Conservation Biology

Essay

A Regional Perspective on the Diversity and Conservation of Tropical Andean Fishes

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Abstract: *The tropical Andes harbor an extraordinarily varied concentration of species in a landscape under increasing pressure from human activities. Conservation of the region's native plants and animals has received considerable international attention, but the focus has been on terrestrial biota. The conservation of freshwater fauna, particularly the conservation of fishes, has not been emphasized. Tropical Andean fishes are among the most understudied vertebrates in the world. We estimate that between 400 and 600 fish species inhabit the diverse aquatic environments in the region. Nearly 40% of these species are endemic. Tropical Andean fishes are vulnerable to ongoing environmental changes related to deforestation, water withdrawals, water pollution, species introductions, and hydropower development. Additionally, their distributions and population dynamics may be affected by hydrologic alterations and warmer water temperatures associated with projected climate change. Presently, at least three species are considered extinct, some populations are endangered, and some species are likely to decline or disappear. The long-term persistence of tropical Andean fishes will depend on greater consideration of freshwater systems in regional conservation initiatives.*

Keywords: elevational gradients, freshwater, mountain, Neotropics, river, South America

Una Perspectiva Regional de la Diversidad y Conservación de Peces Andinos Tropicales

Resumen: *Los Andes tropicales albergan una concentración de especies extraordinariamente variada en un paisaje bajo presión creciente de actividades humanas. La conservación de las plantas y animales nativos de la región ha recibido considerable atención internacional, pero la biota terrestre ha sido el principal objetivo. La conservación de la fauna de agua dulce, particularmente la conservación de peces, no ha sido enfatizada. Los peces Andinos tropicales se encuentran entre los vertebrados menos estudiados en el mundo. Estimamos que en los diferentes ambientes acuáticos de la región habitan entre 400 y 600 especies de peces. Casi 40% de ellas son endémicas. Los peces Andinos tropicales son vulnerables a los cambios ambientales actuales relacionados con la deforestación, la pérdida de cuerpos de agua, la contaminación acuática, la introducción de especies y el desarrollo de hidroeléctricas. Adicionalmente, sus distribuciones y dinámicas poblacionales pueden ser afectadas por las alteraciones hidrológicas y las temperaturas de agua más cálidas asociadas con el cambio climático proyectado. Actualmente, por lo menos tres especies están consideradas extintas, algunas poblaciones están en peligro y es probable que algunas especies declinen o desaparezcan. La persistencia a largo plazo de los peces Andinos tropicales dependerá de una mayor consideración de los sistemas dulceacuícolas en las iniciativas regionales de conservación.*

Palabras Clave: agua dulce, América del Sur, gradientes altitudinales, montaña, Neotrópico, río

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Introduction

The tropical Andes Mountains of South America—extending from northwestern Venezuela through Colombia, Ecuador, Peru, and Bolivia—harbor an extraordinary richness of species and a high concentration of endemic species in many taxonomic groups. Latitudinal, elevational, and climatic gradients have created a highly heterogeneous landscape, and 133 ecosystem types have been identified in the region (Josse et al. 2009). An estimated 45,000 species of plants and 3,400 species of vertebrates (excluding fishes) inhabit the tropical Andes, and they represent approximately 15% and 12% of all known species, respectively. Nearly half these species are endemic (Myers et al. 2000).

The tropical Andes is also a rapidly changing landscape. Growth of human populations and exploitation of natural resources have led to extensive reductions in native vegetation and the subsequent identification of many species as vulnerable, threatened, or endangered (Brooks et al. 2002; Greyner et al. 2006). In parts of the northern Andes, human activities have affected 60–75% of the land area between 500 and 3000 m (Etter & van Wyngaarden 2000). The tropical Andes has been designated one of the world's 25 most species rich and exceptionally threatened areas (Myers et al. 2000). Of these, the tropical Andes is among the most likely to experience high levels of species loss in the future, given present deforestation trends and projected climate change (Brooks et al. 2002; Malcolm et al. 2006). Accordingly, considerable funding has been directed toward the region for conservation of biological diversity.

Nevertheless, conservation efforts in the region have not emphasized one group of vertebrates: fishes. Fishes are not usually included in statistics on species diversity for the tropical Andes (e.g., Myers et al. 2000), and most current scientific research and conservation initiatives are focused on terrestrial flora and fauna or semi-aquatic species (Greyner et al. 2006). Even regional analyses of freshwater resources often do not consider fishes (e.g., Tobon 2009). Because many rivers have never been inventoried, tropical Andean fishes remain among the least studied and described vertebrates on Earth (Jacobsen 2008). It is known that tropical Andean fishes are highly endemic and adapted to extreme abiotic conditions (Maldonado-Ocampo et al. 2005). Effects of human activities and climate change could irreversibly alter tropical Andean freshwater ecosystems and result in the decline or disappearance of species. Here, we summarize current knowledge of the diversity and distribution of tropical Andean fishes, discuss the main factors that may affect their long-term persistence, and highlight opportunities for conservation.

Fishes of the Tropical Andes

The Neotropics is the global center of species richness of freshwater fishes and is believed to harbor 5000–8000 species, of which about 4500 have been described (Malabarba et al. 1998; Reis et al. 2003). Globally, approximately 20–25% of all fishes and 50% of all freshwater fishes are Neotropical species. Recent estimates suggest at least 2500 of these species inhabit the Amazon basin (Junk et al. 2007) and at least 995 inhabit the Orinoco basin (Lasso et al. 2004). The tropical Andes encompass the headwaters of these basins and several Pacific and Caribbean drainages (e.g., Guayas and Esmeraldas rivers in Ecuador; San Juan, Atrato, and Magdalena-Cauca rivers in Colombia). Most knowledge of Neotropical fishes is derived from the lowlands of major river systems. Comparatively, fishes in montane and piedmont areas of the tropical Andes have been much less studied (Table 1).

Patterns of Species Richness and Distribution

We estimate that 400–600 freshwater fish species inhabit the tropical Andes. Country-level data suggest Colombia has the highest species richness. Of 1435 fish species recorded in Colombia, 223 are found in the Andean region, and 85 of these species (37%) are endemic (Maldonado-Ocampo et al. 2008). To date, 92 Andean species have been recorded in Ecuador, 123 in Peru, and 155 in Bolivia (Maldonado et al. 2010).

Two orders, Siluriformes (catfishes) and Characiformes (tetras), account for approximately 44% and 40% of tropical Andean species, respectively. The remaining 16% are distributed among the Cyprinodontiformes (livebearers, killifishes), Gymnotiformes (electric knifefishes), Perciformes (cichlids), Myliobatiformes (freshwater stingrays), and Synbranchiformes (swamp eels) (Fig. 1). The Cyprinodontiformes are represented largely by an endemic group of *Orestias* spp. inhabiting Lake Titicaca and surrounding environments of the Altiplano above 3600 m in Peru and Bolivia (46 described *Orestias* species; Vila et al. 2007). Taxonomic knowledge of tropical Andean fishes remains incomplete. New species are still being described in the main Andean genera: *Astroblepus* (Astroblepidae); *Trichomycterus* (Trichomycteridae); *Chaestostoma*, *Dolichancistrus*, *Cordylancistrus* (Loricariidae); *Bryconamericus*, and *Grundulus* (Characidae). Results of recent phylogenetic analyses show that some Andean genera may be paraphyletic (e.g., *Cordylancistrus*) (Armbruster 2008), which is consistent with the limited taxonomic understanding of these fishes.

There are several broad patterns of species richness and distribution of tropical Andean fishes. Species richness is highest between 500 and 2200 m (Fig. 2). Overall,

Table 1. Selected results of recent biological inventories of fishes in tropical Andean aquatic systems.

Tropical Andean river basin	*Elevation range (m asl)*	*Number of species documented*	*Number of species potentially not described previously*	*Reference*
Streams of the central Andes, Colombia	228–2242	62	3	Jaramillo-Villa et al. 2008
San Rafael river basin, Colombia	900–2200	20	1	J.A.M., unpublished data
National Natural Park, Puracé-Guácharos, Colombia	1000–2200	21	2	J.A.M., unpublished data
Cane-Iguaque River basin, Colombia	2000–2750	8	–	J.A.M., unpublished data
Lebrija River basin, Colombia	590–2130	21	–	J.A.M., unpublished data
Putumayo River basin, Colombia	530–2170	29	7	A. Ortega-Lara et al., unpublished data
Upía and Magdalena river basins, Colombia	100–2900	12	–	Alvarez-León & Ortíz-Muñoz 2004
Aguarico River basin, Ecuador	450–2600	32	4	Maldonado-Ocampo et al. 2009
Pastaza River basin, Ecuador	500–4000	50	6–8	Rivadeneira et al. 2010; E.P.A., unpublished data;
Upper Pauya River basin, Peru	300–700	21	1	Hidalgo et al. 2002
Urubamba River basin, Megantoni Reserve Peru	750–2200	22	3–5	Hidalgo & Quispe 2004
Apurimac and Urubamba river basins, Peru	500–4800	40	–	M. Hidalgo, unpublished data
Upper Beni River basin, Bolivia	240–1300	28	–	Pouilly et al. 2006

as elevation increases species richness decreases and percentage of endemic species increases, particularly >2500 m (Maldonado et al. 2010). Evenness of abundance among species decreases as elevation increases. For example, in streams of the central Colombian Andes, 3 of 17 species account for 90% of the individuals in streams near 1500 m (Jaramillo-Villa et al. 2010). Spatial turnover in species composition occurs over short distances, apparently driven by elevation, physical and chemical conditions in aquatic environments, and geographic location (Table 2; Pouilly et al. 2006; Jaramillo-Villa et al. 2010). Fish assemblages differ among the northern, central, and southern tropical Andes and among eastern and western slopes, inter-Andean valleys, and the Altiplano (Table 2). These differences manifest primarily at the species level; higher taxonomic levels maintain greater continuity (Maldonado et al. 2010).

The underlying heterogeneity of the tropical Andean landscape helps explain these regional patterns. On geologic time scales, tectonic events associated with Andean uplift produced multiple, isolated river systems and shaped the physiography of these systems (Lundberg et al. 1998). The tropical Andes today contain broad elevational gradients (>5000 m in some places) over which climatic conditions (e.g., temperature, precipitation, wind, solar radiation) change markedly. Rivers follow longitudinal gradients, and the region's rugged topography creates many natural breaks in riverine connectivity (e.g.,

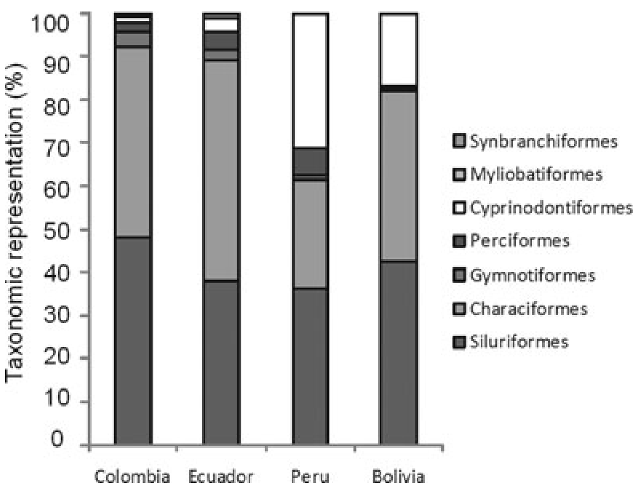

Figure 1. Percentage of taxonomic representation of fishes by order in the tropical Andean region above 400 m.

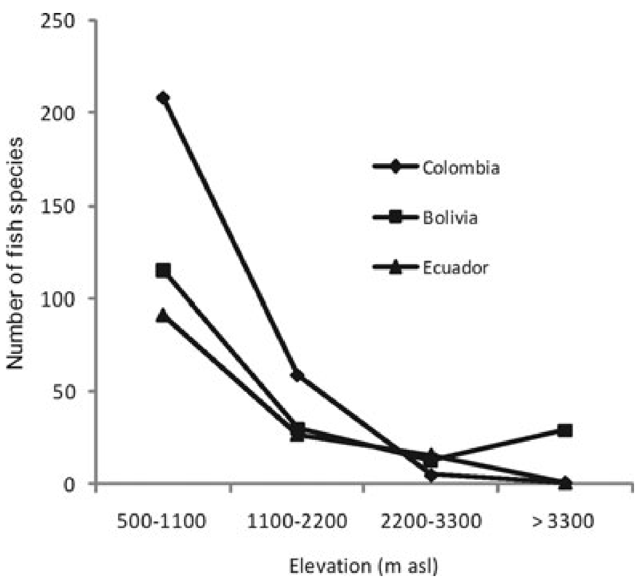

Figure 2. Number of fish species by elevation in three tropical Andean countries.

Table 2. Turnover of fish species by region in the Colombian Andes above 500 m (Maldonado-Ocampo et al. 2005, 2008).

Region	*Number of genera*	*Number of species*	*Number of species found only in this region in Colombia**	*Number of endemic species*
Inter-Andean valleys (Magdalena-Cauca basins)	73	155	107	66
Eastern Andes (Orinoco, Amazon basins)	28	56	33	10
Western Andes (Pacific Ocean drainages)	20	47	11	2
Caribbean (Atrato, Sinú basins)	35	45	12	4
Caribbean (Catatumbo basin)	11	12	11	0

**Species present only in this region in Colombia, but that have been documented in other regions of the tropical Andes in Venezuela, Ecuador, or Peru.*

waterfalls). Together, these factors have created physically and chemically diverse conditions in aquatic environments and have influenced dispersal of tropical Andean fishes (Fig. 3; Maldonado et al. 2010).

Characteristics of Tropical Andean Fishes

Fishes exhibit conspicuous morphological and physiological adaptations for survival in tropical Andean aquatic environments. Some of these adaptations have also facilitated their dispersal along elevational gradients. Tropical Andean fishes are generally classified by body form and habitat into three groups (Maldonado-Ocampo et al. 2005). Torrent species (e.g., *Astroblepus* spp., *Chaetostoma* spp.; Fig. 4) typically have depressed bodies, large pectoral fins, reduced swim bladders, and fleshy oral disks. They occur in streams characterized by cold temperatures, fast currents, and steep gradients. Pelagic species (e.g., *Salminus* spp.; Fig. 4) exhibit a compressed and streamlined body form, allowing them to inhabit the main water column in fast-flowing areas. Pool species (e.g., *Rivulus* spp.) generally lack adaptations

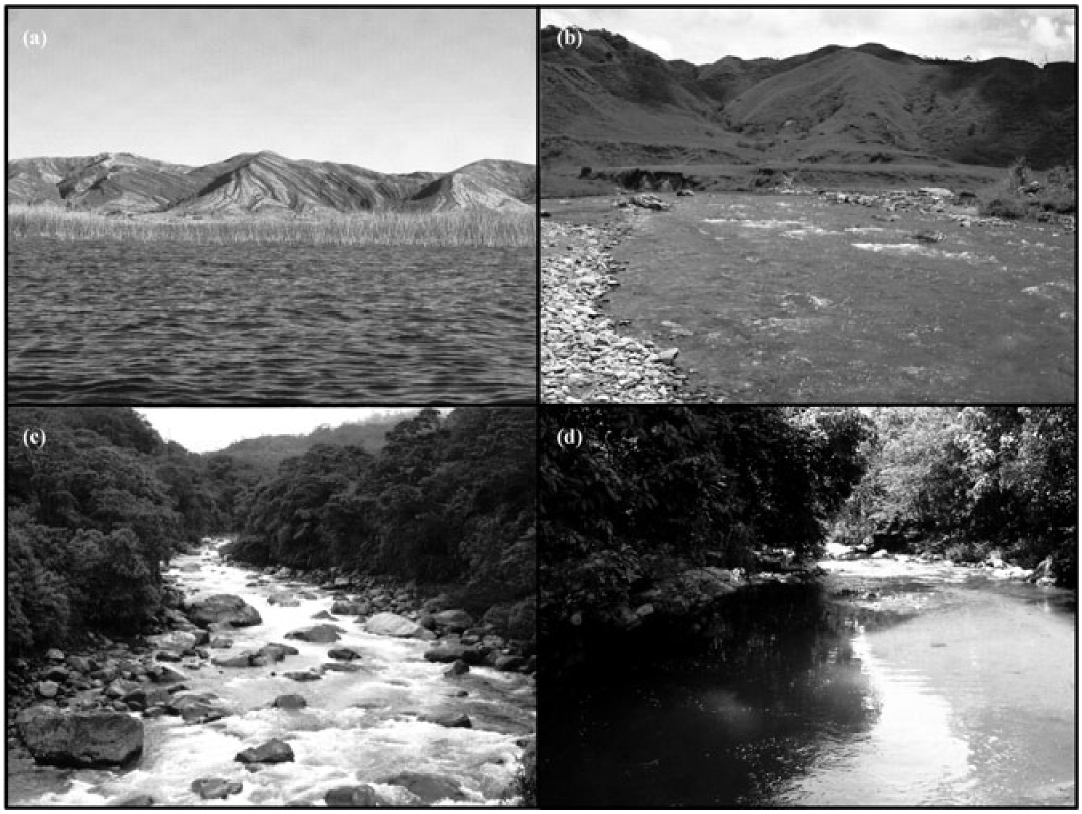

Figure 3. Freshwater environments of the tropical Andes: (a) Lake Titicaca, Bolivia, near 4000 m (photo by E.P.A.), (b) Concepción River, Nare River basin, Antioquia, Colombia, 1631 m (photo by U. Jaramillo), (c) Topo River, Pastaza River basin, eastern Ecuador, 1200 m (photo by E.P.A.), and (d) Burbura stream, Catatumbo River basin, Colombia, 570 m (photo by C.L. Maecha).

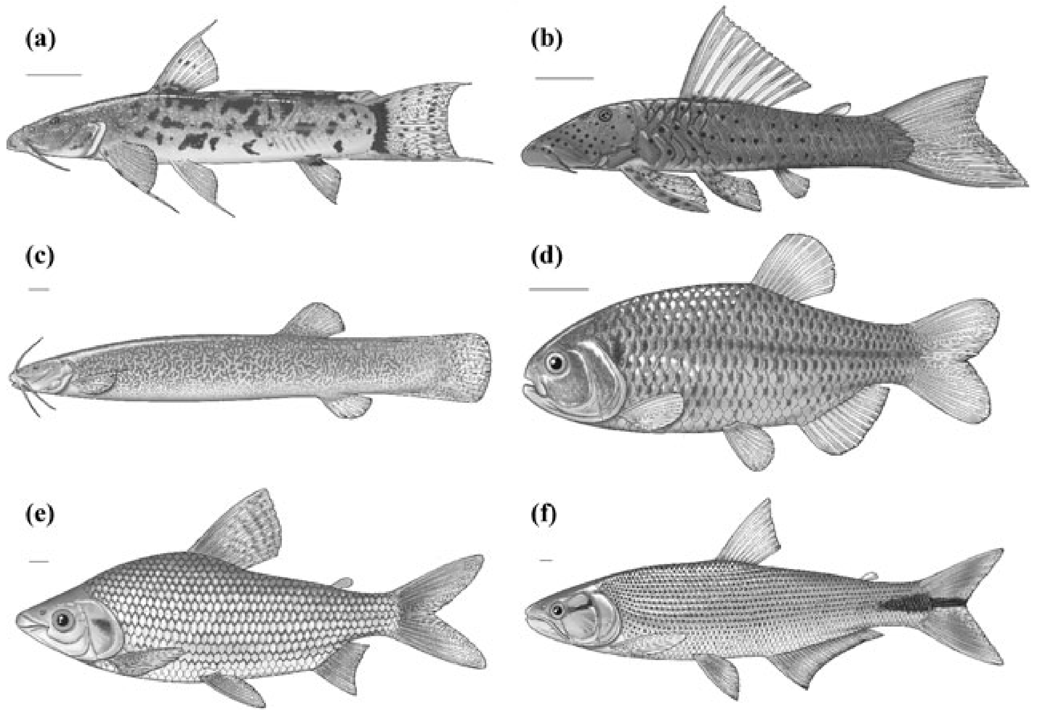

Figure 4. Common species of tropical Andean fishes: (a) Astroblepus grixalvii *(Astroblepidae), (b)* Chaetostoma milesi *(Loricariidae), (c)* Eremophilus mutisii *(Trichomycteridae), (d)* Grundulus bogotensis *(Characidae), (e)* Prochilodus magdalenae *(Prochilodontidae), and (f)* Salminus affinis *(Characidae). Lines under letters are 1-cm scale bars. Illustrations by J.C. Cristobal.*

to fast waters and are restricted to lentic, marginal, or slow-moving areas.

Catfishes (Siluriformes) of the tropical Andes are morphologically distinctive, occur over a broad range of elevations, and their taxonomy is poorly known. Most are torrent species with an oral disk, which allows them to attach to substrates and withstand high water velocities (Astroblepidae, Loricariidae), or anguilliform, which allows them to occupy interstitial spaces between rocks and avoid the current (Trichomycteridae). *Astroblepus* (Astroblepidae; climbing catfishes), a genus endemic to the Andes, occurs from Venezuela to northern Bolivia from roughly 300–3200 m. The taxonomy of this genus is rudimentary. To date, 54 species have been described (Schaefer 2003). A fleshy oral disk allows *Astroblepus* spp. to adhere to smooth surfaces, and their highly muscularized and mobile pectoral girdle allows them to ascend vertical and overhanging rock. The family Loricariidae (armored catfishes) (*Chaetostoma*, *Dolichancistrus*, *Cordylancistrus*, *Leptoancistrus*, and *Lipopterichthys*, among others) also displays morphological adaptations to steep, fast-water streams in the form of oral disks and large pectoral fins. Within the Siluriformes, Loricariidae and Astroblepidae are the most species rich families in the tropical Andes and thus may be useful in testing biogeographic hypotheses about the influence of geological and ecological factors on diversification of Andean fishes. Trichomycteridae (pencil catfishes) are widely distributed up to roughly 3000 m. Most Andean species belong to the genus *Trichomycterus*, although the family includes two monotypic genera endemic to the Colombian highlands, *Eremophilus* and *Rhizosomichthys*. Body elongation and association with rocky and sandy substrates allow *Trichomycterus* species to withstand fluctuations in flow and high water velocities.

Characiform fishes, mostly in the family Characidae (130–150 species), occur over a broad elevational gradient (500–2100 m), but the majority of species are concentrated in the piedmont region. The few species present at higher elevations, such as species of *Grundulus* and *Bryconamericus*, are associated with both lentic and lotic environments. These species do not display specific morphological adaptations to rheophily; thus, their presence at high elevations could be associated with Andean uplift rather than dispersal from the lowlands through riverine corridors (Maldonado-Ocampo et al. 2005). Taxonomic knowledge of Andean Characiform fishes is also poor. Many new species have been described in recent years, including at least 10 *Bryconamericus*, 9 *Hemibrycon*, and 3 *Creagrutus* in the Colombian Andes.

Several Siluriform and Characiform fishes use Andean rivers as migration corridors up to approximately 1000 m. Large catfishes (*Pseudoplatystoma* spp., *Brachyplatystoma* spp.; Pimelodidae) travel several thousand kilometers from downstream areas of the Amazon and Orinoco to the Andean piedmont to spawn (Barthem & Goulding 1997). Common migratory characids are *Prochilodus* spp., *Brycon* spp., and *Salminus* spp. One of the most widely distributed of the *Prochilodus* spp. in the Amazon, *P. nigricans*, undergoes seasonal, long-distance migrations in schools from the lowlands to Andean rivers as a critical component of their reproductive cycle (Silva & Stewart 2006). These migratory catfish and characid species are among the most important species to lowland fisheries.

Fishes in a Changing Landscape

Although humans have inhabited the tropical Andes for over 10,000 years, their effects on freshwater ecosystems have increased in recent decades as a consequence of deforestation, water withdrawals, pollution, species introductions, and hydropower development (Etter & van Wyngaarden 2000; McClain & Naiman 2008; Josse et al. 2009). These factors, in combination with projected climate change, threaten the long-term persistence of tropical Andean fishes.

Deforestation

Deforestation rates in the tropical Andes are among the highest in South America (Etter & van Wyngaarden 2000; Brooks et al. 2002), and few Andean rivers now drain landscapes of contiguous forest from their headwaters to the Andean piedmont. Frontier deforestation is rapidly advancing toward piedmont regions, particularly on eastern Andean slopes below 1500 m (Mena et al. 2006). These are the same elevations where Andean fish assemblages are most diverse and where many migratory species return to spawn. Frontier deforestation often begins along rivers. Riparian trees are logged and woody debris is frequently harvested from river channels. In the Venezuelan piedmont, Wright and Flecker (2004) found that fish species richness and the number of rare fish species were lower in pools in streams without large pieces of woody debris than in pools with woody debris. Of 30 species observed, 26 were more abundant in pools containing woody debris, including the migratory species *Prochilodus mariae* and *Brycon whiteii*.

Even small losses in percent cover of riparian canopy or short breaks in longitudinal connectivity of riparian forest cover could affect tropical Andean fishes. Results of a study of streams draining an area of fragmented forest in the Ecuadorian piedmont suggest deforestation affects fish community structure and size structure of individual species. Streams with lower percent canopy cover had lower beta diversity and lower percentages of rare species, and the biomass of fish communities was dominated by periphyton-feeding Loricariids. Additionally, mean body size of Loricariids increased as percent canopy cover decreased (Bojsen & Barriga 2002).

Water Withdrawals

Major urban and agricultural areas in the tropical Andes are located above 2000 m. Urban populations, including the capitals of Colombia (Bogota, 2600 m; ~8 million people) and Ecuador (Quito, 2800 m; ~2 million people), rely on Andean rivers for water (Bradley et al. 2006; Buytaert et al. 2006). Agricultural production at elevations over 2000 m typically requires irrigation, and many Andean rivers experience extremely low or zero flow conditions during dry periods because of water withdrawals by chains of irrigation projects (Buytaert et al. 2006). Allocation of water to ecosystems is a relatively new consideration in regional water management (Anderson et al. 2010). Many of the streams from which a high proportion of water is withdrawn drain regions with a high concentration of endemic fishes (>2000 m). In Colombia, for example, dewatering of Andean wetlands to meet the demands of urban areas and agricultural and livestock producers has been linked to extirpations and declines of endemic species (*Grundulus bogotensis*, *Eremophilus mutisii*) near Bogota and in the Ubate Valley (Mojica et al. 2002).

Water Pollution

Loading of sediment, nutrients, metals, pesticides, and other contaminants into freshwater systems is linked to decreased growth, reproduction, and survival of native fishes, and consequent declines in species richness (Allan 2004; Fialho et al. 2008). Water pollution in the tropical Andes has multiple sources, including widespread release of untreated industrial and domestic wastewater directly into surface waters, runoff of pesticides and fertilizers from agricultural lands, and wastes from mineral mining operations. Many of these sources of pollution are located at high elevations, but their impacts are far reaching because contaminants are exported downstream and persist over time. In the Bolivian Andes, high concentrations of dissolved metals (Zn, Pb, Cd, and Cu) and low pH (<3) have been recorded in rivers that receive effluent from mines. It is hypothesized that these metals and acidity have negative effects on fishes, including migratory species, but evidence is lacking (Smolders et al. 2002; Van Damme et al. 2008). Results of studies in Colombia suggest that reproduction and survival of tropical Andean fishes are affected by water pollution. In the Magdalena and Orinoco basins, concentrations of heavy metals and organochlorines have been detected in the tissues of fishes of different feeding groups (Donato 1987, 1991; Cala & Sodergren 1999). Results of studies in other parts of South America suggest water pollution strongly affects species richness and evenness of fish assemblages and facilitates expansion of more tolerant introduced species (Barrella & Petrere 2003; Cunico et al. 2006; Habit et al. 2006; Orrego et al. 2009).

Species Introductions

Introductions of non-native species have altered biotic communities in tropical Andean aquatic systems, and their influence extends from high-elevation headwaters to the Andean piedmont. Trout, mainly *Onchorynchus mykiss*, were introduced to the region for aquaculture and fisheries in the 1930s and are now widely distributed in tropical Andean rivers above 1000 m (Forero & Gutiérrez 2002; Ortega et al. 2007). Results of studies in Peru suggest that competition for food resources and space affects the persistence of native Andean fish species in the presence of non-native trout. In streams of the Río Abiseo National Park (1680–3990 m), *O. mykiss* and native *Astroblepus* spp. co-occurred at only 2 of 51 sites sampled, and at these 2 sites *Astroblepus* persisted only along steep slopes. *Astroblepus* were also found in the stomach contents of trout (Ortega et al. 2007).

Non-native species have affected other tropical Andean aquatic systems similarly. At Fúquene Lake in Colombia, endemic species (*Eremophilus mutisii*, *Grundulus bogotensis*) compete for food and space with non-native species (*Cyprinus carpio*, *Carassius auratus*), which now account for the majority of fish biomass (Valderrama 2007). In the Lake Titicaca system, trout and *Odonthestes bonariensis* (Atherinidae), a temperate South American species accidentally introduced in the 1960s, have had a direct, irreversible effect on native fishes. Through competition and predation, these non-native species have contributed to the extinction of one native fish, *Orestias cuvieri*, and to declines in abundance of many others (e.g., *Oligosarcus schindleri*; Ortega et al. 2007; Van Damme et al. 2009). African tilapias (*Oreochromis* and *Tilapia* spp.) and guppies (*Poecilia reticulata*) are also present in tropical Andean streams, mainly below 1500 m.

Hydropower Development

Dams on tropical Andean rivers alter local physical and chemical conditions and disrupt hydrologic connectivity along longitudinal and elevational gradients. Regionally, hydropower accounts for about 50% of electricity generation. Nevertheless, many sources of hydropower are untapped and hundreds of new dams of different types and sizes are under consideration (Anderson et al. 2010). Andean rivers, particularly between 500 and 1100 m, are targets for new hydropower development. This is the same elevation band where species richness of tropical Andean fishes peaks and where lowland species migrate seasonally to Andean rivers.

The impacts of large dam projects in the lowlands (<500 m), especially restriction of movement of migratory fishes, are likely to be transmitted upstream to Andean aquatic ecosystems. For example, the presence of the Urrá Dam in the lowlands (170 m) on the Sinu River, Colombia, has been linked to decreases in abundance of migratory fish species, including *Prochilodus magdalenae*, *Brycon moorei*, and *Salminus affinis* (Valderrama 2002; Valderrama & Solano 2004). The Madeira River project, a proposed complex of four major dams near the border of northern Bolivia with Brazil, is another example. The Madeira River sub-basin accounts for roughly 20% of the Amazon Basin, and its headwaters encompass several major Andean rivers: the Madre de Dios, Beni, and Mamoré. Although the exact effects of the Madeira River project are unknown, it is likely the project will restrict access of migratory species to upland Andean aquatic ecosystems. Studies from other areas document a loss of critical ecosystem function in the absence of migratory species, particularly *Prochilodus*. In Venezuelan streams, *Prochilodus* account for nearly half of all nitrogen recycling (McIntyre et al. 2007). Removal of *Prochilodus* from Venezuelan streams resulted in increased primary production and decreased downstream transport of organic carbon (Taylor et al. 2006). No other species in Andean streams appear to have a functional role similar to that of *Prochilodus* (Taylor et al. 2006).

Climate Change

The magnitude of warming at high elevations in the tropical Andes may approximate that projected for the world's high latitudes (Bradley et al. 2006; Urrutia & Vuille 2009). The probable consequences of this warming include melting glaciers and drying Andean páramos (high-elevation grasslands), which would alter flows of Andean rivers and reduce the area of wetland at high elevations. The effects of climate change on flows in Andean rivers are likely to have high social and economic costs (Bradley et al. 2006); however, effects of climate change on freshwater biota have not been well studied. In temperate regions, extension or contraction of the distribution of fishes along elevational or longitudinal gradients and changes in assemblage structure may occur as a result of climate change (Buisson et al. 2008; Buisson & Grenouillet 2009). Despite scant biological data, we believe hydrologic alterations and increased water temperatures associated with climate change could influence the future distribution and population dynamics of fish species in the tropical Andes. Species typical of high-elevation streams and wetlands could shift their ranges downslope if warming causes a loss of habitat. Warmer water temperatures may facilitate colonization by lowland species of areas further upslope, where topographic relief or dams are not barriers.

Opportunities for Conservation

Globally, declines of freshwater animals have been much greater than losses of animals in terrestrial systems, and freshwater fishes are among the world's most endangered vertebrates. Tropical Andean fishes have restricted distributions and limited dispersal ability along elevational gradients and are adapted to narrow ranges of extreme abiotic conditions. These factors can increase the probability of species loss and imperilment, but limited knowledge of the taxonomy, distribution, and natural history of tropical Andean fishes makes estimating extirpation, extinction, and status difficult. At least three species associated with high-elevation systems in the tropical Andes are probably extinct: in Colombia *Rhizisomichthys totae* (Mojica et al. 2002) and *Trichomycterus venulosus* (Prada-Pedreros et al. 2006) and in Bolivia *Orestias cuvieri* (Van Damme et al. 2009). Populations of *Astroblepus ubidiai* in Ecuador may be critically endangered (Velez-Espino 2005). At least 23 species present in the Colombian Andes are included in the Red Book of Freshwater Fishes of Colombia (Mojica et al. 2002). Of the 42 fishes in the Red Book of Vertebrate Fauna of Bolivia, 24 (57%) are Andean species (Van Damme et al. 2009).

Several opportunities exist for improving conservation of tropical Andean fishes. First, Colombia, Ecuador, and Peru are in the process of revising water resources legislation. Concepts such as environmental flows are being proposed for inclusion in new legislation, which increases the prospect for greater coordination among institutions with respect to management of water withdrawals and waste streams, and overall conservation of freshwater systems (Anderson et al. 2010). This coordination is important because protection of tropical Andean fishes often depends on multiple legislative and institutional jurisdictions (M. Hidalgo, personal communication). Second, there is strong interest in establishing biological corridors to link existing protected areas in the tropical Andes (S. Fuentes, personal communication). These corridors could be situated along river courses. Additionally, as of January 2010 at least 16 wetlands of international importance had been designated in the tropical Andes by the RAMSAR convention, and regional initiatives were underway to form conservation corridors between high-elevation wetlands. These efforts increase possibilities for protection of endemic fish species in highland lentic environments.

Moreover, adoption of watershed-level perspectives in conservation planning or designation of freshwater protected areas (see Abell et al. 2007) could provide an avenue for conservation of tropical Andean fishes along elevational and longitudinal gradients. Results of studies from the Aroa Mountains, Venezuela, show that protected areas can effectively minimize the influence of human activities on aquatic ecosystems and fish assemblages (Rodriguez-Olarte et al. 2006). The recently established La Bonita-Cofanes-Chingual conservation area in Ecuador includes the majority of the headwaters of the Aguarico River and spans an elevational gradient of about 3500 m. One of the primary motivations for its creation was the protection of freshwater resources. Its location adjacent to existing protected areas in the lowlands further increases opportunities for conservation of fishes along critical elevational and longitudinal pathways (Maldonado-Ocampo et al. 2009).

More research on fishes in the tropical Andes would help guide freshwater conservation initiatives regionally. Studies of alpha taxonomy and phylogenetics are needed to improve basic scientific knowledge of tropical Andean species. Further documentation of elevational and longitudinal patterns of species richness and distribution could aid in identification of priority areas for protection or restoration. A better understanding of the life history and ecology (e.g., reproduction, habitat, thermal tolerance, population dynamics) of tropical Andean species would be particularly useful for assessment of environmental flows and for designing conservation strategies for adaptation to climate change. Investigation of the interactive and additive effects of multiple stressors on fishes is also a priority, especially given ongoing environmental changes in the tropical Andes.

Fish assemblages in montane areas are similar in terms of species richness and trophic structure, and fishes inhabiting high-elevation streams on different continents have similar adaptations to their environments (Ibañez et al. 2009). The Himalayas, like the tropical Andes, are at the headwaters of some of the world's largest rivers—the Indus, Ganges, Brahmaputra, and Mekong—where freshwater conservation and research initiatives are often focused on the lowlands. Rivers draining another global center of species richness, the Eastern Arc Mountains in southern Kenya and Tanzania, are being increasingly subjected to riparian deforestation and water withdrawals and harbor a largely unknown aquatic fauna. There is a critical need to increase scientific understanding and effective conservation of the fishes that inhabit uplands of the tropical Andes and other montane regions.

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