

Habitat Fragmentation and Genetic Diversity

What We can Learn by Studying Alpine Aquatic Insects

The fragmentation of natural habitats has important implications for the distribution of organisms and the genetic structure of populations. For the past four years, we have studied how fragmentation of alpine streams by lakes and reservoirs affects the dispersal ability and the genetic structure of stream insects. One of two mayfly species studied, *Baetis alpinus*, showed genetic differences between fragmented populations. Adults are poor flyers and generally fly upstream along the water course to lay eggs. The second mayfly, *Rhithrogena loyolaea*, is a better flyer and disperses in all directions, suggesting it can cross the unsuitable habitat between fragments. Interestingly, genetic differences in *B. alpinus* were only detected across geologically old lakes suggesting that human-caused habitat fragmentation may be too recent to detect genetic effects.

The habitats of many species have become fragmented naturally or by humans into smaller “islands”. This process of habitat fragmentation can transform one large population into several smaller populations. The reduction of population size is called a genetic bottleneck and can result in a serious loss of genetic diversity within each of the smaller populations increasing the probability of local extinction [1]. It is possible that genetic diversity can be increased by gene flow, defined as the influx of new genetic variation from other populations. But the isolation of populations very often limits the amount of gene flow, thereby confounding the problem.

Does Habitat Fragmentation Affect Genetic Diversity of Stream Insects?

Many aquatic insects are restricted to flowing water habitats. These flowing water habitats can be fragmented into discrete reaches by standing water bodies such as natural lakes and human-made reservoirs (Fig. 1). Aquatic insects living in flowing waters may not be able to transverse lakes, thereby causing population isolation and possible changes in genetic diversity. Over the past four years, we have examined how natural and human-made fragmentation of alpine streams has affected the population genetics of stream insects in the Swiss Alps.

Understanding how fragmentation affects organisms is important in Alpine regions because of their large number of endemic plants and animals.

The Study Sites

We conducted our study in several headwater streams of the Rhine, Inn, and Ticino rivers (Fig. 2). Six streams were fragmented by lakes, 2 streams were fragmented by

reservoirs, and 3 of the streams were unfragmented, providing “controls”. Organisms were collected from above and below each lake or reservoir or from 2 points along the unfragmented streams (Fig. 2). The purpose of the design was to compare naturally fragmented streams (lakes) with human-fragmented streams (reservoirs), the primary difference being that reservoirs are much more recent features of the landscape. They were constructed mostly within the last 100 years, while most of the lakes we studied were formed by the retreat of Alpine glaciers.

The Study Animals

We investigated two mayfly (Ephemeroptera) species with different dispersal abilities, *Baetis alpinus* and *Rhithrogena loyolaea*. These animals spend most of their lives as larvae on the stream bottom. *Baetis* lives 6–9 months, and *Rhithrogena* 2–3 years in the stream before emerging as flying adults. As adults, they live from only a few hours up to a few days, hence the names “Eintagsfliegen” and “éphémères”. *B. alpinus* is a wide-



Fig. 1: Fragmented alpine streams: Natural fragmentation by the Jöriseen ...

spread and abundant alpine species [2]. Adults have poor flying ability and generally fly in an upstream direction. *R. loyolaea* also is widespread but occurs at fewer locations. It is considered to be a stronger flyer than *B. alpinus* and other studies of *Rhithrogena* suggests it flies in all directions rather than just upstream.

The Genetic Analyses

We used 2 kinds of genetic analyses to answer questions about the effects of habitat fragmentation. The first technique was allozyme electrophoresis, where genetically different forms of the same enzyme, so-called allozymes, migrate different distances in an electric field (Fig. 3). From this we can examine how many different enzyme forms are present in a population, that is the **genetic diversity**, and how different one population is from another population, that is the **genetic difference** (θ). From this second measure, we can estimate the amount of gene flow that occurs among fragmented populations. Small genetic differences ($\theta < 0.05$) between subpopulations indicate

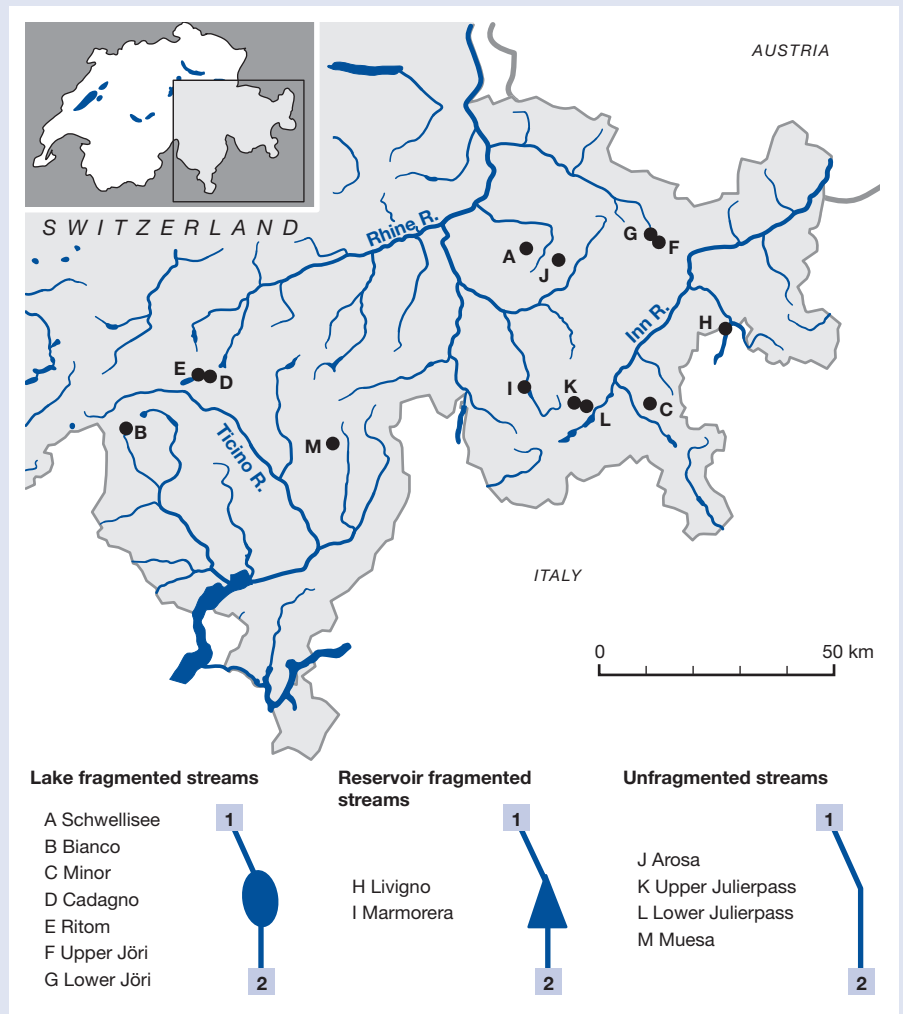


Fig. 2: Location of studied streams. Streams A–G fragmented by lakes, streams H–I fragmented by reservoirs, and control streams J–M without fragmentation. Numbers 1 and 2 indicate the sampling sites.

that dispersal occurs frequently, whereas large genetic differences ($\theta > 0.05$) indicates limited dispersal and low population mixing

because animals do not cross the standing water habitat. The second technique was amplified fragment polymorphism (AFLP), a



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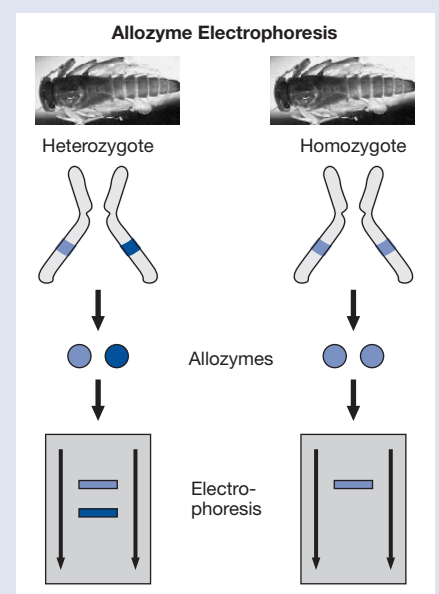
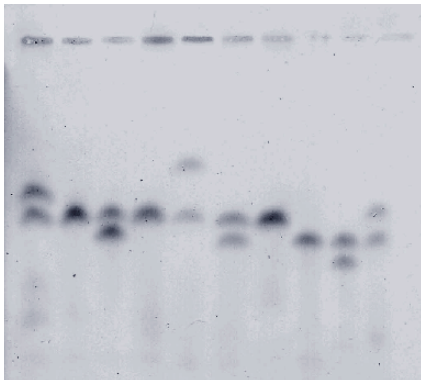


Fig. 3: Principle of allozyme electrophoresis.



The polymorphic allozyme locus *Pep-B* analyzed for 10 individuals of *Baetis alpinus*. Differences in migration distance of dark bands (from the top of the figure) indicate 5 genetically different forms of the enzyme.

DNA “fingerprinting” technique that allows for more sensitive analysis of genetic differences among populations. The data analyses are carried out using specialized programs for population genetics including FSTAT [3] and ARLEQUIN [4].

Limited Dispersal Among Habitat Fragments

The allozyme data indicate no reduction of genetic diversity in habitat fragments for either *B. alpinus* or *R. loyolaea*. However, there were large genetic differences between populations of *B. alpinus* within all of the streams fragmented by lakes except for the Jöri lakes (Fig. 4) [5]. These allozyme data were directly supported by the more sensitive AFLP data as well (results not shown). In contrast to *B. alpinus*, there were no detectable genetic differences between populations of *R. loyolaea* within any of the study streams.

We attribute the difference among the two species to adult flight and egg-laying behavior. *B. alpinus* normally fly upstream, staying close to the stream course. Upon reaching standing water without exposed rocks to deposit their eggs, they are likely to stop flying and lay their eggs in the stream.

This is in contrast to *R. loyolaea*, which flies in several directions, even away from the stream. As a consequence, *R. loyolaea* appears to be able to cross unfavorable habitats such as lakes and disperse among habitat fragments [6].

An unexplained result is the finding that populations of *B. alpinus* were not genetically different across the two Jöri lakes and the two reservoirs (Fig. 4). Our suggestion is that valley history might play an important role in determining the genetic structure of populations and that genetic differences across geologically younger lakes and reservoirs could not be detected within the first 100 to 1000 years of fragmentation. Indeed, the Jöri glacier has remained active throughout the Holocene and extended into one of the study lakes during the Little Ice Age ca 150 years ago. This recent alteration of the stream course may mean that fragmented populations probably have not had enough time to become genetically different. Reservoirs are even more recent, having been constructed in the 20th century.

Conclusions and Next Steps

Two important results from our research are (1) habitat fragmentation can reduce disper-

sal of alpine stream insects, leading to genetic differences among populations, and (2) human-caused habitat fragmentation may be too recent to detect genetic effects. One important goal of our continuing research is to separate historical from present-day genetic effects to better understand how organisms respond to environmental modification (natural and man-made).



Michael T. Monaghan recently completed his PhD in the Limnology Department of EAWAG studying the effects of habitat fragmentation on genetic diversity and species diversity of alpine stream insects.

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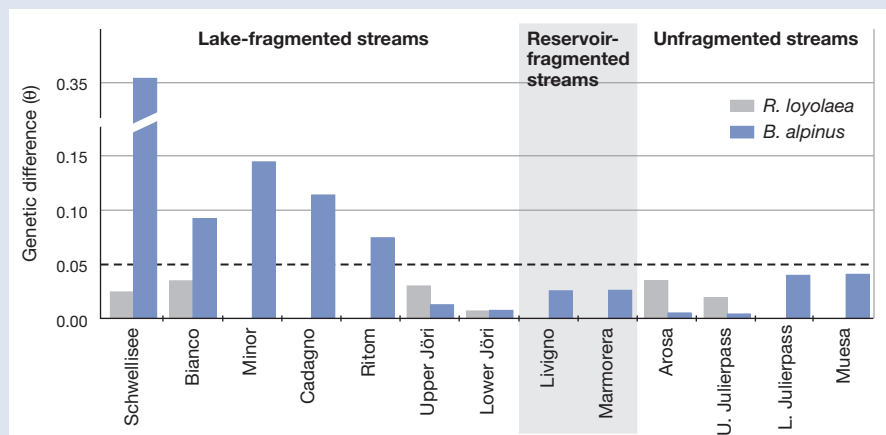


Fig. 4: Genetic differences (θ) between fragmented populations of two mayflies (*Baetis alpinus* and *Rhithrogena loyolaea*) with values >0.05 indicating limited gene flow.

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