

Review

Biological Diversity in Headwater Streams

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Abstract: Headwaters, the sources of all stream networks, provide habitats that are unique from other freshwater environments and are used by a specialised subset of aquatic species. The features of headwaters that provide special habitats include predator-free or competitor-free spaces; specific resources (particularly detrital based); and moderate variations in flows, temperature and discharge. Headwaters provide key habitats for all or some life stages for a large number of species across just about all freshwater phyla and divisions. Some features of headwaters, including isolation and small population sizes, have allowed for the evolutionary radiation of many groups of organisms within and beyond those habitats. As small and easily engineered physical spaces, headwaters are easily degraded by streambank development, ditching and even burial. Headwater streams are among the most sensitive of freshwater ecosystems due to their intimate linkage with their catchments and how easily they are impacted. As a unique ecosystem with many specialist species, headwater streams deserve better stewardship.

Keywords: cold stenotherms; detritus; ecological function; lotic; refuge; richness; species radiation

1. Introduction

Headwater streams exist in all landscapes as source streams but are variously defined, and a search of the word “headwater” will attest to that. Here, I define headwaters as the first perennially flowing streams in a network, i.e., having no permanent tributaries [1]. Headwaters originate anywhere that the surfacing of groundwater (e.g., springs, swales, etc.) is sufficient to create fluvial characteristics such as the washing away of accumulated organic materials and other sediment movements. However, even continuous flow is not necessary, as intermittent and ephemeral streams are included as headwaters. We often think of headwaters as being surrounded by forest, but they can originate in alpine or subalpine areas [2], grasslands or savannahs [3], or any other type of landscape (Figure 1). Streams originating from glaciers have their own distinctive characteristics, as discussed in the paper by Füreder (this issue). Headwaters can also emerge as the outflows of lakes, mires and other wetlands, with special characteristics of their own [4]. By this way of defining headwaters, a second or third-order stream would not be counted as a headwater stream, and we have encouraged this distinction where we refer to second and higher-order streams as “small streams” [5]. There are always exceptions to any definition, and as examples, the Metolius River (3.17 m³/s at its origin, Oregon, USA) or San Marcos River (4.3 m³/s at its source, Texas, USA) come out of spring sources as large streams, which might stretch our definition of headwater streams.

The characteristic scale of headwaters varies depending on the definition and the hydrological region. Several studies have noted a shift from the reach to catchment-scale influence at about 1 km², which aligns well with the definitions of headwaters [1,6,7]. Headwater streams can have perennial flow, flow during an extended period of the year (intermittent) or only following flow after large storms or for a few months of the year (ephemeral). The duration of flow persistence determines what kind of organisms can sustain populations in the channels and thus affects species richness [8]. Relatively

fewer organisms are found in ephemeral streams, but there are some species capable of surviving long periods of absence of flow [8,9]. Given that headwaters have relatively small contributing areas, hence small amounts of groundwater storage, streams that have perennial flow in an average year may be vulnerable to loss of surface flow in a drier than average year [10]. Although headwaters are individually small environments, some estimates suggest that they may cumulatively make up to 80% of total stream lengths around the world [1,11].



Figure 1. Examples of headwater streams in different biomes: (A) near Marlborough Sound, New Zealand; (B) Iceland near Hlaupungufoss; (C) near Caleta Chaihuín, Chile; (D) East Creek, Malcolm Knapp Research Forest, British Columbia, Canada; (E) Middle Bush Stream, Cass, New Zealand; (F) near Grundarfjörður, Iceland; and (G) near Pudasjärvi, Finland.

In this review, I examine the biological diversity of headwaters from several aspects. This article is not intended to mention all the many species found in headwaters around the world but rather to illustrate the reasons they occur in those habitats using examples from many regions. First, I survey the physical and chemical processes and structures that differentiate headwater habitats from other freshwaters. Next, I consider the ecological functions of headwater systems that lead to organisms' preferential or exclusive use of those habitats. I also look at how these functions may vary by landscape. Third, I provide an overview of the kinds of species and communities found in headwaters. I use examples of these species from a perspective of taxonomic groups, trait groups and community types. Finally, I end with a discussion of the conservation threats of headwater ecosystems and their species and some suggestions for future research. This paper builds on previous reviews of headwater biodiversity [11–13].

2. Characteristics and Functions

2.1. Characteristics of Headwater Streams

How do small streams provide a different set of processes, structures and resources in comparison to larger streams or other freshwaters? That is, in what ways are they unique among freshwaters? There are some general differences between headwater streams and other freshwaters that set the environmental stage for the biodiversity of headwaters (Table 1): For instance, isolation, stability of some aspects of the environment and higher variation in other features, dependence on allochthonous

resources, and potential refuge from larger-bodied predators. Headwaters are the end member in the hierarchy of branches of a stream network and, as such, have properties related to their isolation, their size and their often steeper than downstream topography [14–16]. However, headwater streams vary enormously across the globe [12,13], which I expand upon in the next section.

Table 1. The characteristics that distinguish headwater streams from other freshwaters: Small size and small volume are not included, as those are implied by the definition of headwater streams. These characteristics are generalizations, and there is variation across landscapes.

Characteristic	Difference from Other Freshwaters	Influence	Conservation Issue
Edge: Area	Highest with the possible exception of springs	High sensitivity to conditions along stream edges	Most vulnerable to catchment alterations
Shading	High probability of shading by vegetation (trees, shrubs or herbs) or topographic shading	Reduces thermal inputs and may restrict primary production	Removal of vegetation due to land use
Temperatures	Less variation (cooler in summer, warmer in winter), close to groundwater temperatures	Provides habitat for cool, stenothermic organisms	Land use can remove the vegetative cover leading to warming and loss of cool-water and cold-water species
Discharge	Highly responsive to runoff generation, i.e., “flashy” peak flows; less capacity to buffer against droughts	Disappearance of surface flows and loss of larger-bodied species	In dry years, populations may go locally extinct
Energy sources	Allochthonous, at least in forested areas	Detritus-based food webs, including dissolved organic carbon (DOC)	Impacted by forestry and other land-use changes that alter types of inputs
Chemistry	More similar to groundwater	Often but not always oligotrophic	Low productivity and perhaps small local populations
Geomorphology	Colluvial to alluvial but may have very small sediment grain sizes depending on slope and geology	Morphology depends on gradients, parent material and peak flows	Disruption of structure can take centuries to recover, including changes in large wood supply.
Disturbance regimes	Low frequency but high intensity structural changes as debris flows (depending on slope); excessively low flows (see discharge)	Punctuated shifts and long periods to recover	Sensitive to land-use changes that modify peak and minimum discharges

Headwater streams generally provide small habitat spaces, resulting in relatively small and isolated populations [13,14], which can lead to the genetic differentiation of populations of species through selection, drift or both [17–19]. This isolation may also be a mechanism leading to the obvious radiation of some taxonomic groups from headwater streams. In these small habitats, there are few species of large size, and thus, the majority of occupants are typically small-bodied. At the same time that diversification can occur, these headwater populations are extremely vulnerable to local extinction due to spatial isolation and small population size [14].

Headwater streams are characterised by high connectivity with their surroundings. Shading provided by forest canopy or even shrub-level vegetation can moderate stream heating to maintain cooler conditions than elsewhere. Cross-ecosystem resource subsidies in the forms of leaf litter, seeds, terrestrial invertebrates and others can dominate the basal resource base of such detrital-based streams [20,21]. A corollary of the importance of allochthonous resources is that primary production is sometimes very low. Even in places lacking vegetation cover, there is a large imprint of the surroundings in terms of hydrology, nutrients and dissolved organic carbon inputs, and particulate inputs from vegetation. For instance, in non-glacial, alpine streams in the Alps, stable isotope signatures of stream invertebrates showed clear signals of allochthonous resources as a major basal resource despite the lack of a vegetated canopy, in contrast to autochthony common to glacial streams [2]. Even in open fens in Sweden, stream invertebrates were mostly dependent on allochthonous materials to support their food web [22].

A high proportion of the flow in headwaters may be generated from groundwater, which picks up a larger chemical imprint of their catchment than can be measured in surface flows further downstream [23]. Thermal variation through the year tends to be lower, but not always, due to the prevalence of groundwater inputs as a large portion of total discharge [24] even in tropical settings [25]. However, the small depths and small volumes of water can heat up rapidly when vegetative cover is removed through land use.

Headwater streams can be vulnerable to surface dewatering, as there is less buffering against drought due to their smaller catchment areas. This results in headwaters often classified as having

ephemeral, intermittent or perennial flows, and organisms adapted to the characteristic flow regimes of such classes. However, there is evidence that some of the invertebrates that live in these small streams can withstand very low flows [26,27]. In a comparison of intermittent streams with a nearby (but still small) perennial stream in Oregon, there were more aquatic insect species in the intermittent streams [9]. Certainly many headwater species are adapted to life in seasonally low flows.

Headwater streams can vary enormously, even within a single region. Structural variation due to differences in geology, surrounding vegetation, slopes, contributing areas and others can be important contributors to species sorting by environmental filters (see Section 3.1). Geology can affect the size, specific gravity, shape and even the surface roughness of clasts in headwaters. Headwaters can be colluvial, i.e., their flows are not competent to move the largest of the clasts in the channel [28,29], providing highly heterogeneous channels. Headwaters are often (but not always) surrounded by vegetation that can contribute large wood and small wood, which can remain in the channels for a long time if they are larger than the stream's capacity to flush them away. Large wood accumulations can provide important habitats for many organisms, a stabilizing feature for geomorphology and even a source of biological energy to food webs.

The network position hypothesis has been proposed to account for distributions of organisms across stream networks, but a recent test of the hypothesis suggests different taxonomic groups may be subject to different environmental filters and, therefore, different patterns of distribution [30]. Network positions along streams, and not overland position, often (but not always) provide a good prediction for distribution and population dispersal [14,16].

2.2. Use of Headwaters by Organisms—Functions

Balian et al. [31] estimate there are at least 126,000 freshwater animal species (14.5% are vertebrates) and over 2600 aquatic macrophytes. There are no similar estimates for algae, bacteria, fungi or protists. Many groups are still poorly sampled and described; for instance, estimates are that fewer than 3% of freshwater nematodes have been described [31]. There are no estimates of what fraction of the world's freshwater species are unique to headwater streams. Nevertheless, headwater streams sustain species that may be found nowhere else downstream for a variety of reasons (Table 2).

Table 2. Species' uses of headwaters for particular functions that differentiate headwaters from other freshwater environments: The characteristics of these sites vary geographically depending on forest cover, topography and extent of groundwater inputs, and thus, these are generalizations.

Ecological Process	Characteristic	Example	Citation
Enemy-free space	None or few large-bodied predators	<i>Anablepsoides hartii</i>	[32]
Lack of competition	Headwaters may be unsuitable for some species of competitors	<i>Gammarus</i> sp. or <i>Juga</i> sp.	[9]
Unique physical and chemical niche space	Physically stable, low variation in flows and temperatures in forest sites; chemical imprint of groundwater	<i>Cordulegaster</i> spp.	[33]
Seasonal environmental refuge, e.g., thermal, flow	Move to cooler sites during warm periods	Steelhead trout <i>Oncorhynchus mykiss</i>	[34]
Breeding and rearing sites	Small habitats with physical and biological processes resulting in higher survival and growth rates (likely coupled with lower predation)	Brook trout, <i>Salvelinus fontinalis</i> <i>Atya</i> shrimp	[15,35]
Detrital-based food web	High retention of detritus due to modest flows and high inputs	Scopariidae stoneflies	[36,37]

Headwaters can provide an enemy-free refuge from some kinds of predators, especially large bodied-predators, which enables some prey species to persist with the relaxation of predation. For instance, in Trinidad streams, *Anablepsoides hartii* (formerly *Rivulus hartii*) is found almost exclusively in headwater streams, and even there, they occur at lower densities or average body size when the predator *Hoplias* or the competitor *Poecilia reticulata* are present [32]. Subsequent experimental introductions of *P. reticulata* have shown this to be a result of predation and perhaps some competition [38]. An alternate hypothesis is that *Anablepsoides* is temperature sensitive, but the evidence shows that the species can exist in the warmer, lowland streams if the predators are absent [32].

Species such as the big-headed turtle (*Platysternon megacephalum*) and their crab prey in southeast Asia may occupy headwaters as a refuge from predators [39]. The use of headwaters by *Atya lanipes* and *Xiphocaris elongata* shrimps in Puerto Rico is interpreted as providing refuge from predation by fishes in downstream reaches [15].

In the same way that small streams may lack predators, it is possible that some competitor species are incapable of surviving there. It is suggested that summer-dry streams in Oregon may have high invertebrate diversity due to the absence of competition from the snail *Juga* sp. or the amphipod *Gammarus* sp. due to the inability of these latter species to persist through periods lacking surface water [9]. The rare mayfly *Paraleptophlebia werneri* in Europe is also considered to find refuge from competition in headwaters [40].

Headwater streams in forested ecosystems are often heavily dependent on detrital materials as basal resources supporting food webs [41]. This can even be true in alpine systems [2] and open-canopy fens [22] where stable isotope analyses have confirmed the dependence of stream communities on allochthonous inputs. As such, another reason for a unique composition of biological communities is the kinds of resources, such as decomposing leaf litter [42]. High input rates of detritus from the forest and the local retention of that organic matter within headwaters contributes to the importance of detritus to these food webs. Detritivore species consuming leaf litter typically decrease in abundance as streams get larger [43]. Some species, for example, the peltoperlid stoneflies *Tallaperla* and *Yoraperla*, are restricted to small streams because of their dependence on detrital food sources [37,44]. However, the relative importance of detritus as an energy source to macroconsumers is not global, and several studies from tropical regions [45,46] demonstrate detritus is processed predominantly by microbes and not invertebrates as in temperate regions.

Headwater streams tend to be cooler than downstream reaches and, thus, provide a thermal refuge for some species [47]. Water temperatures also tend to vary less in headwaters, which may benefit some species. Bull trout (*Salvelinus confluentus*), a cold-water species, are restricted to streams with a summer maxima of about 12 °C. Moreover, bull trout are easily outcompeted by species with broader temperature tolerances such as non-native brown trout, brook trout and rainbow trout [48]. The lower seasonal variation in headwater stream temperatures provides for cool-water and cold-water species to maintain appropriate habitats or even thermal refuges from the extremes [24]. Even in warmer climates, headwaters tend to provide a slightly cooler or more stable habitat [25] due to the shading by vegetation and the larger contribution of groundwater to flow. Many headwater amphibians, such as torrent salamanders, are considered to be associated with headwaters due to the colder conditions there, favouring their growth and survival [49].

There are many examples of species that make seasonal use of headwaters. Some species make seasonal movements to headwaters, such as larger individuals of the arctic grayling (*Thymallus arcticus*). In Alaska, adult arctic grayling can move upstream 10 s of km during the summer after spawning and manage to competitively relegate smaller individuals to downstream [50]. These large graylings are hypothesised to move upstream to preferred feeding areas. Some species of freshwater shrimp move seasonally to headwaters to breed [15]. Some frogs move in autumn into headwater streams, then swim downstream to find hibernation sites and move back upstream the following summer to breed [51]. *Desmognathus* salamanders showed a propensity for upstream movements towards headwaters [16]. Adult mayflies fly from productive mainstem rivers to cooler headwaters to oviposit, and their predators, steelhead trout, appear to follow that movement to cooler streams for a thermal refuge [34]. All these examples demonstrate an active movement of individuals within a species moving upstream at some point in their life cycles.

2.3. Variations across Landscapes

Headwater streams can originate anywhere that groundwater reaches the surface at a sufficient rate to support a flowing-water environment, normally defined as showing evidence of fluvial processes (e.g., erosion of accumulated organic materials, lack of rooted vegetation, etc.). However,

headwaters in alpine or grassland areas are obviously different from streams in wooded, temperate areas. The community assembly in headwaters is subject to many environmental filters, including geology, climate, elevation, riparian forest composition and others. Our knowledge of headwater streams is uneven geographically, and particularly in tropical regions, there is much less known than in temperate zones [45], although that is slowly improving in the past two decades. However, one should not assume that all tropical streams are similar [46], just as one would not assume all temperate streams function in the same way. There are also differences to be expected between headwater streams of arid versus wet regions. Headwaters in arid regions or areas without forest cover form a stark contrast against the terrestrial matrix and may result in a greater relative isolation and lower dispersal probabilities than streams in a moister region [52].

Studies show that taxon richness often declines with increasing elevation, although not always [53,54]. Across a 4000 m elevational gradient in Ecuador, the macroinvertebrate family richness decreased as elevation increased even though there were some taxa only found at higher elevations [53]. Similarly, Lujan et al. [54] found the significantly decreasing taxa richness of fishes and macroinvertebrates in small tributaries along another 4000 m elevational range in Peru although the relations were not linear. In a set of 71 streams in an Amazonian (Brazil) stream network, the fish diversity declined with elevation, controlling for stream size, even over an elevational range of only approx. 200 m [55].

Water quality differences may express themselves along stream networks, such as headwaters being cooler and more highly oxygenated, although this is not likely to be a robust generalisation. There is some evidence of a higher diversity and aromaticity of dissolved organic carbon molecules in headwaters [56]. Turbidity is often characterized as being lower in headwaters than downstream reaches [54,57]. These patterns might occur within a catchment, but a variation between catchments would overwhelm any generalization.

Headwaters are often conceived of as being steep but, in reality, can have any gradient, including in prairies [3]. Certainly, a large proportion of our literature comes from temperate-forest streams and is biased towards that sense of headwater streams. Headwater streams in very steep landscapes and with large clasts are often colluvial and underrepresented in our knowledge of the organisms that occur there. For example, sampling in small, colluvial channels might underestimate the densities and diversity and might require different sampling approaches [29]. Typical sampling equipment is ineffective in these habitats, and we know little about whether biological diversity in those habitat types might differ from less steep streams.

3. Species and Communities of Headwater Streams

3.1. Examples of Headwater Stream Communities

A small number of headwater streams have been intensively studied and have provided insights into the uniqueness of organisms found there (Table 3). Among the best studied of headwater streams is the Breitenbach, Germany, in which over 1800 species, including >1000 species of insects, have been found [58], Wagner pers. comm. Studies of invertebrates in Oregon, USA found 300 taxa in Berry Creek [59], over 457 taxa in three streams in the H.J. Andrews Forest and 194 taxa in a set of 18 coastal headwaters [60]. Even in seven temporary streams of coastal Oregon, over 204 taxa of invertebrates were collected [9]. In Broadstone Stream, England, over 130 taxa of invertebrates have been recorded [61]. Feminella [8] found 171 invertebrate taxa across 6 small streams in Alabama, and in three small streams in the Appalachian Mountains, Meyer et al. [12] listed over 290 species of invertebrates. Studies of single cell algae in headwaters have found 72, 88 and 172 species, respectively [60,62,63]. These studies indicate there may be hundreds to over a thousand species of organisms in such streams.

Table 3. Examples of the taxon richness in studies of headwater streams.

Site	Taxonomic Diversity	Comments	Source
Breitenbach, Germany	>1831 taxa, including >1556 invertebrates, 135 algae, 140 ciliates	Long-term study	[58]
Broadstone, England	131 invertebrate taxa, mostly identified to species	Increased richness over 40 years of study as stream recovered from acidification	[61]
Corvallis, Oregon, USA	204 aquatic insect taxa in 7 “summer-dry” headwater streams	Described 13 new species	[9]
Coweeta Hydrological Laboratory, North Carolina, USA	>290 invertebrate taxa	Three headwater streams	[12]
Alabama	>171 taxa of invertebrates	Combined for 6 headwater streams	[8]
Oregon, USA	72 species of single-celled algae	Mostly diatoms	[60]
Bolivia	172 species of single-celled algae	Mostly diatoms	[63]
Colorado, USA	88 species of single-celled algae	Diatoms and Chlorophyta dominant	[62]

Most of the studies mentioned above have characterised algae, macroinvertebrates and vertebrates. In most studies, it is rare to have a similar effort at sampling across all taxonomic groups; for instance, there are relatively few studies of free-living nematodes, which may reach densities of millions per m² and represent hundreds or thousands of species [64]. Also, there are few studies that have considered protists [65], microinvertebrates or bacteria [56].

One observation that is repeatedly noted through surveys is the high degree of beta diversity found among headwater streams [66]. For instance, in 18 streams in Oregon, Danehy et al. [60] found 194 invertebrate taxa, but 42 of these were found at only a single site and only 7 were found in all 18 streams. High degrees of beta diversity at the genetic and community levels for chironomids and a black fly were found between headwater streams, consistent with the high variation in environments between sites, isolation and different scales of variation in genetic drift [18], and similarly for bacteria [56]. The variation in abiotic environments among headwaters accounted for a large portion of variation in the metacommunity structure through species sorting for several taxonomic groups [67,68]. These conditions of isolation, environmental differences, small population sizes and genetic drift all foster beta diversity and diversification of taxa (see Section 3.3).

3.2. Species of Headwaters

Headwater streams are the primary habitat for many species. In this section, I provide examples from many taxonomic groups, but it would be impossible to refer to all the species known to use these habitats from around the world. There are suggestions that headwater streams may have been less intensively sampled than fish-bearing reaches of streams, although that is difficult to quantify. The trophic roles of particular taxonomic groups are not the same globally, and many authors have noted that the aquatic insects that play a large role in detritivory in temperate regions may be replaced by decapods or fishes in tropical regions [45,46,54]. Other such shifts have likewise been noted. I have not attempted to distinguish the species that are exclusively found in headwaters as opposed to small streams in general. One needs to consider the local environmental controls on composition (environmental filtering) versus the regional source pools of taxa [69].

3.2.1. Algae and Other Microbiota

Many of the diatom species found in headwater streams [60,70] are cosmopolitan and also found in larger streams and even lakes (<http://www.algaebase.org/> accessed 6 July 2018). Danehy et al. [60] reported that of the 72 algae species found in the headwaters of Oregon, USA, they were almost entirely of the prostrate diatom species. In their Oregon streams, they found a single species, *Planothidium lanceolatum* (listed as *Achnanthes lanceolata* (Brébisson) Grunow), often made up half of the relative abundances of algae at the 18 sites they evaluated. Danehy et al. [60] found some green algae and Cyanobacteria species but very few. Similarly, of the 172 algae species determined from small, cloud forest streams in Bolivia, most were diatoms [63], and diatoms were predominant in two small, shaded streams of Australia [71]. However, in an experimental study of the influence of current velocity

and substrate in Colorado, USA, there were 88 taxa identified in that mountain stream, including 57 diatoms, 21 chlorophytes, 8 Cyanobacteria and 2 Chrysophyta [62]. In that study [62], Cyanobacteria were only common in the lowest of flow conditions and prostrate diatoms tended to predominate in the faster currents. It has been suggested that most of the diatom taxa associated with headwaters are there due to the typically oligotrophic nutrient status of those areas [70]. Many species of algae, especially diatoms and other unicellular algae, are considered to be cosmopolitan according to some authors [69].

Fungi in freshwaters are considered to be ubiquitous throughout surface water, whether streams, lakes or wetlands. Given that their spores can be dispersed aurally around the world, this is not surprising. There appears to be no evidence of species of aquatic fungi being restricted in distribution to headwaters (Felix Bärlocher, pers. comm.). There are relatively few studies of other microbes, but one study showed that bacterial diversity was both higher in headwaters than downstream reaches and also that there was a large beta diversity consistent with distances through the stream network [56], as seen in many other taxa groups as noted above.

3.2.2. Plants

Vascular plants can be found in headwater streams, such as the genera *Ranunculus* and *Callitriche*, but in general, macrophytes living under water are uncommon in steep, small streams [72,73]. Along low-gradient, headwater stream margins, there are many emergent angiosperms, but the majority are in the wet banks rather than with their roots submerged in the stream bed [74]. Most of the plants found in headwater streams are bryophytes (mosses and liverworts). Fritz et al. [75] found at least 60 taxa of bryophytes representing 20 families across ephemeral, intermittent and perennial streams in the USA, with fewer taxa in streams with less permanent flows. They found that over half of the species were found in only one of their 95 sites [75]. Suren [76] found 83 taxa of bryophytes in small streams of New Zealand, and the composition of bryophyte assemblages showed that liverworts and mosses formed separate groupings in his statistical classification of sites. Bryophytes were most commonly found on relatively immovable large cobbles and boulders, a reflection of their slow-growing characteristics [76]. In 108 small, high-elevation streams in Nepal, a total of 44 species of bryophytes were found [77]. In general, bryophytes are not considered to be freshwater obligates, and some taxa found in streams also exist beyond the water.

3.2.3. Invertebrates

Among freshwater animals, over 60% are insects or crustaceans [31]. Some invertebrates are found solely within headwaters, and other groups have apparently diversified from cool-water, headwater environments. For instance, the spiketail dragonfly (*Cordulegaster* spp.) larvae are primarily found in headwater streams, and adults spend their lives in the forest and forest canopy [33]. The stonefly genus *Scopura* (Scopuridae) is restricted to small, montane streams of Japan and the Koreas [36]. This family of about seven species are unusual in having wingless adults. The larval stages appear to grow slowly and may take up to four years to reach the adult stage, during which they are detritivorous, feeding on leaf litter, which is typically abundant in small, forested streams. In some tropical streams, shrimps such as *Atya*, *Xiphocaris*, and others migrate seasonally back to headwaters to breed from the estuaries where they spend part of the year [15,45]. Decapods (e.g., crabs and *Macrobrachium* shrimp), snails and other taxa can be found predominantly in headwaters, and some may be obligate headwater species [15,45]. Many other taxa, such as mountain midges (Blephariceridae), are headwater specialists as well.

Within the Trichoptera, Wiggins and Mackay [78] identified patterns at the generic level. In particular, within the filter-feeding group Hydropsychidae, they suggest *Parapsyche*, *Arctopsyche* and *Dipletrona* are typical of headwater streams. *Parapsyche* and *Arctopsyche* occupy steep streams, using the microhabitats between cobbles and boulders with hydraulic jumps to place their nets, associated with their predatory habits [42,79]. *Dipletrona* appears to require cool water [80]. Other Trichoptera genera

also are primarily associated with headwater streams, particularly some of the cased genera belonging to the family Goeridae and the subfamily Pseudostenophylacinae [78]. The genus *Eocosmoecus* (Trichoptera) appears to be another high-elevation, headwater specialist, perhaps because of their detrital food [81].

3.2.4. Amphibians

Many forest amphibians are associated with headwater streams and some obligately so. For instance, many torrent salamanders (*Rhyacotriton* spp.), coastal giant salamanders (*Dicamptodon* spp.) and the tailed frog (*Ascaphus truei*) of the Pacific Northwest of the USA are primarily found in or around headwater streams [82,83]. Cool summer temperatures are regarded as one of the key features of these headwaters contributing to the persistence of such stream-associated amphibians [49]. Campbell Grant et al. [16] found stream-dwelling *Desmognathus* species in eastern USA occupied the headwaters and showed evidence of upstream-directed movements. Many species are found in the smallest of streams as a refuge from predation. Some species are associated with special conditions associated with springs, caves and other small headwater features, such as the Blind salamander (*Proteus anguinus*) of the Pyrénées mountains of France. In the tropics, there are large numbers of species found solely or predominantly in headwater streams, such as many clades of the Bufonidae.

3.2.5. Fish

There are an estimated 12,470 freshwater fish species [31], but it is not possible to tally how many of these are predominantly found in headwaters. One example of fishes found primarily in headwaters is *Anablepsoides hartii* as detailed in Section 2.2 above. Some taxa, such as the tetras (Characidae) of South America have taxa unique to headwaters [84]. Some groups of fishes are mostly restricted to headwater habitats, including the darters, *Etheostoma* (Percidae) [19], and many species of the genus *Galaxias* (Galaxiidae) [85]. Many fishes migrate seasonally to headwaters to breed or rear where predation rates may be relatively lower, food resources might be greater, temperatures or flows may be more appropriate, or for other reasons.

Fishes show distribution patterns consistent with some species being headwater specialists. In a study from Oklahoma, 21 of 58 species were unique to headwaters across 65 sites in a drainage from 1st to 5th order streams [86]. They determined that large differences in species composition (beta diversity) among headwaters was attributed more to turnover than nestedness as a mechanism. In a stream system in Colombia, three species of Astroblepidae were found only in the smallest of streams out of a fauna of 27 species [87].

3.2.6. Others

A number of other vertebrate species are associated with headwaters as a source of food or nesting areas. For instance, desmans (*Galemys pyrenaicus*) are a mammalian insectivore that swims to the bottom of fast-flowing streams to capture stream invertebrates [88], in a similar pattern to water shrews. The small invertivorous birds known as Dippers (*Cinclus* spp.) are found in many small streams, although they are found in cobble-bottom streams that can be quite large, so they are not particularly a headwater specialist. Several of the Asian turtles are stream dwellers and are mostly found (and exploited) in headwater streams, such as the big-headed turtle, *Platysternon megacephalum* found in southeast Asia [39].

3.3. Taxonomic Richness, Life History Traits and Diversification

There is ongoing interest in patterns of the amount of alpha diversity, or species richness, in streams of different sizes. Many studies find lower taxonomic richness in headwaters than in downstream reaches [52], but others find higher richness in headwaters [89]. Most often, the evidence suggests that species richness may be relatively lower in headwater streams. However, it has been shown repeatedly that there is high beta diversity among headwater streams (for an exception,

see Reference [66]), so while the richness of species in a particular headwater may not be exceptional, there is relatively less overlap in the species composition in headwater streams in a region [52,60]. In a study of headwater streams in Oregon, from the 194 invertebrate taxa identified, 42 of those taxa each occurred in only a single stream out of their 18 streams [60].

Genetic differentiation between populations in headwaters appears high and is attributed to small, isolated populations with limited gene flow [18,19]. Dispersal is limited within stream networks [90], and headwaters may be isolated by distances down to tributaries and then back up to other headwaters [14]. Modelling results suggest that headwaters should have high F_{ST} values and low genetic diversity [91], consistent with empirical observations.

Darters (genus *Etheostoma*) in eastern North America are a good example of a taxon that has apparently diversified in headwater streams [19]. This apparent radiation of species occurs due to small populations with limited dispersal abilities across the riverscape. Likewise, some tetras (Characidae) in South America show similar patterns of high diversity between headwater streams [84]. Some groups of amphibians appear to have differentiated in headwater systems, such as the torrent salamanders (*Rhyacotriton* spp.), dusky salamanders (*Desmognathus* spp.) and bufonids. The toad family, Bufonidae, has nearly 600 species, most of which occur in the tropics. Many clades in the bufonid phylogeny are derived from the evolutionary radiation of headwater lineages (e.g., *Atelopus*, *Rhaebo* and *Rhinella*) [92], and this has occurred repeatedly on several continents. The caddisfly family Limnephilidae is proposed to have diversified from cool stream ecosystems [78], as have several other lineages of freshwater invertebrates, and likely other taxa. Some lineages of snails and clams in southeast Asia appear to have differentiated in headwater streams and show a high degree of endemism [45]. Thus, it seems the combination of isolation of populations in headwaters, relatively small population sizes, drift and low genetic diversity can be the leading causes of diversification in freshwaters.

Life history traits such as dispersal, drought tolerance, resting stages (e.g., diapause), egg banks and other attributes may differ between headwaters and larger streams. Fishes in Brazilian headwater streams tended to have traits such as smaller body size, less piscivory, higher algivory and detritivory, less use of sensorial barbels for foraging and less parental care compared to larger streams [57]. Headwater species may have limited tolerance for thermal changes. However, this thermal breadth may differ by elevation in different parts of the world. In a temperate region, thermal breadth decreased with elevation, but in contrast, populations in a tropical region (Ecuador) had greater thermal breadth as elevation increased [93], emphasising that life history traits are likely to vary in complex ways across the globe. Species may also take on trophic roles in headwater streams atypical for their genus or family, such as larvae of black flies in headwaters that have secondarily lost their filtering fans and instead have become grazers of biofilms [94].

4. Conservation and Stewardship and Future Research Directions

4.1. Threats from Land Use

Headwater streams are very easy to ignore due to their high number in the landscape and small size, resulting in redirection (Figure 2A), burial (Figure 2C), channelization and other bank modifications (Figure 2D). In forestry and agricultural landscapes, headwaters receive little to no protection on average around the world [95], and the past two decades has seen an increased focus on these source streams, mostly for their impacts on water supplies and fish habitats downstream. Headwaters are also important providers of materials and nutrients to downstream environments [96–99].

Because of the large influence of the surrounding landscape, headwaters can also be vulnerable to pesticides and other chemical inputs, to the alteration of hydrology, to insolation and to other effects. These impacts added to the small habitats and lack of refuge make headwaters among the most vulnerable of ecosystems. This influence relative to the stream area can quickly degrade headwaters, with the resulting lack of function and loss of ecosystem services. Importantly, all these

impacts can accumulate as water moves downstream and as it meets water from other sources, leading to cumulative effects from the perturbations of the range of land uses and from major disturbance downstream.



Figure 2. Examples of the adverse alterations of headwater streams: (A) A notice of a creek being “relocated” to enable development in British Columbia, Canada (October 2017); (B) a culvert at a road crossing in British Columbia; (C) the origin of Wilket Creek, part of the West Don River in Toronto, Canada emerging from its subterranean network now mostly in storm drains (note the person standing in front of the opening); (D) an ephemeral stream in Toronto with a mowed lawn to its edge; (E) a headwater stream converted to a ditch near Umeå, Sweden. Figure 2C,D are courtesy of Brian Kielstra, the University of British Columbia, and Figure 2E is courtesy of Lenka Kuglerová, Swedish Agricultural University.

Forest harvesting around headwaters is a large issue that has been studied extensively around the world [44,60,83]. Most evidence demonstrates biodiversity is lost with the increasing intensity of land use. Foundation species, such as bryophytes, are easily lost as a result of land-use impacts of forestry, agriculture and urban development [76] and may take decades to recover following the disturbance, including by “restoration” activities [100]. The global extent of forestry makes this one of the leading threats to headwaters internationally. However, forests can regenerate, but we know little about the rates and mechanisms by which the rarer and less mobile species recover from harvesting [14], particularly in plantation forests that are common in many parts of the world.

Headwaters are also easily channelized, redirected or buried (Figure 2C). In some agricultural and urban landscapes, a large portion of the catchment’s headwaters can end up in pipes [101,102]. Burying streams more-or-less eliminates their roles in flood mitigation and the provision of ecosystem services [103]. In agricultural lands, streams are ditched and subject to excessive erosion, nutrient additions, loss of structure, pesticides and livestock disturbances [3]. In some places, e.g., the eastern USA, mountaintop mining digs out the tops of mountains to gain access to coal, filling the stream valley with the overburden of mineral materials and burying streams deep below rock [104]. As a consequence of damage to headwater streams, there has been a lot of effort at stream restoration, but mostly in fish-bearing reaches, where the simple assumption that physical habitat is limiting is usually applied. Restoration efforts are typically based on engineered, structural features without regard to what processes and attributes have been disturbed, often at great expense and with little effect [105,106] or even making the problems worse [100].

4.2. Threats from Isolation

Flow regulation by dams typically occurs further downstream, but this can alienate critical seasonal habitats that species that migrate require. For instance, some of the species discussed above that breed in headwaters and move downstream as they increase in size may not be able to move back upstream past barriers due to movements created by dams. In some landscapes, headwaters may provide water sources to local communities and thereby be drained of water, particularly during seasons of water scarcity. Even culverts for stream passage under roads may create significant barriers to the upstream movements of species, particularly if those pipes become “perched” by erosion at the downstream end [107] (Figure 2B).

Fagan [14] notes that headwaters are the most isolated stream segments simply due to the fact that there is only one way to colonise, that is, from the downstream end. That simple observation indicates that headwater populations are subject to higher risks of local extinction, particularly from seasonal low waters, which may be exacerbated in the face of global change (see Section 4.3). Dams downstream, whether large or small, will further diminish the rates of colonising other headwater streams for species limited to the stream network. Moreover, urban development can also result in the loss of connectivity and genetic differentiation of headwater populations, such as Brook Trout [108]. As discussed above, this isolation of populations coupled with small population sizes provide the conditions for genetic divergence and even diversification [90]. However, that diversification may mean that unique species might be lost before we appreciate their taxonomic status. In some parts of the world, groundwater extraction may provide local water supplies and the reduced recharge of headwater channels leads to a longer duration of intermittency and can imperil the persistence of headwater specialist species of macroinvertebrates [40].

The caddisflies (Trichoptera) *Thremma gallicum* (Uenoidae) and *Drusus discolor* (Limnephilidae) of Europe show disjunct distributions linked to post-glacial refuge, presumably associated with cooler temperatures of higher elevation headwaters in mountainous regions [109]. Patterns of disjunct distributions, particularly of higher elevation species is probably common but little explored. This isolation into refuge areas that are themselves subject to global warming may lead to species' extinction.

There are few comprehensive surveys of biological diversity of headwaters in general, and those that have been published are generally for temperate regions. Moreover, most of these studies are for forested regions. Thus, there is a large opportunity to document the taxonomic, trait and functional diversity of headwater streams over large portions of the earth. Developing clear and testable hypotheses about the functional use of headwaters by species should also be a future goal of ecological research.

4.3. Global Change

Global warming may overrun species' abilities to adapt to warming conditions, and headwaters may no longer provide the thermal refuge that some species need [110]. Furthermore, global change is altering hydrologic regimes in a way that may diminish water quantity and, thereby, habitat space needed by populations in these small aquatic environments. Smaller volumes of water receiving long-wave solar radiation coupled with higher rates of other heat exchanges will mean a reduced habitat space and warmer conditions, not conducive to the protection of modern headwater ecosystems. Moreover, this warmer water will feed into downstream networks, threatening coolwater species in larger streams or lakes.

The hydrological alterations noted above also predict a greater degree of intermittency of small channels [27]. This intermittency may reduce the duration of flows needed for some species to take advantage of the functions of headwaters discussed above, such as refuge from predators and competitors, thermal refuge and others. This is another topic that will require more study, including experimental dewatering, to appreciate the potential risks [27].

Headwater streams in mountain regions of the world are changing quickly as many glaciers recede and seasonal snowpacks diminish. Species associated with these areas may be at risk, such as the two nemourid stoneflies, *Lednia tumana* and *Zapada glacier* of the Rocky Mountains of western North America, both of which were proposed as candidates for listing as endangered in the USA. However, these habitats are poorly studied, and such species may be more widely distributed than previously considered. However, as we study these species closer, we learn that there may be different species that we did not recognise earlier as turned out to be the case for the stonefly genus *Lednia* once more sampling effort was expended [111]. Whether these particular species are considered threatened depends on additional criteria. More attention to montane headwater streams is needed, especially in the face of predictions of greater rates of change to the hydrology of alpine areas.

However, headwaters are not all montane and are abundant habitats everywhere as the first surface water sources. As such, these areas come into potential conflict with many land uses.

Headwater streams are very vulnerable to anthropogenic disturbance, whether by local land use (forestry, mining, agriculture and urbanization) or global change (climate, aerial dispersal of pesticides and other contaminants). The tolerance of headwater populations and communities to changes in the face of environmental extremes is not well-tested. In their own right, these systems may be imperilled. However, these are also the sources of ecosystem services we depend upon as they flow into larger systems where we take advantage of them. Protecting these headwater sources protects our own interests as well as conserving biological diversity.

4.4. Solutions

The protection of headwaters around the world is challenging. Even in the USA, controversy over whether headwaters warrant protection under the Clean Water Act is not settled [112,113]. In many parts of the world, the values of headwaters are not recognised against the backdrop of the economic value of development of the surrounding landscape right up against stream margins. In forestry, agricultural and urban settings of some jurisdictions, riparian buffers of vegetation (preferably native species) are retained to protect headwaters [114] but are rarely sufficient to protect these ecosystems entirely. Other solutions, such as protected areas, are key in some landscapes undergoing rapid development [45]. Once damage is incurred, it is difficult or impossible to restore in human time frames and much less expensive to avoid damaging these ecosystems in the first place [106]. Efforts at restricting pollution sources, such as from nutrient and pesticide runoffs, have made progress, but it is insufficient in many places around the world. More recognition of the value of headwaters for their ecosystem services and unique habitat values and as source areas could result in better management [97].

5. Summary

Headwater streams are the source for downstream environments and provide support for the stream network in terms of the amount and quality of water, as well as resources such as organic matter. These small streams provide small, somewhat isolated habitats (nowhere to go but downstream) and can show high degrees of environmental differences among headwaters promoting diversification and endemism among the organisms found there. There are many functions that make headwaters unique environments, including seasonally moderated temperatures and flows, enemy-free space, unique resources and relatively more stable physical environments. The very large influence of the surrounding landscape on headwaters makes these streams more vulnerable to physical change and less likely to have the resilience provided by multiple refugia as found in stream networks. However, they are the stream environment that is most likely to receive the least protection from land use and probably require more conservation action.

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