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THE CONTRIBUTION OF HEADWATER STREAMS TO BIODIVERSITY IN RIVER NETWORKS[1]

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ABSTRACT: The diversity of life in headwater streams (intermittent, first and second order) contributes to the biodiversity of a river system and its riparian network. Small streams differ widely in physical, chemical, and biotic attributes, thus providing habitats for a range of unique species. Headwater species include permanent residents as well as migrants that travel to headwaters at particular seasons or life stages. Movement by migrants links headwaters with downstream and terrestrial ecosystems, as do exports such as emerging and drifting insects. We review the diversity of taxa dependent on headwaters. Exemplifying this diversity are three unmapped headwaters that support over 290 taxa. Even intermittent streams may support rich and distinctive biological communities, in part because of the predictability of dry periods. The influence of headwaters on downstream systems emerges from their attributes that meet unique habitat requirements of residents and migrants by: offering a refuge from temperature and flow extremes, competitors, predators, and introduced species; serving as a source of colonists; providing spawning sites and rearing areas; being a rich source of food; and creating migration corridors throughout the landscape. Degradation and loss of headwaters and their connectivity to ecosystems downstream threaten the biological integrity of entire river networks.

(KEY TERMS: biotic integrity; intermittent; first-order streams; small streams; invertebrates; fish.)

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INTRODUCTION

Headwaters (i.e., springs and intermittent, first- and second-order streams) are abundant and unique components of a river network. They are found throughout the network, flowing into other first-order streams or into ones that are much larger. Small streams and springs occur across the range of climatic, geologic, riparian, and biogeographic settings of the United States This diversity produces differences in temperature, light, and hydrologic regimes, water chemistry, substrate type, food resources, and species pools, all of which affect the abundance and diversity of the biota. Because their catchments are not large and are easily influenced by small-scale differences in local conditions, headwater streams are arguably the most varied of all running-water habitats. They offer an enormous array of habitats for microbial, plant, and animal life, but their small size

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also makes them especially sensitive to disruption. Despite their abundance on the landscape and importance as habitat and as the origin of water resources, they are ignored in commonly used cartographic depictions. Small streams are neither named nor adequately indicated on standard topographic maps (1:24,000, USGS 7.5 min quads) (Meyer and Wallace, 2001).

The biota of headwater streams can be placed in five broad groups: (1) species that are unique to these small ecosystems; (2) species that are found in these and larger streams, although their abundance may vary with stream size; (3) species that move into headwaters seasonally as the stream network expands and contracts or as downstream conditions grow less favorable; (4) species that spend most of their lives in downstream ecosystems, but require headwaters at particular life-history stages (e.g., for spawning or nursery areas); and (5) species that live around but not in headwater streams, requiring the moist habitat they provide or feeding on the products of headwaters (e.g., benthic, emerging or drifting insects).

Headwaters are important for all of these groups and therefore are integral to the maintenance of biological diversity in the river network. In the following sections, we (1) provide an overview of the diversity of organisms that depend on small streams, (2) discuss the ecological factors that make these habitats favorable for so many species, (3) illustrate the ecological connectivity that exists between headwater and downstream ecosystems, and (4) discuss the ways in which downstream biota depend upon headwater ecosystems.

BIOLOGICAL DIVERSITY IN SMALL STREAMS

Primary Producers

The algal communities of headwaters are dominated by diatoms (e.g., *Cymbella*, *Gomphoneis*, *Fragilaria*), cyanobacteria (e.g., *Schizothrix*, *Phormidium*), red algae (e.g., *Batrachospermum*), and green algae (e.g., *Stigeoclonium*) (Biggs, 1996). In systems where the headwaters are shaded and low in nutrients, 30-60 algal species are commonly encountered, some of which are not found elsewhere in the river network (Rex Lowe, personal communication). For example, the algal community of a rivulet flowing from an Ontario spring consisted of 34 taxa, 32 of which were diatoms (Sherwood *et al.*, 2000). Although algal taxa richness increased downstream, eight of the taxa found in the first 20 m of the stream were not found at stations further downstream (Sherwood *et al.*, 2000). Rocks and bryophytes in a shaded headwater stream in the southern Appalachians supported 40 algal taxa, 30 of which were diatoms (Greenwood, 2004; Greenwood and Rosemond, 2005). Only a few taxa were abundant; two taxa each represented >20% of the biovolume, whereas each of 29 other taxa represented <1% (Greenwood and Rosemond, 2005). Recent research in continuously flowing Alaskan springs has revealed a diverse algal assemblage that serves as a source of propagules for the downstream flora once those larger streams begin to thaw (Huryn *et al.*, 2005).

Bryophytes (mosses and liverworts) commonly dominate the biomass of primary producers in small streams. Mosses can use only carbon dioxide in photosynthesis and are most diverse and abundant in headwater streams and seeps where water is rich in carbon dioxide (Stream Bryophyte Group, 1999). Bryophyte species richness ranged from 0 to 14 species in small boreal streams (Heino *et al.*, 2005). Four species dominate the bryophyte flora of small, high-gradient Appalachian streams; *Fontinalis dalecarlica* and *Hygroamblystegietum fluviatile* are most abundant in first through third-order streams (Glime, 1968). Mosses and liverworts attach to hard substrates and provide habitat that supports many invertebrate species (Stream Bryophyte Group, 1999).

The types of primary producers found in headwater streams vary greatly as a function of light and hydrologic regime. In well-lit, hydrologically stable springs, a diversity of vascular plants can be found including species endemic to springs such as *Zizania texana* (Texas wild rice) (Hubbs, 1995). A survey of macrophyte diversity in 79 small (mean width 1.9 m), unshaded, lowland streams found 11-24 species per stream (mean = 18.5 species) and a total of 131 species (Baattrup-Pedersen *et al.*, 2003). The headwaters of the Upper Mississippi River flow through bogs and swamps with high vascular plant diversity (Delong, 2005). In headwater streams flowing through steeper and forested catchments, angiosperm diversity is often low and increases as stream width increases. For example, the first 20 m of an Ontario spring-fed stream housed only three vascular plant species, whereas 9-14 species occurred at sites further downstream (Sherwood *et al.*, 2000). In addition to being primary producers in small streams, vascular plants can act as sieves, trapping particles of organic matter (Horvath, 2004). This increases the organic matter availability to consumers in the headwaters, but decreases organic matter transport downstream.

Decomposers

From a taxonomic perspective, bacteria are the least known organisms in headwater streams; however, we know much about their functional role in stream biogeochemical cycles and food webs (e.g., Hall and Meyer, 1998). They are critical to processing of organic matter, which alters nutrient and organic matter exports from small streams to downstream ecosystems as described elsewhere in this series of papers (Wipfli *et al.*, this issue). Dissolved organic carbon (DOC) provides the C source supporting bacterial metabolism and is the most abundant form of organic matter exported from headwaters to downstream ecosystems (Allan, 1995). Leaching of leaf litter is one source of DOC in headwaters that generates a diversity of compounds that differ in their availability to bacteria. Highly labile DOC supports local bacterial metabolism, whereas DOC of intermediate lability is exported and supports bacterial metabolism downstream (Wiegner *et al.*, 2005). Bacteria from headwater sites were able to grow on DOC leached from a nearby riparian species, whereas bacteria collected further downstream were able to use DOC leached from a wider array of species (Koetsier *et al.*, 1997). Genetic diversity of bacteria did not vary significantly with distance downstream in a blackwater stream (McArthur *et al.*, 1992). However, genetic similarity between sites decreased with increasing distance downstream, suggesting genetic differences among headwater and downstream populations of a species (McArthur *et al.*, 1992). Methods for assessing bacterial diversity are recent and still developing, and have not been applied to the entire bacterial assemblages in headwater streams. On the basis of what has been discovered in soils (Tiedje *et al.*, 1999), we would expect the sediments and biofilm of headwater streams to contain at least hundreds to thousands of types of bacteria.

Fungi are also crucial to organic matter dynamics and food webs in headwater streams, and we know considerably more about their diversity than about bacterial diversity. Fungi in headwater streams are primarily hyphomycetes, ascomycetes, and oomycetes. Species composition changes markedly along the course of a stream (Tsui *et al.*, 2001), but is high even in very small streams (Suberkropp and Wallace, 1992; Gulis and Suberkropp, 2004). Over 51 taxa of aquatic hyphomycete fungi have been found in two tiny streams in the southern Appalachians, where inputs of leaf litter from the surrounding forest are high (Gulis and Suberkropp, 2004). When leaf litter inputs to a headwater stream were experimentally eliminated, fungal taxa richness declined from 43 to 36 taxa (Gulis and Suberkropp, 2003). Fungal species composition and richness in headwater streams are strongly influenced by the species composition of riparian vegetation and water chemistry (Bärlocher and Graca, 2002; Gulis and Suberkropp, 2004).

Insects

As water first emerges from the ground in a spring or seep, it provides habitat for an array of insect species. Thirteen species of caddisfly were found within 20 m of the source of an Appalachian springbrook (McCabe and Sykora, 2000). As many as 18 caddisfly species were found in individual California springs (Erman and Erman, 1995), and from 5 to 38 chironomid taxa were identified from individual springs in the High Plains (Blackwood *et al.*, 1995). Unique faunal assemblages have been linked to characteristic water chemistries of springs, reflecting different levels of contamination of their ground-water sources (Williams *et al.*, 1997).

The springs and small seeps that provide habitats at the beginnings of a river network are inadequately mapped. A study in headwater streams of West Virginia and Kentucky illustrates this point. From February through April 2000, Stout and Wallace (2003) sampled from the first continuous flowing water downstream to either a confluence or the point on a topographic map where a solid blue line stream began; i.e., they sampled 34 flowing streams that were unmapped or indicated as intermittent. Their samples included over 86 insect genera in 47 families. Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa richness, commonly used as an indicator of water quality, increased with distance from the source in these unnamed streams (Figure 1). The seeps where water first emerged from the ground had

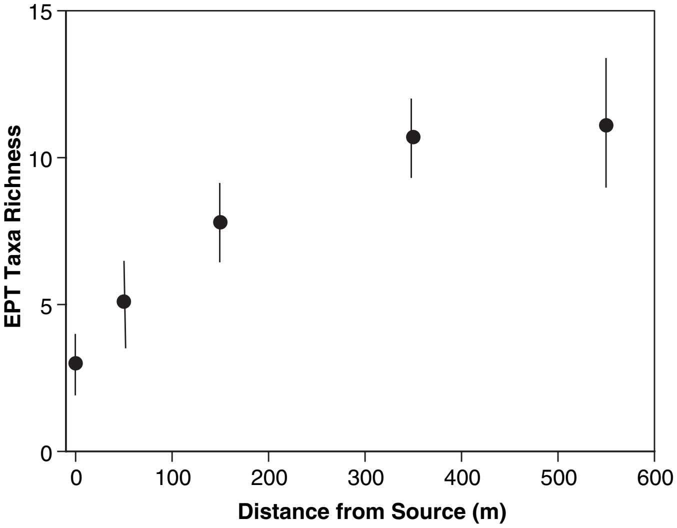

FIGURE 1. Taxa Richness (Mean ± 95% CI) for Insects in the Orders Ephemeroptera, Plecoptera, and Trichoptera Collected From 34 Unmapped Headwater Streams in Kentucky and West Virginia. Richness is plotted *vs.* distance from the point at which water emerged from the ground. Data are from Stout and Wallace (2003).

an average of three EPT taxa; sites within only 150 m of the source had an average of eight EPT taxa; and EPT taxa richness was similar (11 taxa) at 350 and 500 m from the source. Although these streams were either unmapped or designated as intermittent, EPT and other insect taxa with multiyear aquatic life cycles were found in these streams, some with catchments as small as 4 ha (Stout and Wallace, 2003).

Long-term stream research at Coweeta Hydrologic Laboratory in North Carolina provides further evidence of the diversity of aquatic insects in very small, unmapped streams (Table 1). At least 51 families and 145 genera of aquatic insects have been collected over three decades of sampling in eight headwater streams with catchments ranging in size from 5 to 61 ha. None of these streams is shown on standard topographic maps. Putting this taxonomic diversity into some perspective, there are only 33 families and 80 genera of freshwater fishes in the entire state of North Carolina (Menhinick, 1991).

TABLE 1. Diversity in Aquatic Insects Found in Headwater Streams of Coweeta Hydrologic Laboratory in the Southern Appalachian Mountains of Western North Carolina (Courtney, 1994, 2000; Gurtz, 1981; Huryn, 1990; Huryn and Wallace, 1985, 1987a,b, 1988; Lugthart and Wallace, 1992; Wallace *et al.*, 1991, 1999).

Order	**Number of Families**	**Number of Genera**
Ephemeroptera (mayflies)	5	10
Odonata (dragonflies, damselflies)	2	2
Plecoptera (stoneflies)	8	15
Megaloptera (alderflies, dobsonflies)	1	1
Coleoptera (beetles)	3	4
Trichoptera (caddisflies)	13	22
Diptera (true flies)	19	91*
Total	51	145

*Includes Chironomidae.

Small streams contain unique as well as widely distributed insect species. A list of eastern North American stoneflies that occur only in first- and second-order streams includes 60 species in 24 genera and 8 families (R.F. Kirchner and B.C. Kondratieff in Stout and Wallace, 2003). Thirty-six of the 78 caddisfly species in a Sierra Nevada stream network were found only in springs; eight of these were restricted to constant temperature springs (Erman and Erman, 1995). Species composition differed greatly among individual streams; on average, only 23% of species were similar among streams (Erman and Erman, 1995). Insect samples from seven central Oregon springs and seeps included 106 species; 92% of those were found only in the springs and seeps and not in the main creek (Anderson and Anderson, 1995). Most of the uniquely spring species were dipterans.

Aquatic insect diversity is high in the southeastern United States; 40% of the North American aquatic insect fauna can be found in the Southeast (Morse *et al.*, 1997). Much of this richness is in small springs and streams (Morse *et al.*, 1997). For example, extensive sampling in a Louisiana spring complex captured 43 caddisfly species including 5 endemics (Morse and Barr, 1990). Over 650 insect species have been found in Upper Three Runs Creek, a fourth-order stream on South Carolina's Coastal Plain; 180 species are found in its second-order tributaries, and many are found only in the headwaters (Morse *et al.*, 1980, 1983; John Morse personal communication). The spring-fed ravine ecosystems of northern Florida harbor 138 caddisfly and 23 stonefly species, which represent 70% and 55%, respectively, of all Florida species in these orders (Rasmussen, 2004). The high-gradient streams of the Appalachians are also rich in insect species, with collector-gatherers and shredders as the largest contributors to secondary production in the headwaters (Wallace *et al.*, 1992).

Even small streams that do not flow continuously may contain a rich and sometimes unique insect fauna. An intensive study of seven "summer-dry" (i.e., intermittent) streams in western Oregon < 12 km apart found 202 aquatic or semi-aquatic insect species, at least 13 of which were new to science (Dieterich and Anderson, 2000). The two intermittent streams that were in forest settings had more insect species (125-126 species) than a permanent headwater stream (100 species) in the same setting. Considering the entire species pool, 8% were found only in permanent headwaters, 25% were restricted to intermittent streams, and 67% were found in both. Over half of the species found were dipterans, and EPT taxa comprised about 30% of the insect fauna (Dieterich and Anderson, 2000). Somewhat higher taxonomic richness was observed in permanently flowing streams (71-92 taxa) than in intermittent streams (54-93 taxa) in another group of western Oregon streams, although the peak emergence biomass was three times higher in the intermittent streams (Progar and Moldenke, 2002). This emerging biomass provides a food resource for riparian consumers. In these streams, only two EPT genera were unique to the intermittent channels, and most taxa were common to both stream types. In the southeastern United States, 171 taxa were found in six small Alabama streams that varied in their permanence (Feminella, 1996). Only 7% of taxa were found exclusively in intermittent streams, whereas 75% of taxa were found in both perennial and intermittent streams. In the Southwestern United States, 10 species of winter-emerging stoneflies were found in New

Mexico streams that are dry for long periods in spring and autumn (Jacobi and Cary, 1996). Adaptations for life under these conditions include small size, rapid development, and a period of diapause during egg or larval stages. Subarctic Alaskan streams do not flow in winter because they are frozen. Although some dipteran species have adaptations that allow them to survive freezing, most aquatic invertebrates die when streambeds freeze; these species survive by migrating away from a freezing front or remaining in habitats such as headwater springs that do not freeze (Irons *et al.*, 1993; Huryn *et al.*, 2005). These refugia serve as sources of colonists when streams begin to thaw (Huryn *et al.*, 2005).

Mollusks, Crustaceans, and Other Invertebrates

The invertebrate fauna of hardwater springs is dominated by crustaceans, triclads, and mollusks (Glazier, 1991). Although mollusk diversity is generally the greatest in larger rivers, mollusks can also be conspicuous and abundant in headwaters. Many species are headwater specialists with small geographic ranges. For example, members of the prosobranch family Hydrobiidae frequent springs and spring-fed streams throughout the USA. About 200 rare headwater hydrobiid species occur in the USA. (listed by NatureServe 2005 as imperiled or critically imperiled [G2 or G1]), with dozens of narrowly endemic species from the Southeast, the Great Basin and the Northwest (Herschler, 1994; Frest and Johannes, 1999). Nineteen headwater species are either protected by the Endangered Species Act or are rare enough to be considered for listing. Hydrobiids, physids, and lymnaeids are the most abundant mollusks in hardwater springs in the temperate zone (Glazier, 1991). The pleurocerid snails such as *Goniobasis* and *Juga* are often dominant grazers in headwaters of the Southeast and Northwest (Lamberti, 1996; Steinman, 1996). Their absence from intermittent streams has been suggested as one of the factors responsible for high diversity of insect grazers in those systems (Dieterich and Anderson, 2000). Pearl mussels (*Margaritifera* spp.) can also be extremely abundant (>100 m^{-2}) in small streams (Johnson and Brown, 2000).

Crustaceans such as amphipods, isopods and crayfish are conspicuously abundant in headwaters. Microcrustaceans such as cladocerans, ostracods, and copepods also live in headwaters, where they can reach very high densities (>10,000 m^{-2}, Galassi *et al.*, 2002). Although fewer than 10 species of macrocrustaceans inhabit a typical headwater site, species composition varies greatly across headwaters; North America supports 600-700 species of large freshwater crustaceans, many of them in headwater streams. The NatureServe database lists 31 amphipod, 4 isopod, and 11 crayfish species as found in springs and springbrooks; of these, 30 amphipod, 3 isopod, and 5 crayfish species are considered imperiled or critically imperiled (G1 or G2, Larry Master, personal communication). Amphipods and isopods are most common in relatively constant, cool waters, where they can reach high densities (Covich and Thorp, 1991). The southeastern United States has the highest number of crayfish species (Taylor *et al.*, 1996). Crayfish comprise a large portion of the biomass in many headwater streams; e.g., they comprise >90% of macroinvertebrate biomass in perennial headwaters of coastal Washington (Haggerty *et al.*, 2002). Macrocrustaceans are not confined to perennial streams. In fact, total crayfish densities were higher in intermittent than in perennial streams in the south-central United States; two species (*Orconectes puntimanus* and *O. marchandi*) had significantly greater numbers in intermittent streams, whereas abundance of the other two species did not differ with stream type (Flinders and Magoulick, 2003).

Small streams support many invertebrate taxa other than insects, mollusks and crustaceans (Table 2), although they have not been as extensively studied. A typical headwater stream might contain 30-300 species and 20,000-2,000,000 m^{-2} of these other taxa, such as turbellarians, gastrotrichs, and nematodes (Table 2). Species richness in these groups may be as high in headwaters as in larger streams (e.g., Kolasa, 1983), and many can be found in intermittent streams. Many are unique to headwaters; e.g., most of the endemic lumbriculid oligochaetes recently discovered in the Pacific Northwest live in seeps, springs, and small streams (McKey-Fender and Fender, 1988; Fend and Brinkhurst, 2000; Fend and Gustafson, 2001).

Fishes

Stream fish diversity generally increases with increasing stream size along a gradient of increasing habitat heterogeneity, pool development, and habitat volume (Schlosser, 1987). The extent to which species richness changes with stream size varies considerably. From 3 to 11 species were found in a second-order Kentucky stream *vs.* 12-25 in a fourth-order stream (Kuehne, 1962); a Texas headwater stream contained 22 species, whereas downstream sections had 33 species (Evans and Noble, 1979). In some cases, the increase in fish species with increasing stream size occurs as a result of species additions, so that headwater assemblages represent a nested

TABLE 2. Invertebrates Other Than Mollusks, Crustaceans, and Insects That Are Common in Headwaters.

Group	Typical Species Richness in Headwaters	Typical Density in Headwaters (no./m^2)	Key References
Turbellaria	3–30	1,000–10,000	Kolasa (1983, 2002)
Gastrotricha	3–30 (?)	10,000–300,000 (?)	Strayer and Hummon (2001), Balsamo and Todaro (2002)
Rotifera	20–200	10,000–1,000,000	Schmid-Araya (1998), Wallace and Ricci (2002)
Nematoda	10–100	5,000–500,000	Traunsperger (2002)
Tardigrada	1–10	1,000–10,000 (?)	Nelson and McInnes (2002)
Oligochaeta	3–30	1,000–50,000	Schwank (1981a,b)
Acari	5–50	100–10,000	Di Sabatino *et al.* (2002, 2003)
Total	40–450	28,000–1,880,000	

Question marks indicate substantial uncertainty in poorly studied groups.

subset of species found throughout the network (e.g., Taylor and Warren, 2001). In other cases, diversity increases but the species are different from those found in the headwaters. For example, small insectivorous fishes numerically dominate first- and second-order streams in the southeastern Coastal Plain; the same species are rare in larger streams (Paller, 1994). Because headwater streams may contain a unique species assemblage, they can make a significant contribution to regional fish diversity (e.g., Paller, 1994).

The location of a small stream in the network also affects its richness (Matthews, 1998). The fish assemblages in second-order Texas streams flowing into other second order streams had a Shannon diversity index of 0.94, whereas second-order streams flowing into third and fourth-order streams had diversity indices of 1.13 and 1.84, respectively (Whiteside and McNatt, 1972). The higher diversity in the streams that flow into larger streams is a consequence of species from the larger stream moving into the tributaries.

Small streams are characterized by small-bodied species such as small minnows, madtom catfishes, darters, and sculpins (Schlosser, 1987). For example, small-bodied insectivorous fishes are numerically dominant in first-order streams in Mississippi, with species richness ranging from 2 to 36 species (Smiley *et al.*, 2005). Samples from only 14 first-order streams in managed pine forests included 18% of Mississippi's native fish species (Smiley *et al.*, 2005). The fish fauna in cold eastern and western North American headwater streams usually consists of a salmonid species, a sculpin, and 1-3 species of cyprinids or catastomids (Moyle and Herbold, 1987). In high-gradient Southern Appalachian streams brook trout (*Salvelinus fontinalis*) are found furthest upstream, with sculpin (e.g., *Cottus bairdi*), dace (e.g., *Rhinichthys atratulus*), and darters (e.g., *Etheostoma flabellare*) slightly further downstream (Wallace *et al.*, 1992). Throughout the southeastern United States, darters in the genera *Etheostoma* and *Percina* contribute to fish diversity in headwaters with 73 species whose habitat descriptions in the NatureServe database include the terms springs, small streams, headwaters, or small creeks. That database lists 180 fish species whose distributions include springs and springbrooks (L. Master, personal communication).

Springs and spring runs often contain unique fish faunas, including endemics found in only one or two springs (Hubbs, 1995). The NatureServe database identifies 49 fish species as exclusive to springs and springbrooks; 30 of these species are ranked as critically imperiled, imperiled, or extinct (NatureServe ranks of G1, G2, or GX; L. Master, personal communication). Many extirpated and threatened southwestern fishes are spring inhabitants. For example, 13 species of pupfishes (*Cyprinodon* spp.) are found in springs in the southwestern United States, 12 of which have NatureServe ranks of G1, G2, or GX. Six endemic *Gambusia* species occur in stenothermal Texas springs, and those species are replaced by the widespread mosquitofish *Gambusia affinis* in downstream reaches (Hubbs, 1995). Unique spring species are also found in more mesic regions. For example, *Etheostoma nuchale* is a darter endemic to two springs in Alabama (Hubbs, 1995); the coldwater darter, *E. ditrema*, has a similar limited distribution.

Fish also occur in intermittent stream habitats. Ten intermittent tributaries of a river in Colorado contained 11 native fish species. Five of those species penetrated 7-9 km upstream in tributaries that were dry except for isolated pools, which were maintained by an extensive ground-water aquifer (Fausch and Bramblett, 1991). Rogue River tributaries that were dry in summer supported large spawning populations of steelhead salmon (*Oncorhynchus mykiss*) in winter (Everest, 1973 in Erman and Hawthorne, 1976). A striking 39-47% of adult rainbow trout (*O. mykiss*) in Sagehen Creek, California, spawned in one intermittent tributary and only 10-15% spawned in the perennial main channel (Erman and Hawthorne, 1976). Intermittent streams and ephemeral swamps contributed 15% and 23% of coho salmon (*Oncorhynchus kisutch*) smolts, respectively, during 2 years in the 10 km^2 Carnation Creek catchment (Brown and Hartman, 1988). The proportion of smolts from intermittent tributaries was higher during 1 year because extensive flows washed out smolts in the main channel and lower during the other year because low spring flows decreased the connectivity between the main stem and intermittent habitats. A recent study in coastal Oregon streams found 11-21% of adult coho salmon populations spawning in intermittent streams (Wigington *et al.*, 2006). Furthermore, juvenile coho tagged in the main channel entered intermittent tributaries during high autumn flows, and smolts that used intermittent tributaries were larger than those using permanent tributaries (Wigington *et al.*, in review).

Many fish species that spend most of their lives in larger streams, rivers, or lakes use small streams for spawning and nursery areas. In addition to the coho salmon, steelhead, and rainbow trout just described, cutthroat trout (*Oncorhynchus clarki*) and chum salmon (*Oncorhynchus keta*) migrate into very small tributary streams to spawn, navigating riffles with half of their bodies out of the water. During their first summer of life, 81% of brook trout spawned in a Canadian lake moved into tiny tributary streams to take advantage of favorable flows and temperatures (Curry *et al.*, 1997). Fishes other than salmonids also use small tributaries for spawning and nursery areas. For example, the trispot darter (*Etheostoma trisella*) is an imperiled southeastern species that lives along the edge of a small river but spawns in a seepage stream (<1 m wide) flowing through a marshy pasture (Ryon, 1986); the slackwater darter, *Etheostoma boschungi*, spawns in similar habitats.

Hence, we can identify three broad classes of fishes that use headwater streams and springs. Headwater specialists use small streams throughout the year. This group includes species of minnows (*Phoxinus, Rhinichthys, Hemitremia*), pupfish (*Cyprinodon*), topminnows (*Fundulus*), sculpins (*Cottus*), and darters (*Etheostoma* and *Percina*). A second class includes generalists that use headwaters as one of many habitats. Many trout, minnows such as creek chub, madtom catfish (*Noturus*), and small sunfishes (e.g., pygmy sunfishes, *Elassoma*) are in this group. These species may maintain permanent populations in headwaters or move into and out of them as the stream network expands and contracts. Some can be found in water barely deep enough for them to swim, such as the pygmy sunfishes that occur in inflow regions of southeastern swamps. The third group lives in larger systems but uses small streams for spawning and nursery areas as described above.

Headwater fish species are vulnerable to extirpation. In the southeastern United States 25% of the 16 headwater species and 70% of the 10 spring species are considered to be jeopardized (Table 3 and Etnier, 1997). Small-bodied fishes that spawn, feed or seek shelter on the stream bottom are particularly vulnerable (Burkhead *et al.*, 1997; Burkhead and Jelks, 2000). Highland endemic species, many that occupy headwater habitats, are being replaced by more cosmopolitan species as southern Appalachian streams are degraded (Scott and Helfman, 2001). Threats to headwater fishes are not unique to the southeastern United States. Headwater species account for 29% of

TABLE 3. Southeastern Fish Species Whose Preferred Habitat Is Headwaters or Springs According to Etnier (1997).

Headwater Species	**Spring Species**
Notropis chrosomus (rainbow shiner)	*Hemitremia flammea* (flame chub)
N. signipinnis (flagfin shiner)	*Notropis harperi* (redeye chub)
Phoxinus cumberlandensis (blackside dace)*	*Forbesichthys agassizi* (spring cavefish)
P. erythrogaster (southern redbelly dace)	*Fundulus albolineatus* (whiteline topminnow)*
P. tennesseensis (Tennessee dace)*	*F. julisia* (Barrens topminnow)*
P. sp.cf. *erythrogaster* *	*Cottus pygmaeus* (pygmy sculpin)*
Rhinichthys atratulus (blacknose dace)	*Elassoma alabamae* (spring pygmy sunfish)*
Semotilus atromaculatus (creek chub)	*Etheostoma ditrema* (coldwater darter)*
S. lumbee (sandhills chub)*	*E. nuchale* (watercress darter)*
S. thoreauianus (Dixie chub)	*E. tuscumbia* (Tuscumbia darter)*
Catostomus commersoni (white sucker)	
Salvelinus fontinalis (brook trout)	
Etheostoma parvipinne (goldstripe darter)	
E. sagitta (arrow darter)	
E. spectabile (orangethroat darter)	
E. whipplei (redfin darter)	

*Indicates species that Etnier (1997) identified as jeopardized or extinct. This list does not include species that use headwaters for breeding.

all fish species in the Maumee (98 total species) and Illinois (135 species) rivers, and headwater specialists have been particularly vulnerable to extirpation (Karr *et al.*, 1985). From 50% to 64% of headwater species are either declining or extirpated from those rivers (Karr *et al.*, 1985). A tabulation of headwater and spring fish species that are presumed Extinct or listed as Threatened, Endangered, or Candidate species under the Endangered Species Act includes at least 13 species dependent on small or intermittent streams and 23 spring-dwelling species (Table 4). This is an extremely conservative estimate; many more headwater- and spring-dwelling fishes are recognized as imperiled by the American Fisheries Society (Warren *et al.*, 2000).

In contrast to this pattern of threatened species in headwaters, protected headwater streams can serve as a refuge for species extirpated from other parts of the network. For example, the smallest known parasitic lamprey species (*Lampetra minima*) was thought to be extinct after the endemic population in Miller Lake was eliminated via poisoning in 1958. Later collections in small tributaries revealed previously unknown populations of the species (Lorion *et al.*, 2000).

Amphibians and Reptiles

Stream-dwelling amphibians can be found in streams as both larvae and adults (Petranka, 1998). Many spend their entire life history within streams, whereas others use streams while larvae, venture into terrestrial habitats as adults, and return to streams only to reproduce. In Appalachian streams, amphibians are primarily found in habitats that lack fish, but the *Dicamptodon* of the western United States and *Necturus* of the Southeast share their habitats with fishes. The tadpoles of some *Rana* and *Bufo* also survive where fishes are present.

Salamanders (larvae and adults) and frogs (adults) can be the dominant vertebrate predators in systems where they occur (Burton and Likens, 1975; Werner and McCune, 1979), and tadpoles exert significant grazing pressure on algae (Stebbins and Cohen, 1995). The presence of amphibians in headwater streams increases the biodiversity by acting as keystone predators (e.g., Fauth and Resetarits, 1991).

North American amphibian databases list 84 salamander species in 18 genera whose habitats include small streams, seeps, springs, or headwater streams (Table 5). In high-gradient Appalachian streams, 3-5

TABLE 4. Fish Species Associated with Small Streams and Springs That Are Presumed Extinct (*) or Are Listed as Threatened, Endangered, or Candidate Species under the Endangered Species Act.

Small Stream Species	**Spring Species**
Phoxinus cumberlandensis (blackside dace)	*Eremichthys acros* (desert dace)
Catostomus santaanae (Santa Ana sucker)	*Gila intermedia* (Gila chub)
Oncorhynchus clarkii seleniris (Paiute cutthroat trout)	*Lepidomeda albivallis* (White River spinedace)
O. mykiss pop. 10 (steelhead – southern California)	*L. altivelis* * (Pahranagat spinedace)
O. mykiss whitei (Little Kern golden trout)	*Rhinichthys osculus nevadensis* & other subspp. (Ash Meadows speckled dace)
Gasterosteus aculeatus williamsoni (unarmored threespine stickleback)	*Fundulus albolineatus** (whiteline topminnow)
Etheostoma chienense (relict darter)	*Gambusia gaigei* (Big Bend gambusia)
E. cragini (Arkansas darter)	*G. georgei* (San Marcos gambusia)
E. fonticola (fountain darter)	*G. heterochir* (Clear Creek gambusia)
E. okaloosae (Okaloosa darter)	*G. nobilis* (Pecos gambusia)
E. phytophilum (rush darter)	*Cottus paulus* (pygmy sculpin)
E. scotti (Cherokee darter)	*Crenichthys baileyi* (White River springfish)
E. susanae (Cumberland Johnny darter)	*C. nevadae* (Railroad Valley springfish)
	Cyprinodon arcuatus * (Santa Cruz pupfish)
	C. bovines (Leon Springs pupfish)
	C. *diabolis* (Devil's Hole pupfish)
	C. elegans (Comanche Springs pupfish)
	C. macularius (desert pupfish)
	C. nevadensis (Amargosa pupfish) (2 subspp. extinct)
	C. radiosus (Owens River pupfish)
	Empetrichthys latos (Pahrump poolfish)
	E. merriami * (Ash Meadows poolfish)
	Etheostoma nuchale (watercress darter)

Note: This is a very conservative listing of species considered imperiled by experts; e.g., of the 11 species identified as jeopardized by Etnier (1997) (see Table 3), only four are listed here, and one of those is extinct.

TABLE 5. Reptile and Amphibian Genera with Species Whose Habitats Include Small Streams, Seeps, Springs, or Headwater Streams.

	Genus	No. of Species
Salamanders	*Ambystoma*	6
	Amphiuma	3
	Dicamptodon	4
	Desmognathus	17
	Eurycea	25
	Gyrinophilus	4
	Haideotriton	1
	Hemidactylium	1
	Hydromantes	3
	Necturus	5
	Phaeognathus	1
	Plethodon	2
	Pseudotriton	2
	Rhyacotriton	4
	Pseudobranchus	2
	Siren	2
	Stereochilus	1
	Typhlotriton	1
Frogs	*Acris*	2
	Ascaphus	2
	Hyla	2
	Pseudacris	2
	Rana	18
	Smilisca	1
	*Xenopus**	1
Toads	*Spea*	2
	Bufo	6
Turtles	*Chelydra*	1
	Kinosternon	6
	Sternotherus	4
	Apalone	3
Snakes	*Nerodia*	7
	Regina	4
	Seminatrix	1
	Agkistrodon	1
	Farancia	2

Note: Data are from NatureServe (accessed July and October 2005), AmphibiaWeb (http://www.amphibiaweb.org), Global Amphibian Assessment (http://www.globalamphibians.org), IUCN Red List (http://www.redlist.org), and Center for North American Herpetology (http://www.naherpetology.org, accessed October 2005).

*Introduced into North America.

species of salamanders in the genera *Desmognathus, Eurycea*, *Gyrinophilus*, and *Leurognathus* occur and are the dominant vertebrate predators in the smallest headwaters; their secondary production is higher in first-order streams than in third-order streams (Wallace *et al.*, 1992). Salamander larvae feed almost exclusively on aquatic invertebrates (Johnson and Wallace, 2005). In the northeastern United States, stream amphibian diversity is concentrated in headwater streams (reports cited in Lowe and Bolger, 2002). Population size of the spring salamander, *Gyrinophilus porphyriticus*, was the highest in small streams without brook trout and lower where connectivity with downstream ecosystems was compromised (Lowe and Bolger, 2002).

Several frog and toad species also occur in small streams: 28 species of frogs in seven genera and eight species of toads in two genera occur in small streams and springs (Table 5). At least two of these species are considered rare (G1 or G2 in NatureServe, 2003), and one (*Rana fisheri*) is presumed extinct. Also listed is *Xenopus laevis*, a species native to Africa and introduced to novel habitats in North America; introductions of this exotic species may be responsible for the introduction of Chytrid fungi to the USA (Weldon *et al.*, 2004). This is an example of a headwater species with an impact far beyond the headwaters.

Reptiles (chiefly turtles and snakes) may also be found in headwater habitats including intermittent streams (e.g., Stone, 2001). Fourteen species of turtles in 4 genera and 15 species of snakes in five genera are found associated with small streams (Table 5). Although reptiles are not usually restricted to or most abundant in these habitats (Buhlmann and Gibbons, 1997), species in several genera (e.g., *Nerodia*, *Farancia*, and *Regina*) specialize on aquatic prey items. The genera listed in Table 5 represent taxa with the strongest ties to headwater habitats and do not include several species that are only loosely associated with streams (e.g., certain species of *Carolina*, *Elaphe*, *Thamnophis*, and *Nerodia*).

Birds and Mammals

Only a few species of birds (e.g., dippers, *Cinclus mexicanus*) actually live in small streams, but many depend on headwaters for food, water, habitat, or movement corridors. The preferred habitat of Louisiana and northern water thrushes (*Seiurus noveboracensis* and *S. motacilla*) is small headwater streams (Prosser and Brooks, 1998). The Virginia rail (*Rallus limicola*) is listed as a species exclusive to springs and springbrooks in the NatureServe database (L. Master, personal communication). Many other species are attracted to the large hatches of aquatic insects that emerge from headwater streams. Birds like flycatchers can be especially abundant around streams (Murray and Stauffer, 1995), and overall bird abundance may be elevated near headwater streams (Wiebe and Martin, 1998). Bird species richness and evenness were higher in the riparian zone of the first and second-order Michigan streams than in the uplands, and 12 species were found only in the riparian zone (Bub *et al.*, 2004). Abundance of several bird species was closely correlated with aquatic insect emergence in small prairie streams (Gray, 1993). Birds such as herons and kingfishers feed on fish and aquatic invertebrates in pools of intermittent streams (e.g., Tramer, 1977).

TABLE 6. A Minimum Estimate of Taxa Associated with Three Small, Shaded Streams (Average Discharge <2.5 L/s) on Catchments 53, 54, 55 (5–7.5 ha) at Coweeta Hydrologic Laboratory, NC.

Taxon	**Estimated Number of Taxa**	**Reference**
Algae	30 diatom species 10 other algal taxa	Greenwood (2004), Greenwood and Rosemond (2005)
Bryophyta	7 moss and 4 liverwort taxa	Greenwood (personal communication)
Fungi	51 taxa	Suberkropp and Wallace (1992), Gulis and Suberkropp (2004, 2003)
Protista	>7 taxa	Vila (1996), Vila (personal communication)
Nematoda	>10 taxa	Vila (1996), Vila (personal communication)
Copepoda	5 species	Vila (1996), Vila (personal communication)
Cladocera	1 species	Vila (1996), Vila (personal communication)
Decapoda	1 species	Wallace *et al.* (personal observations)
Ostracoda	1 species	Vila (1996), Vila (personal communication)
Gastrotrichia	>5 taxa	Vila (1996), Vila (personal communication)
Oligochaeta	>4 taxa	Vila (1996), Vila (personal communication)
Branchiobdellida	1 species	Wallace *et al.* (personal observations)
Rotifera	>10 taxa	Vila (1996), Vila (personal communication)
Turbellaria	>4 taxa	Vila (1996), Vila (personal communication)
Tardigrada	2 taxa	Vila (1996), Vila (personal communication)
Acarina	>3 taxa	Vila (1996), Vila (personal communication)
Bivalvia	1 species	Wallace *et al.* (personal observations)
Ephemeroptera	4 families; 7 genera; >7 species	Wallace *et al.* (personal observations), Wallace *et al.* (1991), Lugthart and Wallace (1992), Wallace *et al.* (1999)
Odonata	2 families; 2 genera; >2 species	Wallace *et al.* (personal observations), Wallace *et al.* (1991), Lugthart and Wallace (1992), Wallace *et al.* (1999)
Plecoptera	6 families; 8 genera; >8 species	Wallace *et al.* (personal observations), Wallace *et al.* (1991), Lugthart and Wallace (1992), Wallace *et al.* (1999)
Coleoptera	3 families; 4 genera; >4 species	Wallace *et al.* (personal observations), Wallace *et al.* (1991), Lugthart and Wallace (1992), Wallace *et al.* (1999)
Trichoptera	14 families; 19 genera; > 20 species	Wallace *et al.* (personal observations), Wallace *et al.*(1991), Lugthart and Wallace (1992), Wallace *et al.* (1999)
Diptera (incl. chironomids)	15 families; 55 genera; >59 species	Wallace *et al.* (personal observations), Wallace *et al.* (1991), Lugthart and Wallace (1992), Wallace *et al.* (1999), Courtney (1994, 2000)
Hemiptera	2 genera; 2 species	Wallace *et al.* (personal observations)
Collembola	1 family; 1 genus; >1 species	Wallace *et al.* (personal observations)
Arachnida	19 genera*	Sanzone (2001)
Amphibia	2 genera; 5 species	Johnson (2001)
Reptilia	> 3 species	Wallace *et al.* (personal observations)
Aves	2 species	Wallace *et al.* (personal observations)
Mammals	4 species	Wallace *et al.* (personal observations)
TOTAL	> 293 taxa	

*Estimated from data on a site ~2 km downstream.

Several bat species forage along streams for emerging insects and drink from the stream (Seidman and Zabel, 2001). Seven bat species in the genera *Myotus*, *Corynorhinus, Lasionycteris* and *Eptesicus* were observed feeding along intermittent streams in California (Seidman and Zabel, 2001). Bat activity was the greatest along the widest intermittent streams, but higher at all stream sizes than at upland sites.

Small mammals found in headwater stream habitats include shrews, voles, and moles. NatureServe (accessed July 2005) lists 5 species of shrews in the genus *Sorex* that are found in and on the banks of headwater streams in the USA. The star-nosed mole (*Condylura cristata*) digs tunnels that lead to small streams and is considered imperiled in the southeastern United States (Harvey and Clark, 1997). Mammals characteristic of small streams in the Pacific Northwest include *Sorex bendirii*, *S. palustris*, *S. pacificus*, *Microtus richardsoni* and *M. longicaudus*; some are obligate headwater species whereas others are widespread but more abundant in headwaters (Richardson *et al.*, 2005). Headwaters are also frequented by species such as raccoon, mink, beaver and otter, which may use them out of proportion to their areal extent on the landscape (Kruuk *et al.*, 1998).

Estimating Biological Diversity in a Headwater Stream

A complete species list does not exist for any headwater stream in the USA. However, based on the studies discussed here, a complete list would likely number in the hundreds to thousands of species. The invertebrate fauna of a first-order German stream (Breitenbach) has been investigated for many years. This 1-m-wide stream is home to 1004 invertebrate taxa (Allan, 1995). Many of these species are small invertebrates living in the hyporheic zone with connections to the ground water. Similar invertebrate diversity is likely to be found in the USA headwater streams. As an example, we consider three first-order, fishless streams (catchments 5-7.5 ha in area and mean discharge < 2.5 l/s) in the southern Appalachian Mountains of North Carolina, which are sites of ongoing long-term ecological research. These heavily shaded streams are in forested catchments and have a dense rhododendron riparian canopy. A list of known diversity in the taxonomic groups found associated with these three small streams is presented in Table 6. The groups about which we know the least (noninsect invertebrates) in these Appalachian streams are very diverse (400 taxa) in the Breitenbach, a small stream where they have been intensely studied (Allan, 1995). It is therefore likely that noninsect invertebrate diversity in the Appalachian streams is considerably higher than what we report here. Birds and reptiles associated with these streams have not been studied, so their diversity is unknown. Thus, we know that at least 293 taxa are associated with these three first-order streams, but their true diversity is likely at least twice that.

Headwater diversity is underestimated not only because of limited sampling, but also because so many headwater species remain undescribed. For example, half of the stonefly species associated with headwaters were described only in the last two to three decades (Stout and Wallace, 2003); new species of hydrobiid snails are continually being described; and a recent survey of ravine streams in the Florida panhandle found a dozen caddisfly species new to science (Rasmussen, 2004). Thorough surveys of small streams routinely discover new species, genera, and even families of invertebrates (Strayer, 2000). This is especially true for the hyporheic fauna living within the streambed, a habitat that is rarely sampled systematically.

THE BIOLOGICAL IMPORTANCE OF SMALL STREAMS IN RIVER NETWORKS

Headwater streams and springs may be small in size, but they provide habitats for a rich array of species, which enhances the biological diversity of the entire river system. Furthermore, the strong biological linkages between these upstream habitats and downstream ecosystems enhance and maintain species diversity downstream. The attributes of headwaters that make them essential habitats and that lead to linkages with other ecosystems are diagrammed in Figure 2 and discussed in this section.

Headwaters Support Many Species That Occur Nowhere Else in the River System

The previous sections provided numerous examples of species found only in headwaters. These species enhance diversity in the entire system (e.g., Paller, 1994). There are many reasons why headwater streams have a unique complement of species; we describe several here.

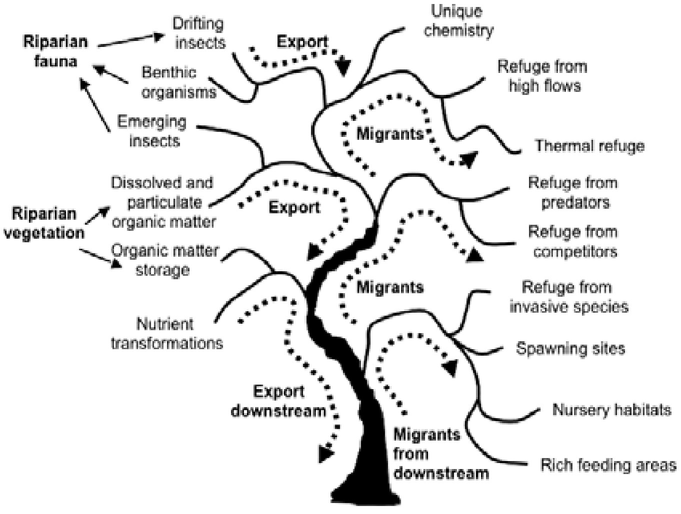

FIGURE 2. Factors That Contribute to the Biological Importance of Headwater Streams in River Networks. Attributes on the right benefit species unique to headwaters and also make headwaters essential seasonal habitats for migrants from downstream. On the left are biological contributions of headwater ecosystems to riparian and downstream ecosystems.

Headwaters Provide Unique and Highly Diverse Physico-chemical Habitats. Headwater streams contribute to species richness in river systems in many ways, chief among which is the diverse array of unique habitats that they provide. As noted by a fish ecologist, "overall, there are probably more environmental, biological and ichthyological differences among different kinds of first-order streams than among stream reaches in higher orders" (Matthews, 1998; p. 311). Headwaters range from steep, swift, and cold mountain streams to warm, low-gradient, swampy tributaries. The light regime in small streams ranges from well lit to heavily shaded. Their chemistry reflects the catchment's soil, geology, and human disturbance regime (e.g., Williams *et al.*, 1997). Their biology reflects the complement of species (both native and introduced) in the region and the presence or absence of barriers to exchange with neighboring ecosystems (e.g., downstream, riparian, or in adjacent valleys). The flow regime in small streams can be fairly constant in ground-water-fed springs, predictably variable from seasonal snow melt, intermittent with isolated pools sustained by ground-water connections, perennial with a flashy hydrograph after rainstorms, or one of many other variations. Small streams can serve as a refuge for species that are vulnerable to being swept downstream. With lower discharge and proximity to refuges from the current, small streams and springs offer a more benign habitat for species unable to maintain position in a strong current (e.g., Glazier, 1991; Dieterich and Anderson, 2000).

Headwaters Provide a Refuge from Predators. The high vulnerability of amphipods to fish predation are considered to be one reason why amphipods reach such high abundance in small fishless springs (Glazier, 1991). Low numbers of predators in intermittent streams is considered to contribute to the high diversity of aquatic insects (Dieterich and Anderson, 2000), the high biomass of emerging insects (Progar and Moldenke, 2002), and crayfish abundance patterns (Flinders and Magoulick, 2003) in those streams. The absence of fish predators in high-elevation Colorado streams results in emerging female mayflies that are larger and more fecund (Peckarsky *et al.*, 2002). The flight of adult stoneflies prior to oviposition is predominantly upstream for distances up to 730 m in a New Hampshire stream network; researchers speculate that this is because of the lower interspecific competition, lower predation risk, and higher food resources in the headwater tributaries (Macneale *et al.*, 2005). The absence of fish predation is considered a factor responsible for the prevalence of salamanders and other amphibians in small streams (Petranka, 1998). The significance of predator-free environments for amphibians is apparent from the lower populations observed in stream networks where trout have been introduced into high mountain lakes (Pilliod and Peterson, 2001).

Headwaters Provide a Refuge from Competitors. Low abundance of competitively dominant species is another explanatory factor for the abundance and diversity of headwater species. The absence of dominant competitors such as the snail *Juga silicula* was considered a factor contributing to the diversity of grazing insects in western intermittent streams (Dieterich and Anderson, 2000). Interannual variation in abundance of native rainbow trout in an intermittent California stream was correlated with the intensity of winter floods, which destroy the eggs of introduced brook trout (*Salvelinus fontinalis*). This leaves fewer brook trout to compete with rainbow trout fry that hatch during the following spring (Erman and Hawthorne, 1976). The brook trout fry are competitive dominants in this stream because they are larger and more aggressive than rainbow trout fry (Erman and Hawthorne, 1976).

Headwaters Provide a Refuge from Alien Species. In the southern Appalachians, populations of native brook trout have been greatly reduced or displaced by the introduced rainbow trout throughout much of the stream network; brook trout persist in small, high-gradient headwater streams (Larson and Moore, 1985; Larson *et al.*, 1995). Headwater pools in a Colorado stream provided habitats for Arkansas darters that were otherwise subjected to predation by an introduced pike (Labbe and Fausch, 2000). Headwater streams are recognized as the refuges for species that have been extirpated downstream and have been identified as the priority targets for freshwater conservation efforts (Saunders *et al.*, 2002).

Headwaters Are Essential for Species Living in Larger Streams

Genetic Linkages. Populations in headwaters are genetically connected to populations living in larger streams, and the genetic structure of stream populations provides a measure of this linkage. Little genetic differentiation from headwaters to downstream reaches was observed for distances up to 2.5 km in a stonefly population (Schultheis *et al.*, 2002), up to 10 km in populations of a mayfly (Monaghan *et al.*, 2001), and up to 20 km in a caddisfly population (Wilcock *et al.*, 2003). This mixing of up- and downstream populations is a result of both larval and adult dispersal and illustrates the scale of biological linkages in river networks.

Species Migrate to Headwaters for Spawning and Nursery Habitats. Small streams serve as vital spawning habitats for species that live in larger streams during most of the year. In addition to the many salmonids that spawn in small streams as discussed earlier, several darters (e.g., *Etheostoma boschungi, E. trisella*) migrate to small streams (<1 m wide) for breeding (Ryon, 1986; Boschung and Mayden, 2004). Many lake-dwelling fish species also migrate to small tributaries for spawning. Examples include kokanee salmon (*Oncorhynchus nerka*, nonanadromous sockeye) and several species of California sucker, including the federally endangered shortnose and Lost River suckers (*Chamistes brevirostris* and *Deltistes luxatus*) (Moyle, 2002). Headwater streams provide a vital rearing habitat for the young of the many species that spawn there. Many of these species support important fisheries and are likely to suffer declines without access to intact headwaters even if the downstream habitats remain intact. Headwaters serve as spawning and nursery grounds for many of the reasons detailed above, namely that they offer a refuge from high flow, competitors, and predators.

Headwaters Provide Rich Feeding Grounds. Small streams are often areas of concentrated food resources for both permanent residents and migrants. Large inputs of leaves from forested riparian zones, the high retention capacity of small streams, and the high rates of primary productivity in unshaded headwaters mean that these streams are rich in food for primary consumers such as crustaceans and insects. Those organisms are eaten by resident and migrant invertebrate and vertebrate predators, and the large hatches of aquatic insects are important to aerial and terrestrial predators. Small streams also receive considerable input of terrestrial insects; e.g., terrestrial invertebrates were a more important food resource for fishes in a first and second-order stream than a third-order stream (Lotrich, 1973).

Headwaters Provide Thermal Refuges. Small streams offer a thermal refuge for species that spend most of their lives in larger systems. They provide warm refuges from freezing for stream fishes during winter (e.g., Power *et al.*, 1999) and cool refuges during summer (e.g., Curry *et al.*, 1997). The Arkansas darter, *Etheostoma cragini*, uses small first-order streams as a summer refuge from heat and drought in the Ozarks (Radwell, 2001). Arkansas darter populations are also found in intermittent streams in Colorado, where their persistence in temporarily isolated pools depends upon a supply of cool groundwater (Labbe and Fausch, 2000). Brook trout in the Ford River, Michigan, retreat to cooler headwaters in summer (Hayes *et al.*, 1998). The success of quillback and introduced carp in midwestern streams has been attributed to the warming of small streams because of human disturbance of the landscape; native species in decline in this region require cooler tributaries (Karr *et al.*, 1985). If headwater streams are thermally degraded, or if barriers to movement are established, downstream species lose access to these thermal refuges.

Headwaters Provide a Source of Colonists and a Network of Movement Corridors. Biological connectivity between headwater and downstream ecosystems is considerable and essential for the maintenance of species diversity in downstream ecosystems (e.g., Labbe and Fausch, 2000). One way in which small streams maintain diversity in the river network is by providing a source of colonists for recovery of downstream systems following disturbance (Lorion *et al.*, 2000; Progar and Moldenke, 2002; Huryn *et al.*, 2005). Small streams also provide movement corridors for plants and animals across the landscape. Their riparian zones provide cooler and more mesic conditions than those found in the uplands (e.g., Richardson *et al.*, 2005). The flight paths of adult aquatic insects are concentrated along streams and riparian zones, which serve as dispersal corridors (e.g., Petersen *et al.*, 2004).

Headwater Biodiversity Affects the Character and Function of Terrestrial and Downstream Ecosystems

Headwaters Supply Food to Neighboring Ecosystems. The diversity of organisms in headwaters creates food resources for other ecosystems and thus provides another ecological linkage between headwater and neighboring ecosystems: "headwater streams are the vertex of a network of trophic arteries flowing from the forest upland to the oceans" (Progar and Moldenke, 2002). Leaf-shredding insects commonly dominate the aquatic insect fauna in forested headwaters, and the fine particles of organic matter that shredders generate are exported as seston to support foodwebs of ecosystems downstream (Vannote *et al.*, 1980). Elimination of aquatic insects from a headwater stream resulted in a 67% reduction in seston export to downstream ecosystems, which was a greater reduction than was caused by a severe drought (Cuffney *et al.*, 1990). Sufficient numbers of drifting aquatic insects and detritus are exported from fishless headwater tributaries to support 100–2,000 young-of-the-year salmonids per kilometer of larger salmon-bearing streams in Alaska (Wipfli and Gregovich, 2002). Emerging insects and transforming amphibians supply food for terrestrial organisms such as spiders, birds, and bats that forage in the riparian zone of small streams (e.g., Richardson *et al.*, 2005). These nutrient and organic matter linkages support riparian and downstream ecosystems. Their significance has been discussed in greater detail elsewhere (Meyer and Wallace, 2001; Freeman *et al.*, this issue; Wipfli *et al.*, this issue).

Biological Activity in Headwaters Affects Connections to Neighboring Ecosystems. Small streams are sites of intense biological activity, whose consequences influence ecosystems downstream. For example, uptake of DOC in headwaters alters the quality and quantity of DOC exported to downstream ecosystems (Wiegner *et al.*, 2005). Uptake of nutrients in headwaters alters nitrogen and phosphorus loading to ecosystems downstream (Meyer and Wallace, 2001; Alexander *et al.*, this issue; Triska *et al.*, this issue).

THREATS TO SMALL STREAMS

Despite their unique contributions to and importance in maintaining the diversity and functional integrity of entire river systems, small streams are continually under threat by human activity (Meyer and Wallace, 2001). The literature describing the biota of headwaters is replete with examples of species threatened by any number of human activities. Threats include ground-water extraction which, in addition to threatening species associated with small springs (e.g., Hubbs, 1995), has caused tributaries of Kansas streams to go dry, resulting in the extirpation of 16 species from the river system (Cross and Moss, 1987). Land-disturbing activities such as agriculture, logging, mining, and urbanization degrade and eliminate headwater habitats (Meyer and Wallace, 2001). These inconspicuous, unnamed, unmapped, and undocumented ecosystems, many of which are on private property, are thus extremely vulnerable to human impacts. The cumulative impact of degraded headwaters contributes to the loss of ecological integrity in ecosystems downstream.

Small streams are thus a vital part of the biological integrity of our nation's waterways. Degradation of headwater habitats and loss of their connections to larger streams have negative consequences not only for inhabitants of small streams but also for the diversity of downstream and riparian ecosystems. In many respects and locales, the biological integrity of entire river networks may be greatly dependent on the individual and cumulative impacts occurring in the many small streams that constitute their headwaters.

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