little reason to believe that any Atlantic mussels recognized it before its invasion. Thus, even if the extremely limited gene flow of *M. edulis* between Europe and North America (29) dis-proportionately influenced northern or southern New England mussels, this effect would not help to explain a population’s predisposition to recognize *Hemigrapsus*. Moreover, even if *M. edulis* recognized *H. sanguineus* before its in-vasion, it is doubtful that the trait would be lost only in northern New England mussels, given the capacity of mussels to maintain cue recognition in the absence of reinforcing predation (17). Alternatively, northern New England mollusks may generally experience lower predation than southern conspecifics (30). Thus, although previous recognition of *H. sanguineus* per se seems unlikely, southern New England mussels may more readily express inducible defenses to many predator species by responding to a lower threshold of cues or with decreased specificity to predators (28). In fact, this potential gradient in cue thresholds and sensitivities may promote the rapid evolution of recognition of a novel, invasive predator in southern New England mussels.

Species interactions can differ on various geographic scales because of local selection and other processes (31, 32). Similarly, there is considerable potential for the evolutionary history of invasive and native species interactions to vary spatially and temporally. Although we have only a nascent understanding of the role of inducible defenses in marine systems (15, 33), this phenomenon is likely highly influenced by the evolutionary history of the interacting species. The confluence of evolutionary and ecological interactions represents an essential field of inquiry to understand fully the impacts of invasive species.

**References and Notes**

11. R. Seeley, personal communication.
18. Details are available in table S1 as supporting material on Science Online.
19. Details are available in Materials and Methods as supporting material on Science Online.
20. Analysis of covariance (ANCOVA) of final STI in laboratory experiment at Nahant, MA (2002): Site(Population) P = 0.0001; Predator P = 0.003; Population P = 0.0207; Site(Population) × Predator P = 0.0001; Population P = 0.0692. (See table S3.)
32. We thank the following: E. Enns, S. Genowese, E. Maney, C. Neefus, G. Trussell, Marine Biological Laboratory (Woods Hole), Great Bay National Estuarine Research Reserve Graduate Research Fellowship, University of New Hampshire (UNH) Graduate School, UNH Marine Program, and UNH Zoology Department. This manuscript was improved by comments from I. Altman, M. Bertness, A. Blakeslee, J. Dijkstra, B. Griffen, M. Lesser, J. Meyer, M. Scott, G. Trussell, and three anonymous reviewers.

**Supporting Online Material**

www.sciencemag.org/cgi/content/full/313/5788/831/DC1

**Materials and Methods**

Tables S1 to S5

References

27 January 2006; accepted 13 June 2006 10.1126/science.1125485

---

**Loss of a Harvested Fish Species Disrupts Carbon Flow in a Diverse Tropical River**

Brad W. Taylor,*† Alexander S. Flecker,* Robert O. Hall Jr.†

Harvesting threatens many vertebrate species, yet few whole-system manipulations have been conducted to predict the consequences of vertebrate losses on ecosystem function. Here, we show that a harvested migratory detrital-feeding fish (*Prochilodontidae: Prochilodus mariae*) modulates carbon flow and ecosystem metabolism. Natural declines in and experimental removal of *Prochilodus* decreased downstream transport of organic carbon and increased primary production and respiration. Thus, besides its economic value, *Prochilodus* is a critical ecological component of South American rivers. Lack of functional redundancy for this species highlights the importance of individual species and, contrary to theory, suggests that losing one species from lower trophic levels can affect ecosystem functioning even in species-rich ecosystems.

Widespread interest in the importance of species to ecosystem functioning stems from concerns that the rapid rate of human-induced species losses could affect ecosystem properties and services negatively (1). Freshwater ecosystems provide essential ecosystem services and contain a large fraction of species diversity that may be declining faster than the diversity in marine or terrestrial ecosystems (2). Humans have over-harvested many of the large, long-lived predatory fishes and are now shifting fishing efforts to the abundant, higher-yielding species at lower trophic levels, such as detritivores (3). Detritus is the major pathway of energy and material flow in most ecosystems, supports higher trophic levels, and is a major source of inorganic nutrient regeneration and uptake; losses of detritivores could disrupt ecosystem functioning (4). Both greater abundance and higher species richness at lower trophic levels

---

*Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA.

†To whom correspondence should be addressed. E-mail: brad.taylor@dartmouth.edu
are assumed to increase functional redundancy (5), but these characteristics also make species like detritivores targets for harvesting. Despite being a large percentage of the fish biomass and catch, manipulations of detritivores are less common than those of predators in freshwater and marine ecosystems.

We investigated the loss of a dominant migratory detritivorous fish, the flannelmouth characin, Prochilodus mariae, alters ecosystem metabolism and organic carbon flow in an Andean piedmont river located in the Orinoco basin (Rio Las Marías, 9°10’N, 69°44’W; 225 m elevation; 331 km² watershed area; 2002 dry season ranges: 0.142 to 0.782 m³ s⁻¹ discharge, 10.1 to 20.5 m wetted width). Piedmont rivers supply the Rio Orinoco with 25 to 90% of its inorganic nutrients and particulate organic carbon (POC) (6). These rivers support a high diversity of fishes (7), with at least 80 species in a 3-km-long segment of Rio Las Marías (8), a fourth-order tributary of the Rio Portuguesa that flows into the Rio Apure. Fish diversity in piedmont streams is dominated by omnivorous tetras (Characidae) and insectivorous catfishes (Heptapteridae), few of which are harvested because of their small body size. In contrast, detritivores, such as prochilodontids, constitute 50 to 80% of the fish biomass and catch in the Orinoco and Amazon basins (7, 9) and are declining throughout the Andean Piedmont (10). Although there are other common benthic feeders in Andean piedmont streams that consume benthic algae and particulate matter [e.g., Parodon apolinaris (Parodontidae) and armored catfishes Ancistrus triradiatus and Chaetostoma milesi (Loricariidae)], they do not reach the biomass of prochilodontids, which are consistently the dominant fish in Rio Las Marías and other South American rivers (10–12). Dams, deforestation, and pollution threaten prochilodontid populations (3, 10), making experimental tests of their removal relevant to current human impacts.

Prochilodus migrations represent a potentially important linkage within river networks, because, by bioturbating, consuming, and egesting large volumes of detritus, this fish may enhance the downstream transport and transformation of materials at a time when hydrologic transport is reduced and algal and bacterial productivities are high in neotropical rivers (6, 13). Replicated small-scale (4-m²) caging experiments showed that Prochilodus decreased benthic particulate matter and changed the composition of microbial biofilms from sediment-dwelling diatoms and heterotrophic bacteria to attached nitrogen-fixing cyanobacteria (8, 14). In addition to their abundance, the effects of Prochilodus may be unique, because, by removing particles that reduce light essential for N fixers, they may facilitate a source of primary production that is independent of N limitation (15). These results provided the basis for the larger-scale manipulations and longer-term observations reported here.

The downstream flux of POC was positively associated with Prochilodus biomass over 6 years [r = 0.76, P = 0.04, d.f. (degrees of freedom) = 4] (Fig. 1) (16). In contrast, interannual variation in discharge and biomass of other fishes were not significantly correlated with POC flux (P > 0.50) (fig. S3). Hence, relative to other physical and biological factors, fluctuations in the biomass of Prochilodus strongly regulated whole-stream transport of POC.

To test the effects of losing Prochilodus on carbon flow and metabolism, we used a large-scale experiment in which we selectively removed this single species from the natural ecosystem and left the remaining fish assemblage intact (16). The experiment was per-
formed in a riffle-run-pool segment of river by installing a 210-m barrier down the center of the river and removing Prochilodus from one side (16). The split-stream experiment allowed us to measure the effects of a wide-ranging consumer on ecosystem processes that occur at large spatial scales and in the presence of other naturally varying biotic and abiotic processes. We measured whole-stream primary production and respiration of organic carbon by using the open-channel diel-oxygen change method (16). We also measured the downstream flux and the benthic biomass of POC and calculated organic carbon turnover length (16, 17), the average distance an organic carbon molecule travels before being respired.

Removing Prochilodus increased benthic particulate matter on the stream bottom (Fig. 2B) and altered multiple components of organic carbon flow (Fig. 3). Impacts of removing Prochilodus on carbon flow equaled or exceeded effects of removing all fish (18), invertebrates (19), shrimps (20), and predatory fish in other streams and lakes (21–23). The biomass of POC on the streambed increased 450% (Fig. 3, A and B) after Prochilodus removal, a result consistent with replicated small-scale experiments demonstrating that Prochilodus effects occurred within 48 hours and persisted for at least 40 days during the 3-month dry season (14). The downstream flux of suspended POC decreased by 60% immediately after Prochilodus removal (Fig. 3, C and D) because of decreased bioturbation, consumption, egestion, and selective sorting of benthic POC by Prochilodus [Supporting Online Material (SOM) Text] (24).

Because benthic POC and biofilms increased after removing Prochilodus, heterotrophic respiration (other than by Prochilodus) increased by 200% in the treatment (Fig. 3, E and F). In addition, gross primary production (GPP) doubled after Prochilodus removal (Fig. 3, G and H). The percent increase in community respiration (CR, equal to autotrophic plus heterotrophic respiration) was greater than the percent increase in GPP; therefore, the ratio of production to respiration (P:R) decreased by 150% after Prochilodus removal (Fig. 3, I and J). Similarly, the deficit in net ecosystem metabolism (NEM = GPP – CR) was 42% greater after removing Prochilodus (Fig. 3, K and L). Thus, removing Prochilodus decreased the proportion and the absolute amount of CR supported by current autotrophic production. Consequently, without Prochilodus, river food webs may be supported by organic carbon produced earlier or imported from upstream and the terrestrial ecosystem rather than by current, local autotrophic production.

Organic carbon turnover length, or the downstream distance an organic carbon molecule travels until metabolized, is a measure of the longitudinal scale at which downstream ecosystems and food webs are linked to those upstream (17). Nutrient spiraling theory predicts consumers should increase turnover length by decreasing the benthic bacterial biomass and increasing the downstream flux of particles (17, 25). Consistent with this theory, removal of Prochilodus decreased turnover length by 35%, from 1.0 to 0.65 km (Fig. 3, M and N). With Prochilodus present, the coupling of materials and energy from upstream to downstream was enhanced. Hence, the loss of Prochilodus decreased the

Fig. 3. Ecosystem properties in the reference and reference area of the split-stream experiment before and after removal of P. mariae. (A to M) Measured values in the treatment (solid circles) and the reference (open squares). (B to N) Differences between measured values of the treatment and the reference. Prochilodus was selectively removed on 31 January 2002 (vertical dashed line) from the treatment. Note the logarithmic y axis. The t and P values were calculated by using the Welch-Satterthwaite-Aspin t test, and SES is the standardized effect size.
spatial scale of organic carbon availability, and the metabolism of organic carbon was more localized during the dry season, a time when hydrologic transport is low.

Given that the removal of Prochilodus altered ecosystem function, we investigated the effects of human harvesting on Prochilodus body size, a determinant of reproductive success and a proxy for changes in population size due to overharvesting (3). We evaluated long-term data on body mass of field and museum specimens of Prochilodus collected throughout the Orinoco basin from 1978 to 2004 (16).

Prochilodus body mass has declined substantially during the past 25 years (Fig. 4A), which we attribute to removal of larger individuals by net-based fishing. The mean maximum body mass decreased from 856 to 201 g, an initial rate of decline of 19 ± 9.1% per year (\(t_{0.95} = -1.80, P = 0.03\)). The current mean maximum body mass of 201 ± 81 g (\(t_{2.5} = 2.50, P = 0.01\)) is 20% below the mean size at which females become reproductively mature (10) and may represent a refugium body mass caused by size-selective harvesting. Concurrently, fishermen have decreased the mesh size of their nets. By making their own cast nets using their fingers to gauge the mesh size, fishermen have decreased their net mesh size from four to two finger widths over the past 25 years (26), a numerical decrease from 6 to 3 cm (Fig. 4B). Hence, the body depth (greatest dorsal-ventral length) of refugium-sized Prochilodus is now 3 to 3.5 cm (16). Decreasing net mesh size and body mass are hallmarks of overfishing and are correlated with decreasing fish population size (3). Decreasing body size may also change pathways of carbon flow, because fish consumption rates generally decrease with decreasing body size. Thus, size-selective harvesting may have long-lasting negative feedbacks on fish populations, ecosystem function, and the flow of protein to humans and other animals, eroding an important ecosystem service (1, 5).

These results have several implications for conservation management and our understanding of ecosystem function. First, the results show low functional redundancy in a diverse ecosystem for a single detritivorous fish species that regulates fundamental ecosystem processes, synthesis and degradation of organic carbon. This finding contradicts the prediction that more individuals and species at lower trophic levels impart a degree of insurance against changes in ecosystem functioning (3). Furthermore, in rivers where Prochilodus migrations have been permanently blocked, compensatory responses by other fishes have not occurred (10). Second, these results are not restricted to spatially localized, short-term processes. POC accumulated on the streambed may eventually be transported downstream during wet season floods; however, most POC transported by floods may not be available or used by many organisms because it is pulsed so rapidly through downstream areas. Moreover, dry season floods are rare or small in magnitude in the Andean Piedmont, so it is unlikely these events would remove much POC or reduce the effects of Prochilodus (fig. S4). Thus, Prochilodus reduces the spatial and temporal variability of organic carbon flow, resulting in a more constant supply of energy and materials, especially during the dry season when detrital resources are scarce and fish growth is low (7, 27). Lastly, the results show the potential ramifications to ecosystem-level carbon flow of losing a species that is currently harvested by humans. Considering the effects we observed in 2002 when Prochilodus biomass was low, we suspect that these effects may be even greater in other years or in other piedmont rivers with higher Prochilodus biomass. In many ecosystems, we know which species or functional groups are threatened by human activities, and selective experimental removals of species targeted by humans could be informative for predicting whether their losses will change ecosystem functioning substantially, especially if traits selected by humans covary with those that enhance species impacts (28).

References and Notes
16. Materials and methods are available as supporting material on Science Online.
29. We thank C. Montañez del Rio for providing museum specimens; D. Taphorn for permits and logistics; the Figueres and the Porens for lodging and field access; and S. Casatti, C. Hodges, B. Roberts, and J. Anderson for field assistance. Three reviewers, B. Daley, R. Irwin, M. Ben-David, B. Koch, F. Kahel, W. Reiners, C. Martínez del Río provided comments. Research was supported by a North American Benthological Society Graduate Award, Sigma Xi, University of Wyoming Office of Research, a Clarke Scholarship, a Plummer Scholarship, Department of Zoology and Physiology, International Programs, Miami University Hampton Funds, and NSF grants 9615349, 0211400, and 0321471.

Supporting Online Material
www.sciencemag.org/cgi/content/full/313/5788/833/DC1
Materials and Methods
Figs. S1 to S4
Table S1
References
3 April 2006; accepted 16 June 2006
10.1126/science.1128223
Supporting Online Material for

Loss of a Harvested Fish Species Disrupts Carbon Flow in a Diverse Tropical River

Brad W. Taylor,* Alexander S. Flecker, Robert O. Hall Jr.

*To whom correspondence should be addressed. E-mail: brad.taylor@dartmouth.edu

Published 11 August 2006, Science 313, 833 (2006)
DOI: 10.1126/science.1128223

This PDF file includes:

Materials and Methods
SOM Text
Figs. S1 to S4
Table S1
References
**Supporting Online Material**

Loss of a harvested fish species disrupts carbon flow in a diverse tropical river  
*To whom correspondence should be addressed.  E-mail: brad.taylor@dartmouth.edu

This PDF file includes:  
Materials and Methods  
Supporting text  
Figs. S1-S4  
Table S1  
Supporting references and notes

**Materials and Methods**  
We estimated fish density by repeated instantaneous visual scans using binoculars and a stepladder to count the number of individuals in six 4-m$^2$ quadrats located throughout a 3-km segment of Rio Las Marías. We computed dry season fish densities for each year from the average of daily censuses at 0700, 1100, 1400, 1700 hrs from 3-8 different pool/run areas on 5-12 different dates. We computed *Prochilodus mariae* biomass (g m$^{-2}$) by multiplying density by the mean wet body mass of individuals collected by electrofishing or fishermen in each year.

During the 2002 dry season, we established a reference (0.19 ha) and treatment (0.11 ha) area by splitting the stream down the center (based on discharge) with heavy-plastic buried 40 cm into the streambed to prevent surface water exchange (fig. S1), and supported with steel concrete-reinforcing rods. Physical properties were similar between the treatment and reference (Table S1). We removed *Prochilodus* from one side of the river by electrofishing and installing wire mesh (3 cm diameter) at each end, which other fishes could swim through but *Prochilodus* could not (S1, S2) (fig. S2). The experiment represented a numerical reduction of *Prochilodus* (from 0.071 m$^{-2}$ to 0.002 m$^{-2}$), rather than a 100% removal, because four *Prochilodus* could not be removed after the experiment began. The contribution of the plastic wall to the total area in each experimental area was < 1%. The wire mesh size was effective for selectively excluding *Prochilodus* because most fishes in Rio Las Marías (65 of 70 species in 2002, fig. S2) have a body depth less than 3 cm (mean ± 1 SD = 1.5 ± 0.6 cm), except for *Prochilodus* (mean ± 1 SD = 6.3 ± 1.5 cm), and four uncommon species that we did not remove if present.

We used the open-channel diel-oxygen change method to quantify metabolism over the entire experimental area (S3, S4, S5). We measured oxygen concentration, percent saturation, and temperature every 10 minutes at the upstream and downstream of each area for 36 hrs (1 day and 2 nights) using Hydrolab MiniSonde 4 probes that were calibrated in the field to within ± 0.1 mg L$^{-1}$ of one another. We estimated average water velocity by dividing the length of the experimental stream unit by the time required for 50% of a conservative tracer (NaCl) to travel from the upstream to the downstream end. The amount of community respiration that was attributed to heterotrophic respiration ($R_H$) was computed as, $R_H = CR - 0.2 \times GPP$ where 0.2 is an estimate of the fraction of GPP that is autotrophic respiration in a partially grazed stream (S6). We converted oxygen to carbon units using their molar ratios and a constant respiratory quotient of 1.
To estimate the air-water exchange of oxygen, we continuously injected sulphur hexafluoride (SF$_6$) and a conservative tracer (NaBr) into the stream, 75 m upstream of the experiment to allow mixing of gas and conservative tracers before they entered each half of the experiment. Each day metabolism was measured, we collected SF$_6$ samples at 10 locations along the length of each stream when the conservative tracer concentration reached equilibrium, and analyzed SF$_6$ samples on a Shimadzu GC-8A with an electron-capture detector. Groundwater inputs, measured by the dilution of a conservative tracer, were undetectable.

At the upstream and downstream ends of each experimental unit, we measured the concentrations of particulate (POC) and dissolved organic carbon (DOC) in the water column every 3-4 h over 24 h. We filtered particulate samples onto Gelman AE glass fiber filters for ash-free dry mass analysis by combustion at 500 °C, and elemental carbon analysis on a Carlo Erba CHN analyzer. Dissolved organic carbon (DOC) samples were filtered through Gelman AE filters, acidified to pH 2-3 with hydrochloric acid, frozen, and analyzed on a Shimadzu 5000A TOC analyzer. To estimate the downstream flux of organic carbon per meter width of stream (g m$^{-1}$ d$^{-1}$), we multiplied instantaneous DOC and POC concentrations (g L$^{-1}$) by stream flow (L s$^{-1}$), integrated these fluxes over 24 h to obtain daily flux (g d$^{-1}$), and divided by stream width (m). During the 1997-2002 dry seasons, we estimated daily fluxes of POC similarly at 6-7 different locations on at least 3-4 dates.

We calculated organic carbon turnover length as,
\[ S_c = \frac{F}{R_H} \]
where \( F \) is the downstream flux of organic carbon standardized for stream width (g C m d$^{-1}$), and \( R_H \) is heterotrophic respiration (g C m$^{-2}$ d$^{-1}$). In rivers with short turnover lengths, organic carbon is metabolized rapidly and near the origin of input or fixation, whereas, in rivers with long turnover lengths, a higher fraction of carbon is exported and deposited or metabolized farther downstream. Standardized effect size was calculated by subtracting the difference between the treatment and reference before and after Prochilodus removal divided by the standard deviation of the differences through time.

We computed the residence time of POC per unit length of stream, as the inverse of the downstream migration velocity of POC, $1/V_p$, (d m$^{-1}$); where $V_p$ was computed by dividing the downstream flux of POC (g d$^{-1}$) by the biomass of benthic POC per unit stream length (g m$^{-1}$), and assumes exchange between the benthic and transported POC compartments (S7).

To quantify changes in Prochilodus mariae body size over the past 25 years, we measured >2000 specimens accessioned from 1978-2004 in the Museo de Zoología, UNELLEZ, Guanare, Venezuela. We predicted wet body mass using the equation, \( W = 0.02L^{3.08} \), where \( W \) is the body mass (g), and \( L \) is the standard body length (cm). To minimize effects of collection bias, we calculated a mean maximum body mass from the mass of individuals above the 90th quantile and regressed the mean maximum body mass against time. We applied a model developed to quantify declines in marine fisheries (S8) to estimate changes in Prochilodus body mass
\[ W(t) = W^* + e^{-rt} (W_0 - W^*) \]
where \( W(t) \) is the maximum body mass at time \( t \), \( W_0 \) is the initial body mass, \( r \) is the rate of decline to \( W^* \), which is the body mass at plateau and may be a refugium body size due to current fishing practices and mesh sizes. To test whether the trend was due to time or collecting procedures that changed over time, we fit a modified form of the model
presented in equation (1) under the assumption of a lognormal error distribution using nonlinear regression (Procedure NLIN in SAS, version 8) with time, watershed where the specimen was collected, and collector ID name assigned to specimens as fixed effects. Because watershed and collector were not significant, these effects were removed and the model as presented in equation (1) was fit. Bias-corrected parameters and standard errors were estimated from 1,000 bootstrap samples (S9).

Supporting text

Our study site was located on the eastern side of the Venezuelan Andes at the transition zone (Piedmont) between the base of the Andes and beginning of the Llanos (savannas). Streams draining the Piedmont supply the Orinoco River with particulate and dissolved nutrients that are disproportionately greater than would be predicted based on discharge (S10, S11). Our study was conducted in Rio Las Marías, a fourth-order tributary of the Rio Portuguesa, which flows into the Rio Apure. The Rio Apure, a major tributary of the Orinoco, supplies the Orinoco with 20% of its suspended sediment and nutrient load (S11, S12). The Piedmont is distinctly seasonal, with a dry season occurring from January to April and a rainy season during the remainder of the year. During the dry season, there is little rainfall (dry season mean ± 1 SD, 123 ± 53 mm; annual mean ± 1 SD, 1621 ± 208 mm, 1950-2002), and stream discharge decreases steadily (e.g., fig. S4). We monitored water stage height with a continuously recording water level indicator and developed a stage-discharge relation to predict discharge on days that is was not measured empirically. Our study area was located in the lower portion of the watershed where the stream has an open canopy. Rio Las Marías is representative of other piedmont streams at similar elevations in being warm (1997-2002 dry season daily mean ± 1 SD, 27 ± 2 °C), with a stream bottom dominated by cobble, gravel, and some extensive sandy areas. Water depth during the dry season varies from 0.1 m in riffles to 1.5 m in the deeper pools, with the majority of the stream composed of 0.3 m slow flowing runs. Our 3-km study area has a channel slope of 0.002 m m⁻¹ and a dry season water velocity of 0.10 ± 0.04 m s⁻¹ (mean ± 1 SD). POC concentrations are variable within and among years (mean ± 1 SD, 1.3 ± 0.7; range 0.3-2.9 mg L⁻¹). The data reported here were collected during the 1997-2002 dry seasons, which spanned a period of considerable variability in fish abundance and stream discharge (Fig. S3).

A conspicuous feature of Andean piedmont rivers is the high density, biomass, and diversity of fishes (S12-S15). We have recorded more than 80 fish species in Rio Las Marías during the dry season, and continue to find new species each field season. The most diverse components of the fish assemblage include: small omnivorous tetras (Characidae), insectivorous catfishes (Heptapteridae), and armored catfishes (Loricariidae) that consume benthic algae and benthic particulate matter. Although Neotropical fishes cannot be easily classified into distinct feeding guilds (S15), benthic-feeding is very common and these fishes generally dominate the biomass of Andean piedmont and tropical South American fish assemblages (S15-S18).

During the dry season, the three largest fishes consistently found at the site are migratory species, Salminus hilari (Characidae), Brycon whitei (Characidae), and Prochilodus mariae (Prochilodontidae). Salminus is a piscivore that feeds on small tetras and armored catfish; whereas, Brycon is primarily a frugivore (S19). In contrast, Prochilodus is a detritivore and typically comprises >50% of the migratory fish biomass
during years with large migrations in Río Las Marías and other piedmont rivers (S20-S22). In addition to their high biomass, Prochilodus has several unique traits that probably enhance the strength of their per biomass effects. They process large quantities of benthic sediments to meet their energetic demands, and are specialized for deriving nutrients from a diet of fine detritus (S21, S23). Prochilodus also has a mouth cavity with a ventral inverted keel that may facilitate selective ingestion of organic particles by allowing inorganic particles to settle and be expelled through their gill slits (S21, B. Taylor personal observation). We focused on the effects of Prochilodus in such a diverse assemblage for two reasons. First, small-scale caging experiments show that this fish species decreases the biomass of benthic particulate matter (S1, S2), by physically disturbing particulate matter, rapidly consuming and egesting them, or selectively sorting particles in their oral cavity, all of which we hypothesized should enhance the downstream transport of POC. Second, by removing benthic particulate matter, Prochilodus alters algal and invertebrate abundance and composition (S1, S2), which we posited should affect rates of ecosystem metabolism. Lastly, prochilodontids constitute as much as 80% of the South American freshwater fishery (S18, S24) and are declining in portions of the Orinoco basin (S22); hence, it is possible that this species and its effects on ecosystem processes could be disrupted by humans.

Besides Prochilodus, there are a number of other benthic-feeding fishes, but they are smaller in body size and generally do not constitute a large percentage of the total fish biomass in Río Las Mariás or other tropical South American rivers (S12-S15). The other abundant benthic-feeding fishes by biomass after Prochilodus are the characoid Parodon apolinari (Parodontidae) and the armored catfishes Ancistrus triradiatus, Chaetostoma milesi, Lasiancistrus sp. (Loricariidae), which are similar in biomass. Parodon is endemic to Andean piedmont streams and forms large mobile schools (S19, S25). Parodon’s mouthparts are well-suited for grazing attached algae (S19), but they may also resuspend benthic POC by direct bioturbation with their mouth and rigid ventral fins or indirectly from turbulence created while swimming near the streambed (S25). Armored catfish are common bottom and wood feeders, with a suctorial ventral mouth that enables them to adhere to substrates and graze algae and perhaps resuspend benthic POC while feeding (S26-S30). The tight association between fishes and sediments in Neotropical streams is evident by their feeding scars (S1, S2, S25, S26, S27, for photographs).
Supporting figures

Fig. S1. A conservative tracer (NaCl) was added in a single pulsed event to the upstream end of the treatment (dashed line) or the reference (solid line) area of the split-stream experiment, and conductivity was monitored every minute using Hydrolab MiniSonde 4 probes at the downstream ends of each area. Arrows indicate the time and the area to which NaCl was added. Percent hydrologic exchange for each side was calculated as the increase in conductivity above background in the side that no NaCl was added divided by the increase in conductivity above background in the side that NaCl was added multiplied by 100. Hydrologic exchange measured on 30 January 2002 and 19 February 2002 was <1% between the two areas.
**Fig. S2.** The size frequency distribution of the greatest body depth (GBD) of fishes in Rio Las Marías is highly skewed. Many species have body depths smaller than the diameter of the mesh used to selectively exclude *Prochilodus*. GBD measurements were obtained from field measurements and published values (*S19*).
Fig. S3. Interannual whole-stream flux of suspended particulate organic carbon was not significantly associated with mean dry season discharge of Rio Las Marías \((r = 0.22, \ P = 0.68, \ d.f. = 4)\).
Fig. S4. Temporal changes in stream discharge in Rio Las Marias during the 2002 dry season. The solid line indicates the period during which the split-stream experiment was conducted. Due to a rare rainfall event on 15 February, discharge increased 23% (175 to 215 L s\(^{-1}\)).
### Supporting tables

**Table S1.** Physical variables measured in the reference and treatment streams pre and post *Prochilodus* removal.

<table>
<thead>
<tr>
<th>Time</th>
<th>Day</th>
<th>Discharge (L s(^{-1}))</th>
<th>Depth (m)(^*)</th>
<th>Width (m)</th>
<th>Velocity (m s(^{-1}))</th>
<th>(k_{O_2})§ (d(^{-1}))</th>
<th>Discharge (L s(^{-1}))</th>
<th>Depth (m)(^*)</th>
<th>Width (m)</th>
<th>Velocity (m s(^{-1}))</th>
<th>(k_{O_2})§ (d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reference</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-removal</td>
<td>20 Jan</td>
<td>324</td>
<td>0.41</td>
<td>5.3</td>
<td>24</td>
<td>3.4</td>
<td></td>
<td>310</td>
<td>0.19</td>
<td>10.4</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>22 Jan</td>
<td>324</td>
<td>0.41</td>
<td>5.3</td>
<td>23</td>
<td>3.4</td>
<td></td>
<td>310</td>
<td>0.20</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>26 Jan</td>
<td>213</td>
<td>0.31</td>
<td>5.2</td>
<td>26</td>
<td>4.5</td>
<td></td>
<td>177</td>
<td>0.14</td>
<td>9.6</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>30 Jan</td>
<td>188</td>
<td>0.31</td>
<td>5.2</td>
<td>30</td>
<td>4.5</td>
<td></td>
<td>165</td>
<td>0.17</td>
<td>9.6</td>
<td>34</td>
</tr>
<tr>
<td>Post-removal</td>
<td>03 Feb</td>
<td>142</td>
<td>0.26</td>
<td>5.1</td>
<td>33</td>
<td>5.3</td>
<td></td>
<td>143</td>
<td>0.14</td>
<td>9.3</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>09 Feb</td>
<td>140</td>
<td>0.33</td>
<td>5.0</td>
<td>41</td>
<td>4.3</td>
<td></td>
<td>103</td>
<td>0.13</td>
<td>8.9</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>13 Feb</td>
<td>78</td>
<td>0.21</td>
<td>5.0</td>
<td>47</td>
<td>6.6</td>
<td></td>
<td>75</td>
<td>0.12</td>
<td>8.6</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>16 Feb</td>
<td>72</td>
<td>0.22</td>
<td>5.1</td>
<td>55</td>
<td>6.3</td>
<td></td>
<td>53</td>
<td>0.10</td>
<td>8.6</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>21 Feb</td>
<td>57</td>
<td>0.24</td>
<td>5.0</td>
<td>72</td>
<td>5.8</td>
<td></td>
<td>43</td>
<td>0.11</td>
<td>8.3</td>
<td>74</td>
</tr>
<tr>
<td>*<em>Mean ± 95% CI</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>171 (78)</td>
<td>0.3 (0.1)</td>
<td>5.1 (0.1)</td>
<td>39 (13)</td>
<td>4.9 (0.9)</td>
<td></td>
<td>153 (77)</td>
<td>0.14 (0.1)</td>
<td>9.3 (0.6)</td>
<td>40 (14)</td>
</tr>
</tbody>
</table>

* Confidence interval.
§ Standardized to 20\(^0\)C.
\(^*\) Estimated as: discharge/(width\(\times\)velocity).
Supporting references and notes