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Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration

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Abstract

Headwater streams channelized for water transport of timber in Finland are being restored to their pre-channelization state. The primary motivation is the enhancement of sport fisheries, but restoration probably has profound impacts also on other stream organisms. We assessed how such "single-goal" restorations affect benthic macroinvertebrate communities. We revisited the streams sampled by Laasonen et al. [Aquatic Conservation: Marine and Freshwater Ecosystems 8 (1998)] in the early 1990s when the streams had been recently restored. In 1997, the recovery period of these streams ranged from 4 to 8 years. Habitat structure among the stream types represented a distinct recovery gradient, with streams restored 1 month before sampling and natural streams being the endpoints of a gradient in moss cover (highest in natural, lowest in recently restored streams). Channelized streams supported a characteristic set of indicator species, whereas shifts in species composition between restored and natural streams were more gradual. Macroinvertebrate communities in unmodified streams changed little between the two surveys, whereas communities in restored streams had undergone considerable changes. In-stream restoration is an unpredictable disturbance, to which stream biota cannot have any evolved responses. Therefore, the relatively rapid recovery of habitat structure and macroinvertebrate communities in restored streams is encouraging. However, long-term monitoring of benthic communities in both restored and natural streams is needed to assess whether restoring rivers by these techniques will enhance the recovery of benthic biodiversity in boreal streams. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Channelization is globally one of the major factors causing stream habitat loss and degradation, being thus a serious threat to biodiversity of running water ecosystems (Petersen et al., 1987; Allan and Flecker, 1993). Streams have been channelized for diverse purposes, but consequences to habitat structure and ecosystem functioning are much the same: channelization results in loss of structural complexity, simplified flow patterns, and decreased availability of microhabitats for a wide array of lotic organisms (Petersen et al., 1987). From an ecosystem point of view, one of the most important consequences of channelization is the radical impairment in stream's retentive capacity to allochthonous inputs. Stream ecosystems in forested areas are dependent on the pulsed input of riparian coarse (CPOM) particulate organic matter, part of which is retained by debris dams, aquatic vegetation, cobble ridges, and other bed structures abundant in natural woodland streams (Cummins et al., 1989; Smock et al., 1989; Wallace et al., 1999). Such retentive structures are lost through channelization, resulting in weakening of the aquatic-terrestrial linkage and potentially far-reaching effects on stream ecosystem dynamics (Petersen and Petersen, 1991).

In many parts of the world, considerable effort has now been directed to restoring these degraded streams closer to their natural state. Unfortunately, with the exception of game fishes, little is known about the effects of restoration on stream biota. In particular, observations of long-term responses of stream organisms to habitat restoration are sorely needed, yet are largely lacking at present.

A vast majority of small to medium-sized streams in Finland was dredged in the 1950s and 1960s to facilitate

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water transport of timber. Channelization involved removal of all major impediments to log floating, for example, debris dams, large boulders, etc. This resulted in a radical loss of retention potential to riparian litter inputs (Muotka and Laasonen, unpublished). Log floating became economically infeasible by the late 1970s, and extensive restoration programs have been initiated thereafter to restore these degraded streams to their original, pre-channelization state. The goal is to make the stream bed more heterogeneous, and this is mainly achieved by adding various restoration structures, for example, boulder dams and flow deflectors, to stream channels. Gravel beds are also commonly used to provide trout with better spawning habitats (for a description of the restoration practices used in Finland, see Yrjänä, 1998). Thus, the primary, if not the sole, motivation for stream restoration has been the enhancement of sport fisheries. In this respect, the few tests carried out so far suggest that restoration might indeed benefit salmonid fishes, mainly by increasing the amount of habitat suitable for the youngest age classes (Huusko and Yrjänä, 1997). It is obvious, however, that such intensive habitat modification must have profound impacts on stream organisms other than fish. In a set of leaf release experiments, Muotka and Laasonen (unpublished) showed that in-stream restoration does enhance the retention efficiency of a stream to leaf inputs, and that this improvement is brought about by increased bed heterogeneity. However, this positive effect is almost counterbalanced by the loss of aquatic mosses during restoration works. In addition to being a key retentive structure in many headwater streams, mosses perform many other important ecosystem services (e.g. retention of fine particles, provision of flow refugia for invertebrates; Suren and Winterbourn, 1992). Therefore, the recovery of aquatic mosses after in-stream restoration has potentially wide-ranging consequences on other components of stream biota, as well as on stream ecosystem processes. Unfortunately, little is known about the recolonization rates of aquatic mosses, rendering the prediction of macroinvertebrate community recovery problematic.

Our prime objective in this study was to evaluate how "single-goal" restorations aiming at the enhancement of salmonid fisheries affect other stream biota, using benthic macroinvertebrates as our target organisms. For this purpose, we revisited the streams sampled by Laasonen et al. (1998) in the early 1990s when these streams had been recently (1 month–3 years) restored. Since 3 years is clearly too short a time interval for invertebrate communities to recover from restoration works, we resampled these streams in 1997 when the recovery period ranged from 4 to 8 years. Specifically, we attempted to answer two questions: (1) do the invertebrate assemblages of restored streams differ from those in channelized streams? and (2) do they resemble communities in near-pristine streams, i.e. does restoration enhance the recovery of benthic biodiversity?

2. Materials and methods

2.1. Study sites and sampling protocol

In October 1997, we revisited the streams sampled by Laasonen et al. (1998). We thus had streams restored 4, 6 or 8 years ago, three streams for each group (two for streams restored 4 years ago, cf. +0 streams in Laasonen et al., 1998). In addition, we had two groups of streams (n = 3 for each) that were used as regional references for the restored streams: channelized and natural streams in the same or a contiguous river system. Obviously, any changes in invertebrate community structure in restored streams can only be envisaged relative to channelized, non-restored streams. However, if achieving a natural, or at least near-pristine, ecosystem is the goal of restoration, then changes in restored streams should also be examined in relation to unmodified (non-channelized) streams. It is important to point our here that most headwater streams in northern Finland have been under heavy forestry practices, and their riparian zones have been frequently disturbed by timber harvest and forest draining, especially during the 1950s to 1980s. Therefore, although current legislation provides better protection for stream-side forests, these are still far from mature, and the streams, even if otherwise unmodified, receive little large woody debris, resulting in almost debris-free channels. Thus, streams referred to as "natural" in this study are not truly pristine, because their catchments have been disturbed by forestry activities. Nonetheless, they have unmodified, heterogeneous stream beds, and therefore a higher retention potential than streams channelized for timber floating.

The three natural streams sampled by us were the same as in Laasonen et al.'s (1998) survey, but two of the three channelized streams of that study had been restored before our sampling. We therefore selected, in addition to the one channelized stream still remaining in that condition, two new streams from the same stream system. These streams had been channelized in the 1950s but had not been restored by 1997.

All the streams included in this study drain forested lowland areas, and their riparian zones are dominated by deciduous trees, especially birch (*Betula pubescens*), alder (*Alnus incana*), aspen (*Populus tremula*) and willows (*Salix* spp.). They are circumneutral, oligotrophic headwater (second to third order) streams of two northern boreal drainage systems, rivers Iijoki and Oulankajoki. A more detailed description of the sampling sites and their riparian conditions is given in Laasonen et al. (1998).

The sampling protocol closely followed that used by Laasonen et al. (1998). Samples of benthic invertebrates were collected using the kick-sampling method (net frame 25×25 cm, mesh size 0.25 mm), four timed (1 min) samples being taken at each site. All sampling was done by the same person, and the distance kicked along the stream was exactly 1.0 m for each sample. Samples were preserved in 70% ethanol in the field, and invertebrates were later sorted in the laboratory. Animals were identified to the lowest feasible taxonomic unit, usually species. Simuliids and chironomids were identified only to the family level and were therefore excluded from all statistical analyses. Taxa were assigned to functional feeding groups according to Malmqvist and Brönmark (1985) and Merritt and Cummins (1996).

To quantify changes, if any, in stream habitat structure during the time elapsed since restoration, we measured a number of habitat variables at each site. These were measured for a larger number of sites than included in the benthic sampling; i.e. all second to third order streams of each stream type present in the two stream systems (Rivers Iijoki and Oulankajoki). The sample size per stream group varied from four to six. To characterize the stream habitat structure, we used a stratified random sampling protocol. At each site, we measured water depth (D), water velocity (at $0.6 \times D$), substrate size (largest stone dimension), and moss cover (% cover in 0.25-m^2 quadrats) at 30–50 random points along evenly spaced transects perpendicular to the flow. Stream bed heterogeneity was quantified as bed roughness (k) using a bed profiler modified from Young (1993). The device was 50 cm long, consisting of a continuous row of measuring rods (diameter 0.8 mm). Measurements were made in 1.5-m longitudinal transects, each consisting of three successive 50-cm sections. To obtain a measurement, the device was pressed firmly against the bottom and distance from a horizontal support was measured for each rod. The standard deviation for the length of the rod below the support was calculated as an indicator of substrate roughness for each transect (Statzner et al., 1988), and the mean roughness value across eight 1.5-m transects was calculated for each site. Relative bed roughness, k/D, was used to describe bed heterogeneity (Gordon et al., 1992). Finally, the amount of leaf litter accumulated on the stream bed was quantified by collecting all leaves and leaf fragments from eight randomly placed 0.1-m^2 quadrats at each site. Leaves were dried at 60 °C for 24 h, and weighed to obtain their dry masses.

2.2. Data analyses

Although we were mainly interested in the responses of macroinvertebrate community structure to stream habitat restoration, we first inspected our data for any potential density responses. We used one-way ANOVA

to test for differences among stream groups in the amount of benthic leaf litter (no transformation needed) and densities of two groups of aquatic invertebrates, (1) all detritivorous invertebrates (shredders + collector-gatherers + collector-filterers); and (2) leaf-shredding invertebrates (both $\ln(x+1)$-transformed). We focused on these groups of invertebrates because, on theoretical grounds (Cummins et al., 1989; Dobson and Hildrew, 1992), they could be expected to be directly affected by the enhanced retentive capacity caused by in-stream restoration.

Among-group differences in stream habitat characteristics were examined using discriminant function analysis (DFA). All variables were appropriately transformed (log or arcsine) before entering the analysis. ANOVA, followed by Tukey's test for pairwise differences, was performed on the canonical scores of the sampling sites to find out whether differences in habitat structure among stream types were significant. In addition to the basic data set (streams restored 4, 6 and 8 years ago, plus channelized and natural streams), DFA was also run on data including five recently (i.e. 1 month ago) restored streams. This was done to visualize as effectively as possible the whole recovery gradient from recently restored to unmodified streams.

We used the indicator value method (IndVal) of Dufrene and Legendre (1997) to characterize faunal differences between our a priori stream groups. This method is based on the comparison of relative abundances and relative frequencies of occurrence of taxa in different groups of sites, and it identifies indicator taxa that vary more between groups than would be expected by chance. It is based only on within-species comparisons, independent of the occurrence of other species. The index varies between 0 and 100, and it attains its maximum value when all individuals of a species occur in a single group of sites, and when the species occurs in all sites of that group. The method thus selects indicator species based on both high specificity for and high fidelity to a specific group. IndVal is considered superior to more traditional methods of identifying indicators (e.g. TWINSPAN) on both statistical and practical grounds. For example, it is robust to differences in within-group sample sizes and differences in abundances across species. Furthermore, it allows the significance of individual indicator taxa to be tested using a randomization procedure (Legendre and Legendre, 1998). It therefore has strong appeal in conservation and monitoring studies, and has been recommended to be used when site changes are being monitored (McGeoch and Chown, 1998).

We tested the significance of each invertebrate taxon as an indicator for a stream group using Monte Carlo tests with 1000 permutations. Before any attempt to identify indicator species for stream groups, Multi-response Permutation Procedures (MRPP; Zimmerman et al., 1985; Biondini et al., 1988) were used to test for

significant differences in the invertebrate communities among the a priori stream groups. MRPP is a data-dependent permutation test based on pairwise distance measures, and it is highly appealing for ecological contexts because it makes few assumptions about the distribution structure of the populations under study. The null distribution of the test statistic (R) is based on the collection of all possible permutations of the objects into groups of specified sizes. R (chance-corrected within-group similarity) obtains the maximum value of 1.0 when communities within the predetermined groups do not differ; $R = 0$ when the within-group community heterogeneity equals that expected by chance, and $R < 0$ when heterogeneity exceeds that expected by chance (McCune and Mefford, 1995). As the distance measure in MRPP, we used Sorensen metrics on log-transformed species data.

We applied non-metric multidimensional scaling (NMDS) on data combining samples from Laasonen et al.'s (1998) study and this study. Our goal was to provide an effective visual summary of site-specific changes in benthic community structure by including samples from both studies in the same ordination space. We were primarily interested in seeing whether the macro-invertebrate communities of restored streams converge more on those in natural streams as the recovery period gets longer. NMDS is an ordination method based on ranked distances between samples, and it is highly suitable for ecological data that typically contain numerous zero values (Minchin, 1987). First, a distance matrix was constructed using Sorensen's metrics. To reduce the chance of local optima (Legendre and Legendre, 1998), 10 random starts were carried out, and the one with the lowest stress value was used as the starting configuration for NMDS. A three-dimensional solution was accepted, because change in the stress value (a measure of the monotonicity in the relationship between the distance in the original sample space vs. the reduced ordination space; McCune and Mefford, 1995) was negligible on subsequent dimensions. All species data were log ($\ln x + 1$) transformed before entering the analysis. It is a common practice in ecological applications to exclude rare species from multivariate analyses. We did not do this, however, because it has been argued that omitting rare species may hinder the detection of ecologically meaningful gradients (Cao et al., 1998). Moreover, we ran our analysis also with rare species (occurring in $< 5\%$ of samples) excluded, and this did not affect interpretation of the results. Thus, NMDS appears to cope well with rare species and there is little to be gained by excluding them from the analysis (see also Faith and Norris, 1989).

All multivariate analyses were conducted using the PC-Ord computer package (Version 2.0, McCune and Mefford, 1995), with the exception of DFA which was conducted on SPSS 7.5 for Windows (SPSS Inc., 1997).

Finally, we assessed the persistence in species ranking for all the sites that were sampled in both studies. This was done by calculating Spearman rank correlation between the abundances in 1992/1993 and 1997 of the 15 or 20 species that were most abundant on the earlier sampling occasion (Townsend et al., 1987). Our hypothesis was that benthic communities at restored sites would be more variable in community composition and species' relative abundances than natural communities.

3. Results

3.1. Density responses

Stream types differed significantly in the amount of benthic leaf litter (one-way ANOVA, $F_{4,10} = 5.157$, $P = 0.016$), with streams restored 8 years ago and natural streams supporting significantly higher litter standing stocks than the channelized streams (Tukey's test, $P < 0.05$; see Fig. 1A). Densities of detritivorous (Fig. 1B) and shredding (Fig. 1C) invertebrates were also highest in the natural and $+8$ streams, but, due mainly to high within-group variability and associated low statistical power, differences among stream types were not significant (one-way ANOVA, $P > 0.20$ for both groups; power to detect significant differences if any existed: 0.28 for detritivores, 0.30 for shredders).

3.2. Stream habitat characteristics

Habitat structure among the stream types represented a distinct recovery gradient. This was especially well illustrated by DFA including samples from recently (1 month ago) restored streams ("$+0$ streams" in Fig. 2A). Here, the $+0$ streams and natural streams were the endpoints of a gradient related mainly to moss cover, with highest cover in the natural and $+8$ streams, and lowest in the $+0$ streams (Table 1). However, the same predominant gradient emerged even when the $+0$ streams were omitted from the analysis, the "low moss" endpoint being taken by the $+4$ streams (Fig. 2B). In both analysis, the second DFA axis was mainly related to bed complexity, and the main distinction was between the channelized (low roughness value) vs. natural and $+4$ streams (high bed roughness; see Table 1). This distinction, however, was significant only when the $+0$ streams were omitted from the analysis (Fig. 2B).

3.3. Community patterns

MRPP test showed highly significant among-group differences ($R = 0.1463$, $P < 0.001$), indicating that invertebrate communities in our a priori stream groups were distinctly different. Species characteristic for each
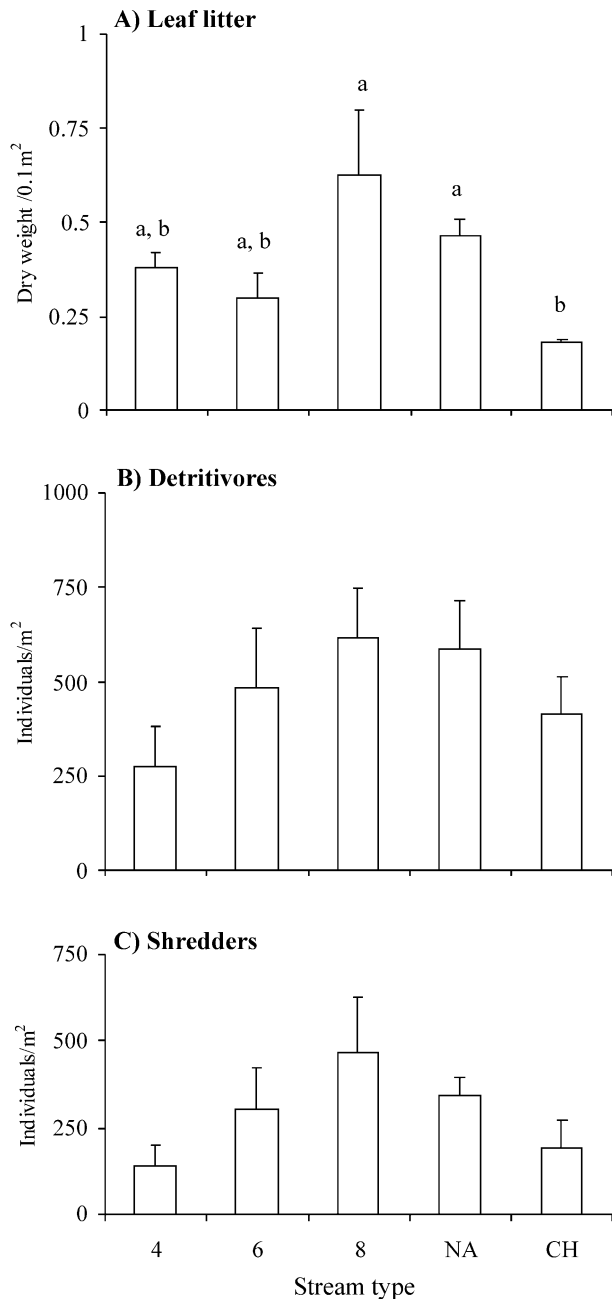
Fig. 1. The standing stock of benthic leaf litter (A) and densities of all detritivorous (B) and shredding (C) invertebrates in various stream groups. Vertical bars indicate 1 S.E. Groups sharing a letter do not differ significantly (Tukey's test, $P < 0.05$).

group are shown in Table 2. The most efficient indicators (almost all individuals present in only one group, occupying all sites in that group; "sympatric" indicators sensu Dufrene and Legendre, 1997) were for channelized streams. For example, filter-feeding invertebrates (e.g. the freshwater mussel *Sphaerium* sp. and the caddis larva *Hydropsyche siltalai*) showed high specificity for this stream type (index value = 91% for both taxa). This group was also characterised, though more vaguely so, by the mayflies *Baetis rhodani* and *Heptagenia sul-*

phurea, and the coleopteran *Elmis aenea*, species commonly described as grazers, i.e. invertebrates feeding on algae and fine detritus on sediment surfaces. The higher heterogeneity of the other stream groups is revealed by the generally lower indicator values of taxa in these groups (Table 2). Four out of the five indicator species for the +8 streams were leaf-shredding invertebrates, whereas the natural streams were characterised by a functionally variable group of invertebrates, including filter-feeders (*Hydropsyche saxonica*), collector-gatherers (*Ameletus inopinatus*; Scirtidae), as well as strictly predatory (*Rhyacophila obliterata*) taxa.

NMDS ordination where the two sampling occasions [Laasonen et al. (1998) vs. this study] were directly compared (Fig. 3A, B) indicates that macroinvertebrate communities in the natural streams changed relatively little between the 2 years, whereas most of the restored streams had undergone considerable changes in community structure. Taxon richness changed very little between the two sampling occasions in the natural and +8 streams (an average increase of 2.7 and 0.3 taxa, respectively), but varied drastically in the +4 and +6 streams (10.0 and 10.7 more taxa in 1997 than 1992/1993; Table 3). Rank correlations between species rankings (across the 15 or 20 taxa most abundant at each site in the earlier survey) in the two sets of samples showed that while macroinvertebrate communities in the natural streams were extremely persistent (high rank correlations), species composition in streams restored 4–6 years ago had changed considerably. Streams restored 8 years ago seemed to vary less than the more recently disturbed streams (Table 3). It thus appears that macroinvertebrate communities vary drastically during the first few years after restoration (+0 and +1 streams in Laasonen et al.'s survey vs. +4 and +6 streams, respectively, in this study), but soon turn more persistent with less year-to-year variability in species composition and species' relative abundances (+3 streams in Laasonen et al. vs. +8 streams in this study).

4. Discussion

The initial goal of restoration in our study streams was to increase habitat heterogeneity, and this was clearly achieved by the enhancement structures used. This, however, incurred a cost: the use of heavy machinery during restoration works caused a drastic loss of mosses and other aquatic vegetation. Mosses have a key role in the trophic dynamics of many woodland streams, not so much because they are directly consumed by herbivores, but more because of their indirect importance as beneficial microhabitats for benthic invertebrates (Suren and Winterbourn, 1992). The loss of mosses during restoration works radically impairs the retention potential of a stream to organic
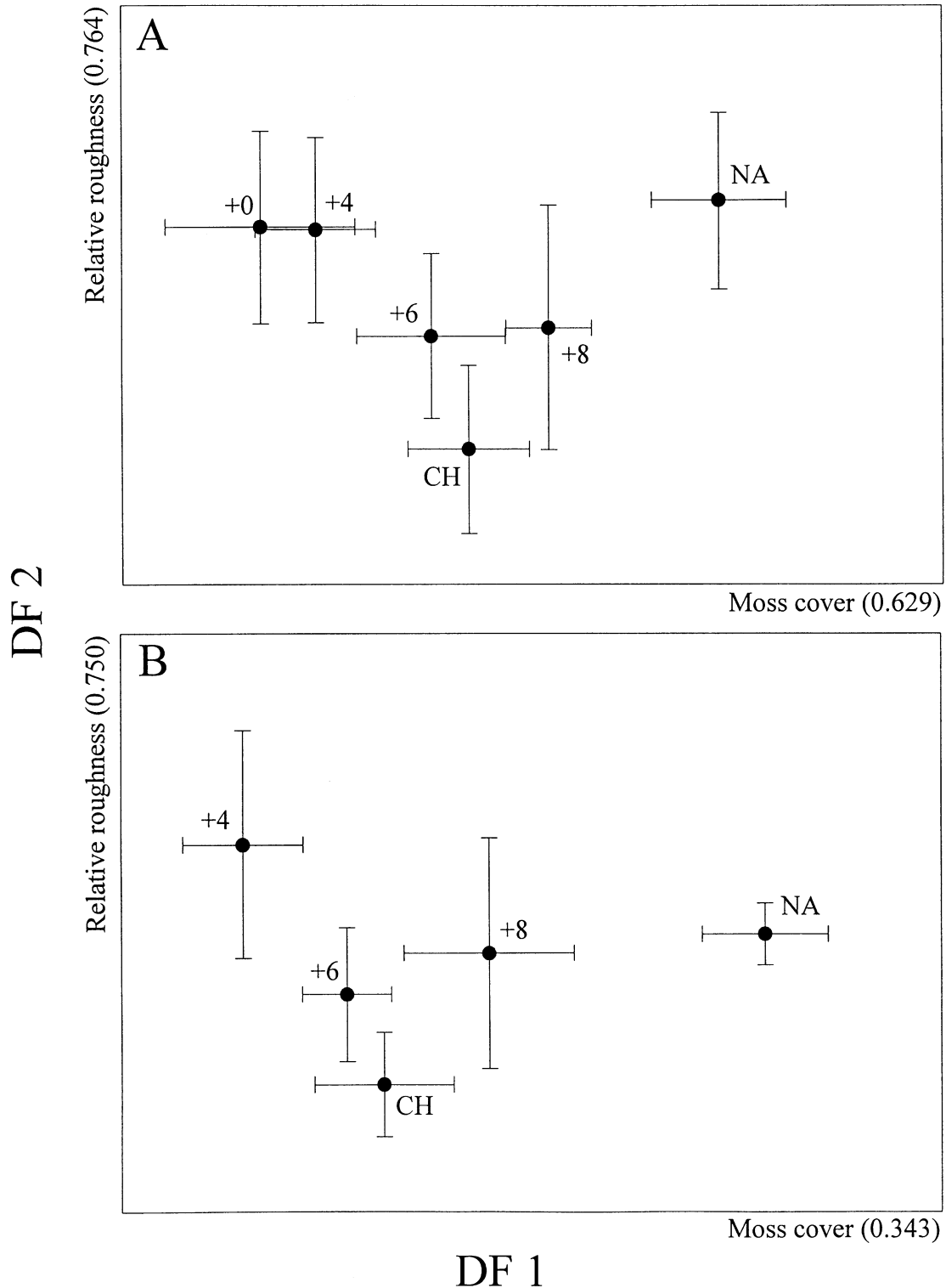
Fig. 2. Discriminant function analysis of stream habitat characteristics; (A) +0 streams (restored 1 month before sampling) included, (B) +0 streams excluded. Numbers refer to years elapsed since restoration; CH, channelized streams; NA, natural streams. One-way ANOVA on DF1 site scores in (A) showed highly significant overall difference among the stream types ($F_{5,20} = 25.80$, $P < 0.001$). Pairwise comparisons (Tukey's test, $P <$ 0.05) revealed the following homogeneous groups: NA; +8, CH, +6; +6, +3; +3, +0 (underlining indicates no significant differences among the stream types). ANOVA on DF2 site scores was non-significant ($P < 0.15$). In (B), ANOVA on DF1 scores was highly significant ($F_{4,17} = 39.10$, $P < 0.001$), with natural streams differing from the other stream types (Tukey's test, $P < 0.05$). ANOVA on DF2 scores was also significant ($F = 5.06$, $P = 0.007$), the only significant pairwise difference being between the channelized and +4 streams (Tukey's test, $P < 0.05$).

Table 1
Habitat characteristics (means and ranges, $n = 4$–6) of the stream groups[a]

	Water depth (cm)	Flow rate (cm/s)	Relative bed roughness	Moss cover (%)	Substrate size (cm)
+0	36 (26–55)	38 (24–60)	0.29 (0.25–0.38)	6 (3–11)	17 (12–20)
+4	39 (30–46)	41 (27–54)	0.24 (0.23–0.26)	19 (13–28)	26 (23–32)
+6	38 (30–49)	42 (37–52)	0.22 (0.18–0.32)	40 (22–59)	17 (15–20)
+8	35 (28–39)	49 (41–60)	0.27 (0.19–0.38)	76 (73–85)	27 (19–33)
CH	37 (30–50)	56 (55–57)	0.19 (0.14–0.22)	65 (50–80)	16 (14–17)
NA	27 (21–37)	38 (31–46)	0.35 (0.33–0.38)	71 (48–92)	30 (22–36)

[a] Grouping is based on the number of years elapsed since restoration; CH, channelized streams; NA, natural streams. Relative bed roughness is the ratio of k/D (substrate roughness/water depth; see Gordon et al., 1992). For substrate size, the largest stone dimension is reported.

Table 2
Indicator values (IndVal) for the most important taxa in each a priori stream group[a]

	Observed IndVal (%)					IndVal from Monte Carlo tests		
	CH	+3	+6	+8	NA	Mean	S.D.	P
Hydropsyche siltalai Döhler	**91**	0	0	0	0	16.5	6.95	0.001
Sphaerium sp.	**91**	0	0	0	0	13.9	6.5	0.001
Rhyacophila nubila Zett.	**72**	1	3	12	4	31.2	7.31	0.001
Wiedemannia sp.	**65**	0	7	3	0	21.9	7.37	0.001
Baetis rhodani Pict.	**60**	5	6	14	14	35.9	5.55	0.001
Heptagenia sulphurea Müll.	**55**	0	7	0	0	15.6	6.47	0.001
Elmis aenea (Müller)	**54**	4	9	18	15	31.4	5.01	0.001
Diura nanseni Kemp.	1	**53**	8	4	10	21.1	5.77	0.001
Arctopsyche ladogensis (Kol.)	0	**45**	3	10	4	19.9	5.79	0.002
Ancylus fluviatilis (Müller)	0	**44**	4	0	0	12.3	5.71	0.003
Micrasema nigrum McL.	1	0	**43**	1	24	26.2	8.36	0.047
Oxyethira spp.	0	6	**30**	2	3	16	6.31	0.041
Brachycentrus subnubilus Curtis	0	0	**25**	1	1	10.9	5.97	0.045
Leuctra hippopus Kempny	2	0	6	**64**	8	24	6.5	0.001
Baetis niger L.	2	6	17	**55**	6	27.7	6.69	0.001
Muscidae sp.	0	0	0	**42**	0	10.4	5.72	0.003
Protonemura meyeri Pict.	10	1	0	**42**	4	21.1	6.99	0.009
Silo pallipes (F.)	0	2	0	**40**	0	13.3	6.52	0.005
Chelifera sp.	0	0	0	0	**33**	9.7	5.59	0.010
Rhyacophila obliterata McL.	1	2	0	0	**32**	11.2	5.62	0.011
Hydropsyche saxonica McL.	1	0	0	0	**30**	12	6.49	0.027
Ameletus inopinatus Etn.	0	9	0	0	**26**	11.2	5.46	0.021
Scirtidae sp.	0	0	0	0	**25**	9.9	5.37	0.025

[a] The highest IndVal for each taxon is given in bold (maximum IndVal: 100%). Monte Carlo tests based on 1000 permutations were used to assess the significance of each species as an indicator for a respective stream group. For each group, up to five taxa with an indicator value of at least 25%, and significant at $\alpha = 0.05$, are given. More than five taxa are shown if these were significant at $\alpha = 0.001$.

inputs (Muotka and Laasonen, unpublished), which may have far-reaching "bottom-up" effects on lotic food webs. Restoration, however, does not completely eliminate mosses from the stream bottom, and it seems that even relatively isolated moss patches may serve as effective sources of recolonization after restoration disturbance. Aquatic mosses are slowly growing organisms (Sand-Jensen et al., 1999) and their recovery after a catastrophic disturbance event should be rather slow; yet, in our streams, moss biomass had recovered almost fully within 6–8 years after restoration. As mosses recover, the restored stream gradually regains its original structural complexity. Lacking historical, pre-channelization data, however, the efficiency of in-stream restoration in regenerating a truly pristine stream environment cannot be fully assessed. This, however, is usually not the ultimate goal of restoration (Osborne et al., 1993), and the more modest aim of habitat improvement is clearly attained by the measures undertaken in our study streams.

In terms of litter standing crop and abundance of detritivorous invertebrates, the restored streams seemed to have recovered rather well. In fact, there even seemed to be a slight overshoot in leaf litter abundance and densities of shredders in the +8 streams, as compared with natural reference streams. This may suggest that the combined effect of increased substratum heterogeneity and high moss cover (once mosses have
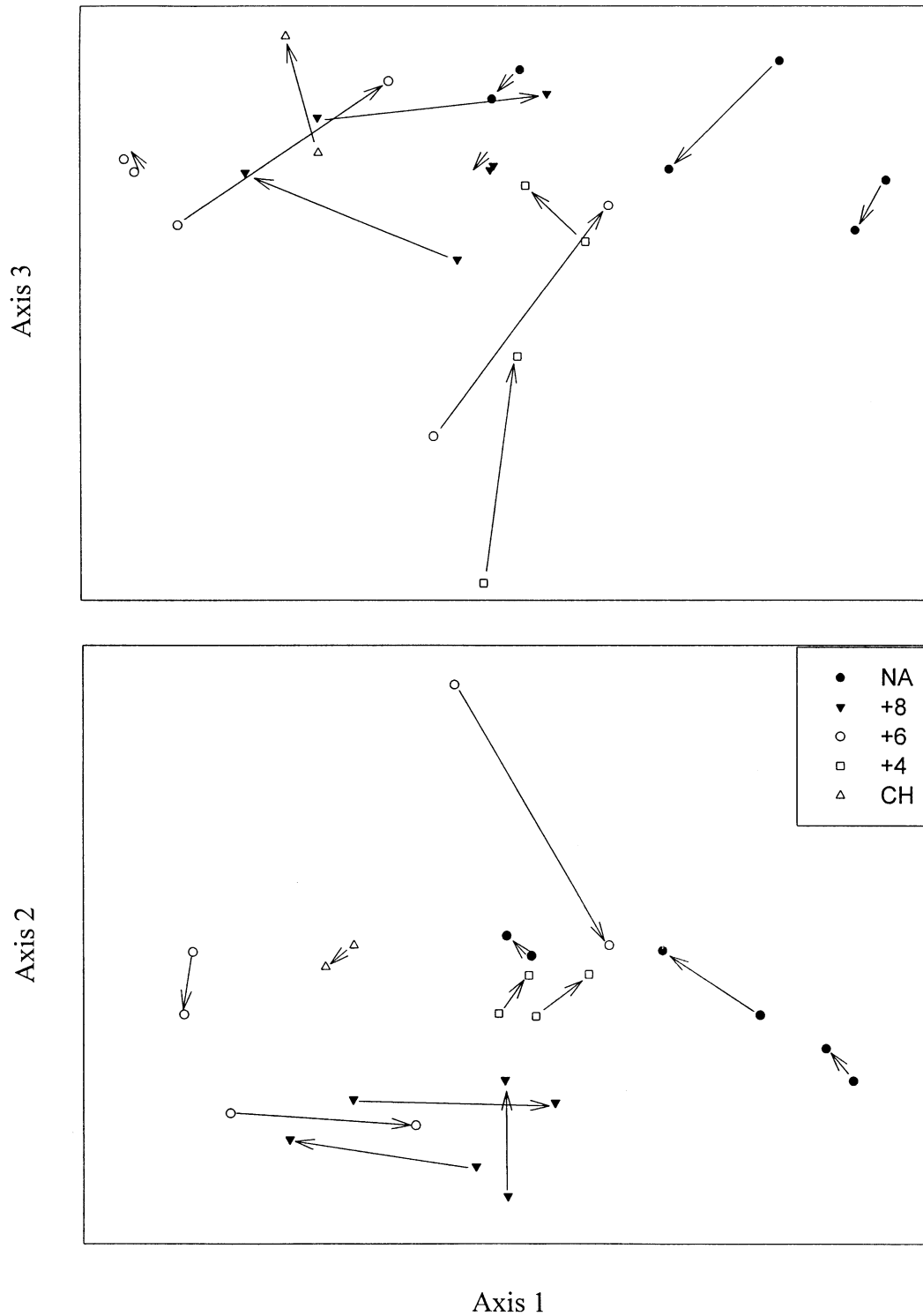
Fig. 3. Non-metric multidimensional scaling (NMDS) ordination combining samples from Laasonen et al.'s (1998) survey (1992/1993) and from this study (1997). The two sampling occasions have been connected by a line, arrow indicating the position of the 1997 samples.

recovered) results in a "supranatural" stream environment with retentive properties exceeding those of natural, unmodified streams. Invertebrate communities, however, seemed less responsive to habitat modifications. Communities in channelized streams were quite

distinctive, with a characteristic set of indicator species, whereas shifts in species composition between the restored and natural streams were more gradual. Since our study streams were located within the same ecoregion and in two adjacent catchments, the regional

Table 3
Changes in species richness (ΔS) between the sampling occasions (1992/1993 vs. 1997), and Spearman rank correlations between the abundances in the 1992/1993 vs. 1997 surveys of the 15 (r_s15) or 20 (r_s20) species that were most abundant in the earlier survey

Stream type	S	r_s15	r_s20
Channelized			
Salmijoki	6	0.595*	0.637**
+4			
Kutinjoki	7	0.361	0.373
Loukusajoki	13	0.147	0.410
+6			
Poika-Loukusa	18	0.640*	0.662**
Livojoki	7	0.119	0.176
Korpuanjoki	7	0.769**	0.568
+8			
Pärjänjoki	−2	0.585*	0.538*
Kouvanjoki	3	0.742**	0.423
Naamankajoki	0	0.482	0.612**
Natural			
Kuusinkijoki	3	0.947***	0.821***
Putaanoja	2	0.875***	0.832***
Merenoja	3	0.512	0.489*

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

species pool (sensu Pärtel et al., 1996) should have been the same for all streams. Apparently, however, channelized streams provide a unique "environmental filter" (Poff, 1997), selecting for species traits and, ultimately, species assemblages that differ distinctly from other stream types. Simplified substratum structure, relatively homogeneous flow patterns and reduced retentive potential are factors that may have a profound impact on stream communities, favouring species traits that might not be as beneficial in structurally more complex and retentive natural (or restored) streams. For example, while filter-feeding and grazing were the predominant feeding modes in channelized streams, shredders and other detritivores seemed to have a primacy in natural and restored streams.

Only a few studies have explicitly addressed the persistence of stream invertebrate community structure through time. In these few studies, the same stream(s) have been sampled repeatedly over time (the "trajectory" approach; McElravy et al., 1989; Giller et al., 1991), or on two occasions a number of years apart (the "snapshot" approach; Townsend et al., 1987). Obviously, the snapshot approach suffers from the lack of temporal replication, and the trajectory approach will give more reliable information of community persistence (Hildrew and Giller, 1994). The fact that communities in our restored streams showed variable responses

might simply reflect among-year differences in environmental conditions that have little to do with recovery from restoration. Nevertheless, the three natural streams showed extremely high temporal consistency, suggesting that either the years were sufficiently similar for an adequate comparison, or that benthic communities in natural streams remain highly persistent in spite of environmental variability. Our analysis of community persistence also indicates that, in addition to having a highly predictable community structure, the three natural streams responded in a profoundly similar way to year-to-year environmental variation, as indicated by their parallel temporal trajectories in the NMDS ordination space. By contrast, restored streams of different "age" groups behaved much more erratically in this respect, streams of the same group often showing contrasting temporal patterns of community change. The high community persistence and similarity in community responses of natural stream assemblages may stem from the fact that headwater streams in forested areas are largely controlled by similar factors, for example, they are strongly dependent on the input of organic matter from the terrestrial surroundings. The recovery of the aquatic-terrestrial coupling, which is partly disrupted in channelized streams due to their poor retention capacity (Haapala and Muotka, 1998), is elemental in the process of ecosystem recovery after in-stream restoration. However, even if riparian inputs remain unaltered after restoration, communities in restored streams may be initially slow to recover, because a restored stream does not regain its original, pre-channelization retentive capacity until many years after restoration. Therefore, it should not be surprising that community changes during the first years after restoration are substantial and unpredictable.

Overall, the benthic assemblages studied here showed a remarkable long-term recovery potential following restoration-related changes in habitat structure and resource availability. Although it is well known that stream communities have high resilience, i.e. they recover rapidly after disturbances (Fisher, 1983; Lake, 1990), the kind of disturbance caused by restoration is exceptional in many respects. First, except for rare catastrophic events (Giller et al., 1991; Lamberti et al., 1991), only rarely do natural disturbances result in such a profound restructuring of the stream habitat. Furthermore, in-stream restoration, as all anthropogenic disturbances, is an evolutionarily novel and unpredictable disturbance, for which stream biota cannot have any evolved responses (Resh et al., 1988). Therefore, from a management point of view, such a rapid recovery from restoration-related disturbance is highly encouraging. This is even more so because these restorations were performed for the sole purpose of fisheries enhancement, with little consideration for other stream biota or ecosystem processes. To this end, it

seems that relatively slight changes in restoration practices (e.g. causing as little damage to mosses as possible; adding large woody debris to increase retention potential) might yield a healthier ecosystem with natural-like food webs and trophic dynamics, and within an even shorter time span. Therefore, consideration of such alternative or, rather, complementary restoration practices could prove ultimately rewarding even for the goal of salmonid fisheries enhancement.

From a biodiversity viewpoint, it is still premature to conclude whether restoring rivers by these techniques will enhance the recovery of benthic biodiversity in boreal streams. Although there were some indications of recovery invertebrate communities in restored streams still differed considerably from those in natural streams 3–4 years after restoration. Only relatively long, quantitative monitoring of benthic communities in both restored and natural streams, using a Before-After-Control-Impact (BACI) type approach (Underwood, 1994), will provide an answer to this question. Nevertheless, if the presence of suitable habitat is a prerequisite for the establishment of a more natural-like invertebrate assemblage, then the fact that the stream habitat had recovered almost fully within less than 10 years shows great promise for the conservation of benthic biodiversity through river restoration.

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