interpreted as a benefit of the channel reconfiguration (i.e., restoration of a natural thermal regime in reconfigured channels), but we also observed no differences in urban catchments where divergence from control would be evidence of a benefit. Thus, any conclusions regarding the influence of channel reconfiguration on the thermal regime are not strongly supported.

We can interpret differences in functional traits related to food resources and habitat stability filters with more confidence. Channel reconfiguration led to differences in taxonomic composition and functional-trait abundances between control and restored reaches in rural and agricultural catchments. Individuals in restored reaches were highly mobile, able to reproduce and grow rapidly, and opportunistic in habitat and food preferences. These characteristics are favorable in disturbed environments. Thus, channel reconfiguration appears to be a disturbance that imposes food-resource and habitat-stability filters in stream ecosystems.

Other lines of evidence in our study suggest that channel reconfiguration imposed a disturbance on aquatic communities following construction. Tolerant taxa appear to replace intolerant taxa in restored reaches in rural and agricultural catchments (Fig. 1A, B). Indicator species analysis suggests a disturbance signal associated with channel reconfiguration. Sensitive taxa (*Dixa* and *Helichus*) were characteristic of control reaches, whereas tolerant taxa (*Chironomus* and *Baetis*; Brigham et al. 1982, Townsend and Hildrew 1994, Merritt and Cummins 1996, Statzner et al. 1997, Lamouroux et al. 2004) were characteristic of restored reaches.

Landscape context in evaluating restoration impacts

Catchment land use strongly influenced the channel reconfiguration signal in our study. In rural and agricultural catchments, causes for channel reconfiguration tended to be local (e.g., bank hardening, damage caused by livestock grazing) rather than catchment-wide. The signal in restored reaches indicated that channel reconfiguration was a disturbance. Thus, the effects of channel reconfiguration in relatively undisturbed catchments might be positive in the long term, but they appear to be detrimental over the short term.

Ecosystem responses to disturbance often are determined by the variability and severity of established disturbance regimes (Poff and Ward 1990). Biological assemblages in relatively undisturbed environments should respond to anthropogenic disturbances (Holling 1973, Connell and Sousa 1983, Resh et al. 1988). In contrast, taxa able to persist in modified and highly variable environments respond more modestly to disturbances than do taxa in natural and more stable environments (Levins 1968, Holling 1973). The dominant taxa and functional traits at our urban sites, both upstream and restored, reflected existing pressure from the urban watershed; i.e., taxa were behaviorally and physiologically flexible with opportunistic life-history traits (Pianka 1970, Poff and Ward 1990). Thus, the biological response to channel reconfiguration in urban reaches might have been minimal because the biota already had been filtered by the effects of urbanization (Paul and Meyer 2001, Konrad and Booth 2005). Thus, the limited improvement in habitat and biological diversity following restoration of urban reaches probably is related to catchment-wide stressors that dominate local-scale filtering processes. This result has implications for the success of restoration activities in urban streams where modified hydrology and water quality at the catchment scale might reduce the effectiveness of instream restoration (Walsh et al. 2005).

Community context in evaluating restoration impacts

Biotic and abiotic responses to channel reconfiguration often were inconsistent with each other. For example, in rural catchments, habitat conditions and biodiversity were similar between control and restored reaches and indicated improved conditions in restored reaches. However, taxonomic and functional-trait composition differed between control and restored reaches in ways that suggested differences in habitat and food resource filters (i.e., a restoration disturbance signal). We see 2 possible explanations for the apparent decoupling of biotic and abiotic responses. 1) Physical-habitat assessments and biodiversity measures might be insensitive indicators of processes driving habitat stability and ecosystem functioning when used as a static snapshot of general condition. 2) Physical-habitat assessments and biodiversity measures might respond faster than taxonomic and functional-trait composition to restoration. Thus, assemblages might still have been recovering from the disturbance associated with project construction, and recolonization by taxa requiring more stable habitat and food resources might not have been complete. It would be useful to know how long disturbance-related taxa and functional traits persist following construction and whether increased habitat diversity and stability of restored channels will increase the relative abundances of habitat specialists (Poff and Allan 1995) and traits unrelated to disturbance (Townsend et al. 1997a). However, continued long-term monitoring is needed to address these questions.

Our study emphasizes the value of using several lines of evidence when evaluating the effectiveness of channel reconfiguration. Compositional and functional differences suggest that channel reconfiguration is a disturbance filter, at least for the years immediately following construction. This result is important because an initial disturbance signal could influence the ability of evaluators to determine the ecological success of a restoration. Moreover, this disturbance signal might provide justification for restoration designers to consider more passive strategies for restoration in areas where abandoning an existing channel is not necessary. However, a disturbance signal was not evident in standard habitat assessment and biodiversity measures. These summary statistics are valuable in reach-wide assessments of general ecosystem condition, but they might be inadequate for evaluation of responses to restoration (Tullos et al. 2006). Moreover, representing community diversity by summary measures is not always appropriate (Ludwig and Reynolds 1988). In contrast, functional analysis of invertebrate traits can be used to distinguish between reference and impacted sites (Charvet et al. 1998, Dolédec et al. 1999, Statzner et al. 2001) and offers mechanistic explanations of effects based on filtering of species attributes by environmental change (Richards et al. 1997). Furthermore, functional-trait analysis may be applied to monitoring restoration activities to identify ways to modify environmental filters driving degradation at local and catchment scales. Assessments based on invertebrates provide specific and causal knowledge (Lake et al. 2007), and monitoring the effectiveness of restoration projects is a learning opportunity (Muotka et al. 2002, Moerke et al. 2004). Therefore, we recommend using functional traits in addition to other measures of physical and biological change to gain insight into mechanisms and processes driving restoration outcomes.

Limitations and applications

We recognize that our statistical approaches were simplistic investigations of complex ecosystems. We considered traits individually and disregarded the complex analytical and theoretical work necessary to untangle interactions and tradeoffs among traits (Roff 1992, Stearns 1992). We did not fuzzy-code our data, and we analyzed all traits, regardless of their evolutionary lability. Moreover, no prerestoration data were available for any of our 24 sites. Nevertheless, our results strongly suggest that channel reconfiguration imposes a disturbance on aquatic communities during the years immediately following construction, that catchment land use filters biological responses to restoration activities, and that substantial value exists in using multiple approaches to monitor the effectiveness of restoration activities.

Our results support application of functional-trait analysis in planning, implementing, and evaluating restoration activities. We emphasize the importance of thorough and mechanistic evaluations of pre- and post-project condition of benthic macroinvertebrate assemblages. Functional-trait analyses offer muchneeded mechanistic explanations of the consequences of simplification and degradation that lead to the need for restoration. If we view channel reconfiguration as a modifier of local environmental filters and understand functional traits associated with those filters, we can: 1) use preproject monitoring to identify missing ecosystem functions to define and target restoration objectives and approaches, 2) develop restoration designs to modify specific environmental filters to maximize the functionality and diversity of the river, and 3) improve postimplementation assessment with informed expectations for recovery duration and trajectory.

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