

Spatial patterns of Ephemeroptera, Plecoptera and Trichoptera diversity in fragmented alpine streams

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Introduction

Habitat fragmentation can affect species diversity by reducing total habitat area, increasing the amount of habitat 'edge', and by isolating fragments. The relative importance of each mechanism can be difficult to assess because of their confounding nature (ANDREN 1994). The fragmentation of streams by a lentic (lake) habitat that is chemically (KLING et al. 2000) and biologically (BREITENMOSER-WÜRSTEN & SARTORI 1995) distinct results in a loss of connectivity among 'patches' of stream, thus increasing the number of isolated fragments. The total loss of lotic habitat within a drainage system is usually minimal and the creation of 'edge' (e.g. lake outlets) is relatively local, as shown by studies of lake outlets and associated species assemblages (RICHARDSON & MACKAY 1991).

At the scale of individual patches, fragmentation by lakes can reduce the connectivity of discrete reaches (e.g. MONAGHAN et al. 2001), which can potentially affect species richness. However, along a stream, increased spatial heterogeneity may lead to greater overall richness, manifested in species turnover among relatively short longitudinal distances. Thus, two components of species diversity relative to habitat fragmentation studies are: species richness (α -diversity) and species turnover (β -diversity). Alpha-diversity (α) represents the number of species present at any given location in a stream, while beta-diversity (β) measures how rapidly species composition changes from one location to another (MAGURRAN 1988). Taken together, these two measures indicate the spatial scale at which biodiversity is structured. For example, low α at multiple sites in a stream, but high β between those sites, indicates that spatial heterogeneity contributes to biodiversity. High α at multiple sites and low β between them indicates that biodiversity lies within any given site.

In order to examine how habitat fragmentation may affect species richness in patches and influence spatial heterogeneity in streams, the α - and β -diversity of Ephemeroptera, Plecoptera and Trichoptera

(EPT) assemblages were examined in fragmented and non-fragmented alpine streams in Switzerland. The first hypothesis was that α -diversity at any given sampling site in fragmented streams would be reduced relative to sites in a non-fragmented stream, primarily because of the reduced connectivity of fragments. The second hypothesis was that increased β -diversity in fragmented streams would result from the presence of a lake outlet and its characteristic species assemblage. This would result in higher total richness (γ) for the whole stream, despite reduced α -diversity at any given site.

Methods

The study was conducted in four alpine streams in the Swiss Alps. Three streams were fragmented by lakes: Lago Bianco (8° 31' 19" E, 46° 27' 14" N), Val Minor (10° 1' 53" E, 46° 26' 22" N), and Jörissee (9° 58' 13" E, 46° 46' 52" N). The fourth stream, Arosa (9° 39' 2" E, 46° 46' 21" N), was non-fragmented. Bianco and Minor each contained a single lake (surface area 3.9 and 0.7 ha, respectively) and sampling sites were located at the inlet, immediately at the lake outlet, and ca. 150 m downstream of the outlet (Fig. 1). Jöri was fragmented by two lakes ca. 200 m apart. Thus, the outlet of the upper lake (5.8 ha) also served as the inlet of the lower lake (9.6 ha) and only the lower lake had a downstream sampling site (Fig. 1). The stream at Arosa was sampled at two locations approximately 300 m apart. All sampling sites were located in alpine tundra, and altitudinal differences between the uppermost and lowermost study sites ranged from 8 m (Bianco) to 175 m (second Jöri lake; Table 1).

Larval zoobenthos were sampled semi-quantitatively at each site using a 100- μ m mesh kick net. Sampling was conducted for 5 min on each occasion to standardize the sampling effort; all habitat types within a 50-m reach of the stream were sampled. Habitat types typically encompassed the main channel, slack water, organic detritus, and all substrate sizes, ranging from sand to large boulders. Samples

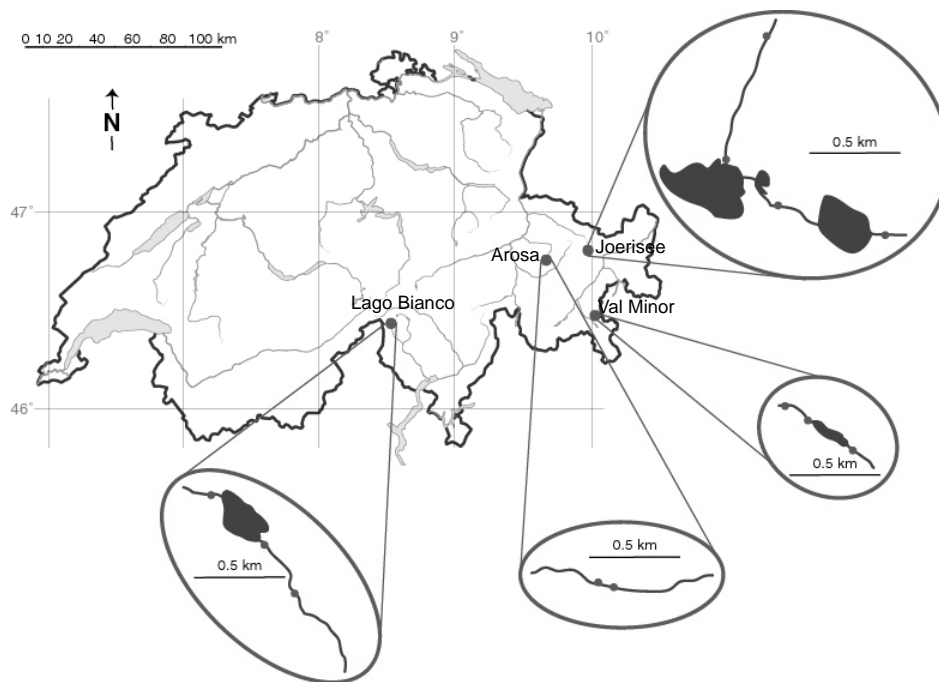


Fig. 1. Map of Switzerland indicating the geographic location of the four study streams. Dots indicate the sampling sites in each stream.

were preserved in the field and sorted in the laboratory using a dissecting microscope (10 \times). Each site was sampled at least three times, once in spring, summer, and autumn in either 1998 or 1999. Bianco, Minor and Jöri outlet-2 were also sampled once in winter (the other sites were inaccessible in winter). For each site, species were placed into abundance categories of low (no more than 1–5 animals in any sample), moderate (6–50 animals in any sample), and high (>50 animals). These categories are distinguished by one, two and three asterisks, respectively, in the results (Table 2).

Species richness was determined for each sampling site (α) and for each stream (γ) by combining samples from the different seasons. Species turnover (β) between sample site pairs in each stream was examined using the Sorenson index C : $C = 2j/(a + b)$, where j is the number of species found in both sites, a is the number of species in site a ; and b is the number of species in site b . The Sorenson index has been found to be most appropriate when using presence-absence data (MAGURRAN 1988). Values of C range from 0 to 1, with a value of 1.0 indicating identical species composition and a value of 0.0 indicating that sites share no species. Three values of C

were calculated for each stream: turnover between the inlet and outlet (C_{il-ol}), between the outlet and downstream (C_{ol-ds}), and between the inlet and downstream (C_{il-ds}). Taken together, this allowed the comparison of the lake outlet with upstream and downstream sites, in order to determine whether assemblages 'recovered' to resemble those at the inlet after a given distance downstream of the outlet.

To measure species turnover along each stream and among different streams, Whittaker's β as $\beta_w = S/\alpha - 1$ was calculated, where S is the total number of species in the system (i.e. within a stream or over the whole study area) and α is mean species richness at each site (MAGURRAN 1988). The level of the similarity of species assemblages is inversely proportional to the value of β_w .

In order to assess habitat changes along longitudinal gradients, 1-L water samples were collected at the same time as zoobenthos from each sample site and returned to the laboratory for analysis (see TOCKNER et al. (1997) for methods). Samples were collected in spring, summer and autumn of 1998 and 1999 ($n = 6$); lake outlets were sampled more frequently in both summers ($n = 10$). Owing to the variance, which probably arises as a result of seasonal effects,

Table 1. Physical characteristics of the study sites. Median substrate size ($n = 50$), mean widths (1 SD), and slope were measured along a 50-m reach at each site in autumn.

Stream	Site	Substrate size (cm)	Wetted width (m)	Bankfull width (m)	Slope (%)	Altitude (m a.s.l.)
Bianco	Inlet	9	6.0 (1.6)	12.5 (2.0)	2	2080
	Outlet	35	6.7 (2.5)	8.6 (1.5)	4	2076
	Downstream	20	4.2 (0.4)	9.7 (2.2)	4	2072
Minor	Inlet	17	8.6 (2.9)	10.3 (2.0)	7	2340
	Outlet	21	3.6 (0.4)	5.0 (0.6)	9	2336
	Downstream	11	5.0 (1.5)	6.4 (1.2)	7	2315
Jöri	Inlet	31	3.1 (1.1)	3.9 (1.5)	17	2525
	Outlet 1	37	6.8 (4.5)	8.8 (4.0)	4	2515
	Outlet 2	18	8.3 (2.4)	10.3 (2.0)	5	2489
	Downstream	17	4.7 (1.9)	5.3 (0.6)	8	2320
Arosa	Upstream	12	1.2 (0.5)	1.2 (0.6)	3	1940
	Downstream	14	1.5 (0.3)	1.5 (0.2)	7	1930

these are reported only as trends in mean values, and statistical analysis has not been performed. In autumn, physical habitat characteristics were examined: benthic substrate size (a-axis of the first particle encountered in 50 randomly chosen locations in a 50-m reach); wetted and bankfull width at five transects using a tape measure; and reach slope using a hand-held clinometer.

Results

Water chemistry parameters showed a general pattern of elevated mean concentrations for dissolved and particulate N and P and particulate organic carbon (POC) at lake outlets (Fig. 2). Exceptions were at Minor, where particulate N and POC were highest at the upstream site and nitrate-N (NO_3^-) was highest downstream. Specific conductance was similar at all sites. In the non-fragmented stream, mean concentrations for all parameters were higher downstream, although mean specific conductance appeared to decrease slightly (Fig. 2). The median substrate size decreased from lake outlets to downstream sites but increased at the downstream site in the reference stream (Table 1). Downstream changes in wetted width, bankfull width, and slope varied among sites and no consistent patterns were evident. For example, lake outlets were wider than inlets and downstream sites at Jöri and Bianco but narrower at

Minor. None of the physical or chemical characteristics were correlated with the values of α -diversity reported below (Pearson correlation, all r -values < 0.6).

A total of 27 Ephemeroptera, Plecoptera and Trichoptera taxa (hereafter referred to as species) were collected among the 12 study sites (Table 2). The total number of species may in fact be higher because of taxonomic uncertainty in the Plecoptera genera *Leuctra*, *Nemoura* and *Protonemura* (AUBERT 1959, V. LUBINI personal communication) and among the Trichoptera genus *Rhyacophila* (WARINGER & GRAF 1997). Alpha (α) diversity ranged from one to 17 species at individual sites, with the highest richness found at downstream sites in two fragmented streams (Table 2). Longitudinal changes in α varied among the streams, with lowest α at the outlet at Bianco and at the inlet at Minor; however, the farthest downstream sampling site always had the highest α -value (Table 2).

The similarity (C) of site pairs within each stream, used to evaluate the uniqueness of lake outlet species composition and the 'recovery' of downstream sites, ranged from 0.13 to 0.91 (Table 3). In Minor and Jöri, the inlet and outlet sites were most similar, followed by the outlet and downstream ($C_{\text{il-ol}} > C_{\text{ol-ds}}$); the lowest similarity was between the inlet and downstream

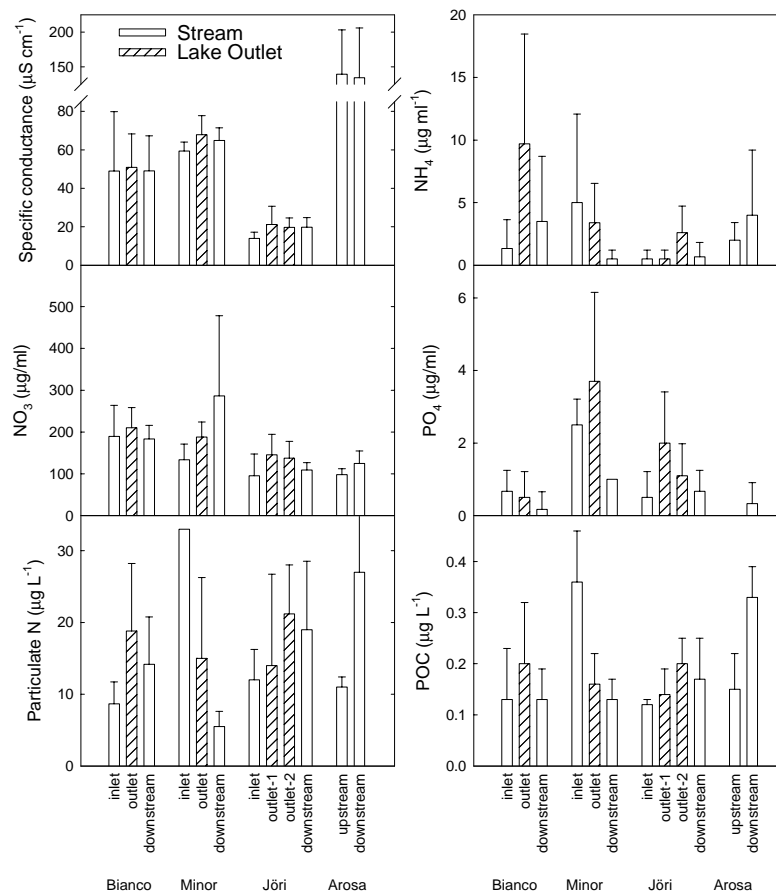


Fig. 2. Chemical characteristics for each study site (mean \pm 1SD) as measured over the course of 2 years (n = 6; lake outlets n = 10).

(Table 3). In contrast, the highest similarity was between the inlet and downstream in Bianco, followed by inlet–outlet and outlet–downstream (Table 3). The two sites in the non-fragmented stream (Arosa) had the highest similarity in any stream (Table 3). Evaluating the role of whole-stream spatial heterogeneity, species turnover (β_w) was greater in the three fragmented streams (2.1–2.8) than in the reference stream (1.2; Table 3). Gamma (γ) diversity also was higher in fragmented streams (14–20) than in the reference stream (12; Table 3). β_w among all sampling sites in the study (3.2) was higher than β_w within any single stream (maximum of 2.8).

Discussion

Habitat fragmentation did not lead to EPT-depauperate patches of stream habitat relative to a non-fragmented stream; the two highest α values occurred at fragmented sites. However, fragmentation did result in a shift in the spatial pattern of species richness in the fragmented streams. In the non-fragmented stream, Arosa, most of the species present were found at both sites and therefore species turnover (β -diversity) was low. It can, therefore, be concluded that the majority of species in this stream should be found at any given site, at least within the hundreds of metres of similar reach. In contrast, there was greater species turnover among sites

Table 2. Species composition and richness (α -diversity) at each site. Asterisks indicate species were present in low (*), moderate (**), or high (***) abundance.

	Bianco Inlet	Bianco Outlet	Bianco Lower	Minor Inlet	Minor Outlet	Minor Lower	Jöri Inlet	Jöri Outlet 1	Jöri Outlet 2	Jöri Lower	Arosa Upper	Arosa Lower
Ephemeroptera												
<i>Baetis alpinus</i>	**	*	***	*	***	**	**	**	*	***	**	**
<i>Ecdyonurus alpinus</i>	*											
<i>Ecdyonurus pitceti</i>			*							*	*	**
<i>Epeorus alpicola</i>										**		*
<i>Rhithrogena endenensis</i>										*	*	*
<i>Rhithrogena loyolaea</i>	**		**			**	**		**	**	**	**
<i>Rhithrogena nivata</i>										**		
Plecoptera												
<i>Dictyogenus alpinum</i>	**					**	**	**	**	**		
<i>Leuctra</i> sp.	**		**			**	**	*	*	**	**	**
<i>Nemoura mortoni</i>			**							**		
<i>Nemoura</i> sp.		***									*	*
<i>Perlodes intricatus</i>	**	*	**		*	*					**	**
<i>Protonemura</i> sp.	*	*	**		*	**				**	*	*
<i>Rhabdiopteryx alpina</i>		*						*		**		
<i>Siphonoperla montana</i>										**		
Trichoptera												
<i>Acrophylax zerberus</i>						*			**			
<i>Anitella obs./Melamophylax mel.</i>					*							
<i>Consorophyllax</i> sp.						**	**	*	*			
<i>Drusus biguttatus</i>						*		**		**		*
<i>Drusus destitutus</i>						*		**				
<i>Drusus discolor</i>	*		**			**	*		*	**	**	**
<i>Drusus mixtus</i>						**		**	*	**		
<i>Drusus monticola</i>						*	***					
<i>Halesus rubricollis</i>										*		
<i>Rhyacophila glareosa</i>						**				**	**	**
<i>Rhyacophila intermedia</i>						**				**	**	**
<i>Rhyacophila sensu stricto</i>	**	**	**									**
α -diversity	9	6	10	1	4	14	7	7	8	17	10	12

within each fragmented stream. This turnover resulted in higher total species richness (γ) in the fragmented streams, despite the fact that two to three sites in each fragmented stream had lower α than the reference stream. Thus, high β -diversity resulted in increased species richness in fragmented streams when a larger spatial scale (although only hundreds of metres of stream) that incorporated the spatial hetero-

geneity of fragments was considered. This finding supports the contention that turnover at multiple spatial scales (β -diversity) is an important measure of biodiversity in aquatic systems (WARD et al. 1999). Additionally, whether richness increases or decreases from environmental heterogeneity depends in part on the spatial scale considered.

The high species turnover in fragmented

Table 3. Species similarity between site pairs (C), total species richness (γ), and turnover (β -diversity) in each stream. Similarity between site pairs within each stream is expressed as a Sorensen index for inlet–outlet (C_{il-ol}), two lakes occurred at the Jöri site), outlet–downstream (C_{ol-ds}), and inlet–downstream (C_{il-ds}) comparisons. Whittaker's β (MAGURRAN 1988) was calculated for each stream and for the entire study.

Study site	C_{il-ol}	C_{ol-ds}	C_{il-ds}	γ	β_w
Bianco	0.53	0.38	0.74	14	2.05
Minor	0.40	0.33	0.13	15	2.81
Jöri	0.57/0.67	0.48	0.42	20	2.4
Arosa	–	–	0.91	12	1.20
Total					3.20

streams did not result from lake outlets harbouring different EPT species. Only four of 27 species identified (*Nemoura* sp., *Rhabdiopteryx alpina*, *Anitella/Melampophylax* and *Drusus destitutus*) were found solely in lake outlets. This is, in part, because many lotic or lentic species typical of lake outlets (e.g. Simuliidae) were not investigated in the present study, although the lake outlets appeared to be chemically richer and perhaps distinct from the stream segments. In addition, little of the expected 'recovery' of downstream sites was observed because the inlet and downstream sites were most similar only at Bianco. This further supports the findings that lake outlets were not taxonomically distinct and indicates that other habitat characteristics of downstream sites may be responsible for the greater observed EPT richness or that the taxonomic 'distinctness' of lake outlet communities declines with increasing elevation. No explanatory relationships were found between physical characteristics and α -diversity, although a lack of strong relationships was not surprising given the small number of sampling sites. Species ability to disperse among disconnected patches appeared to have minimal influence on richness, as inlets and outlets generally were very similar. Thus, local habitat characteristics probably are the primary determinants of EPT response to habitat fragmentation. High diversity downstream of lakes has been observed in other streams and related to increased trans-

ported organic matter (ROBINSON & MINSHALL 1990) and to stream size (MALMQVIST 1999), parameters that were similar among the sites in the present study.

In summary, we examined how lakes within a drainage system may fragment flowing water habitats by assessing changes in species richness and composition of larval Ephemeroptera, Plecoptera and Trichoptera (EPT) in four different alpine streams. Species richness (α -diversity) and turnover (β -diversity) generally increased along longitudinal gradients of 200–300 m that encompassed lake inlets, lake outlets, and sites 100–300 m downstream. Eight of 10 fragmented sites had reduced EPT α -richness, although γ -richness was greater in fragmented streams than in the non-fragmented stream. This was due to high EPT richness at downstream sites rather than to these high elevation lake outlets harbouring distinct EPT assemblages.

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