Life at the edge: Benthic invertebrates in high altitude Andean streams

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Summary

Mountain regions cover about 27% of the Earth's surface, encompassing glacial stocks and freshwater reservoirs that play a valuable role providing ecosystem services to large human populations living downstream. Mountain regions are unique through the heterogeneity of ecosystems and diversity of climates arising from their sharp altitude gradients. When approaching the summits, these factors create exceptional harsh conditions for life, which may be challenged even further by man-made disturbances: life at the edge.

The aim of this thesis was to identify potential drivers of diversity in poorly studied benthic invertebrate assemblages in high altitude Andean streams and to elucidate the mechanisms that enable them to cope with 'life at the edge'. To this purpose, the following objectives were set:

- To describe for the first time the benthic invertebrate assemblages in high altitude Andean streams and to relate their composition to the strong gradients in abiotic factors.
- To unravel the role of melanin as a strategy against harmful UV-B radiation and metal exposure.
- To study the genetic diversity of benthic invertebrates occurring under extreme conditions and showing specific defense strategies.

High altitude creates unique challenging conditions to biota that limit the diversity of benthic communities. Because environmental pollution may add further stress to life at high altitude, in chapter 2 I first explored the effect of metal pollution on macroinvertebrate community composition in Andean streams between 3500 and 4500 m above sea level (a.s.l.) during wet and dry seasons. At polluted sites, showing a high conductivity and a low pH, metal concentrations ranged from 8-fold up to 3500-fold higher than at reference sites. The cumulative criterion unit allowed quantifying the potential toxicity of metal mixtures at the contaminated sites. Principal Component Analysis of physical chemical variables showed that reference sites were more likely to be structured by transparency, water discharge, and current velocity, while polluted sites appeared to be determined by metals and conductivity. Canonical Correspondence Analysis indicated a strong influence of highly correlated metals in structuring invertebrate communities, which were dominated by dipterans, coleopterans, collembolans, and mites at polluted sites. At reference sites crustaceans, ephemeropterans, plecopterans, and trichopterans were the most representative taxa. It was concluded that severe metal pollution induced changes in macroinvertebrate community composition in high altitude Andean streams, with a replacement of sensitive taxa by more tolerant taxa. Yet, relatively species-rich communities persisted under harsh conditions.

In chapter 3 I evaluated the differential effects of metal pollution and altitude on benthic macroinvertebrate community composition. Polluted sites were characterized by high metal concentrations and low pH, and high altitude sites by high ultraviolet-B (UV-B) radiation and low concentrations of dissolved organic matter. Canonical Correspondence Analysis indicated that the patterns in faunal composition were best explained by metal pollution followed by altitude, with dipterans and collembolans occurring mostly under harsh conditions of high altitude and high pollution levels. It was concluded that in highland Andean streams metal leaching from igneous rock and altitude may be important factors modulating benthic macroinvertebrate communities reducing their numbers and changing their composition towards specialized taxa.

High metal concentrations and an elevated UV-B radiation in high altitude Andean streams create highly selective conditions for life, allowing the persistence of only a few specialized taxa, including chironomids. Therefore, the aim of chapter 4 was to determine the mechanisms underlying the persistence of chironomids under these multiple stress conditions, hypothesizing that melanin counteracts both the adverse effects of solar radiation and of metals. Melanin was determined in chironomids from reference and metal polluted streams at 3000 and 4000 m altitude, being 2-fold higher at 4000 m compared to 3000 m, and 2-fold higher in polluted streams than in reference streams at both altitudes. The field observations were experimentally verified by assessing the combined effects of Cu and UV-B on the survival and melanin concentration in larvae of the model species *Chironomus riparius* (Chironomidae, Diptera). In laboratory exposures, the highest melanin concentrations were found in larvae surviving toxic Cu concentrations, but not in those exposed to the highest UV-B radiation. Pre-exposure to UV-B decreased the sensitivity of the larvae to UV-B and to Cu+UV-B. It was concluded that in the field melanin may protect chironomids partially against both elevated metal concentrations and solar radiation, allowing them to persist under the harshest conditions in high altitude streams.

Photoprotective pigments in benthic macroinvertebrates may reduce the damage caused by the blistering UV-B radiation in Andean high altitude streams above 3500 m. Therefore, the aim of chapter 5 was to determine if melanization in macroinvertebrates inhabiting high altitude Andean streams is an adaptive response to high UV-B radiation. To explore if altitude-related differences in melanin concentration between taxa were due to a variable community composition or to population differentiation, mayfly species were identified genetically. I measured UV-B radiation from 650 to 4000 m and compared body melanin concentrations from several benthic macroinvertebrate orders sampled at these altitudes. Five genera belonging to the mayfly family Baetidae were genetically identified to the species level. DNA sequencing was performed in individual larval legs to group genetically similar individuals before pigment analysis in the corresponding bodies. The UV-B radiation at 4000 m was two-fold that at 3200 m, four-fold that at 1900 m, and five-fold that at 650 m. The melanin concentration in families belonging to Ephemeroptera, Trichoptera, Diptera and Turbellaria was two-fold higher at 4000 m compared to 3200 m, but did not differ among taxa or between seasons. Five genera of the family Baetidae were identified: *Americabaetis*, *Dactylobaetis*, *Tupiara*, *Baetodes* and *Thraulodes*. Genetic differences arose between *Americabaetis* sp. at 4000 m from the Cordillera Blanca and at 3200 m from the Rímac River valley, and between *Tupiara* taxa at 650 and 1900 m in the Rímac River. In *Americabaetis* melanin increased five-fold from 1900 to 4000 m, while in *Dactylobaetis* and *Tupiara* it was two-fold higher at 1900 m compared to 650 m. In *Baetodes* melanin at 4000 m was two-fold that at 650 and 1900 m, while in *Thraulodes* it was almost three-fold higher at 4000 m compared to 3200 m. In *Tupiara*, the differences in melanin levels were likely associated to species with different vertical distribution, while in *Dactylobaetis* these differences were interpreted as phenotypic plasticity. These results thus indicate that mayfly species within a single family have both constitutive or adjustable melanin concentrations, enabling them to cope with the strong selective UV-B environment. Adjustable melanin levels have commonly been observed under moderate UV-B regimes, while the constitutive, high melanin concentration is probably an attribute of high altitude invertebrate fauna in the tropics.

As described above, chironomids are among the few dominant insect taxa present under the harshest environmental conditions in polluted high altitude Andean streams. Yet, the question remained if the dominance of chironomids was due to either an adaptive capacity of few species (population differentiation) or to a diversity of species with different capacities to cope with environmental extremes (species composition). To answer this question, in chapter 6 the genetic composition of the chironomid communities from reference and metal polluted streams at 3000 and 4000 m a.s.l. was determined by mitochondrial cytochrome oxidase I (COI) gene sequencing and construction of a phylogenetic tree. At 3000 m the reference site was inhabited by 6 phylogenetic species, completely different from the 3 present at 4000 m, indicating a strong sorting of species according to altitude. Only one phylogenetic species was present at the metal-rich sites. This metal tolerant species was the same at 3000 and 4000 m, and unique for the polluted sites, indicating that the extreme selection pressure by metal exposure overruled altitude driven selection. It was concluded that altitude imposes strict limits to the distribution of chironomid taxa creating a strong vertical zonation on the slopes of the high Andes, yet, selection in acidic metal-rich waters is so strong that altitude driven selection is overruled, leading to predominance of a unique metal tolerant taxon.

In conclusion, high altitude Andean streams harbor a quite diverse benthic community represented by the major groups of invertebrates. Evidence is provided that abundant insect species have not been described taxonomically and that unique genotypes occur, probably as a result of the geological history of the Andes and the strong selection

for high altitude tolerance. Cuticular pigmentation of larvae was demonstrated to form an inducible sunscreen against scorching UV radiation, but the pigment melanin was also effective in mitigating metal stress. Thus a single trait of the fauna enabled species to cope with the combined stressor UV radiation and metal exposure from leaching rock. The only species from the stress tolerant chironomids that survived the most harsh condition of a metal-rich, UV blasted site was a non-identifiable chironomid, characterized as a new haplotype. The vertical zonation of insect fauna on the slopes of the Andes is strong and I identified multiple stress factors such as the mountainous oxygen regime, high UV radiation and metal leaching as drivers of the composition of benthic assemblages in high altitude Andean streams. It is concluded that selection is strong at all altitudes in the Andes, but is most evident at high altitude and high metal exposure: at 'the edges of life'.