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*) disproportionately 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 invasion, 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.

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

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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 overharvested 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

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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 how 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 apolinari* (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 migrates into Andean piedmont rivers to feed during the dry season (January to April) and spawn while returning to floodplains during the wet season (May to December) (10).
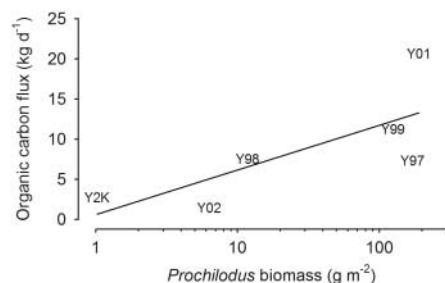
Prochilodus migrations represent a potentially important linkage within river networks, because, by bioturbating, consuming, and egesting large volumes of detritus, this fish may enhance the downstream transport and transformation of materials at a time when hydrologic transport is reduced and algal 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-
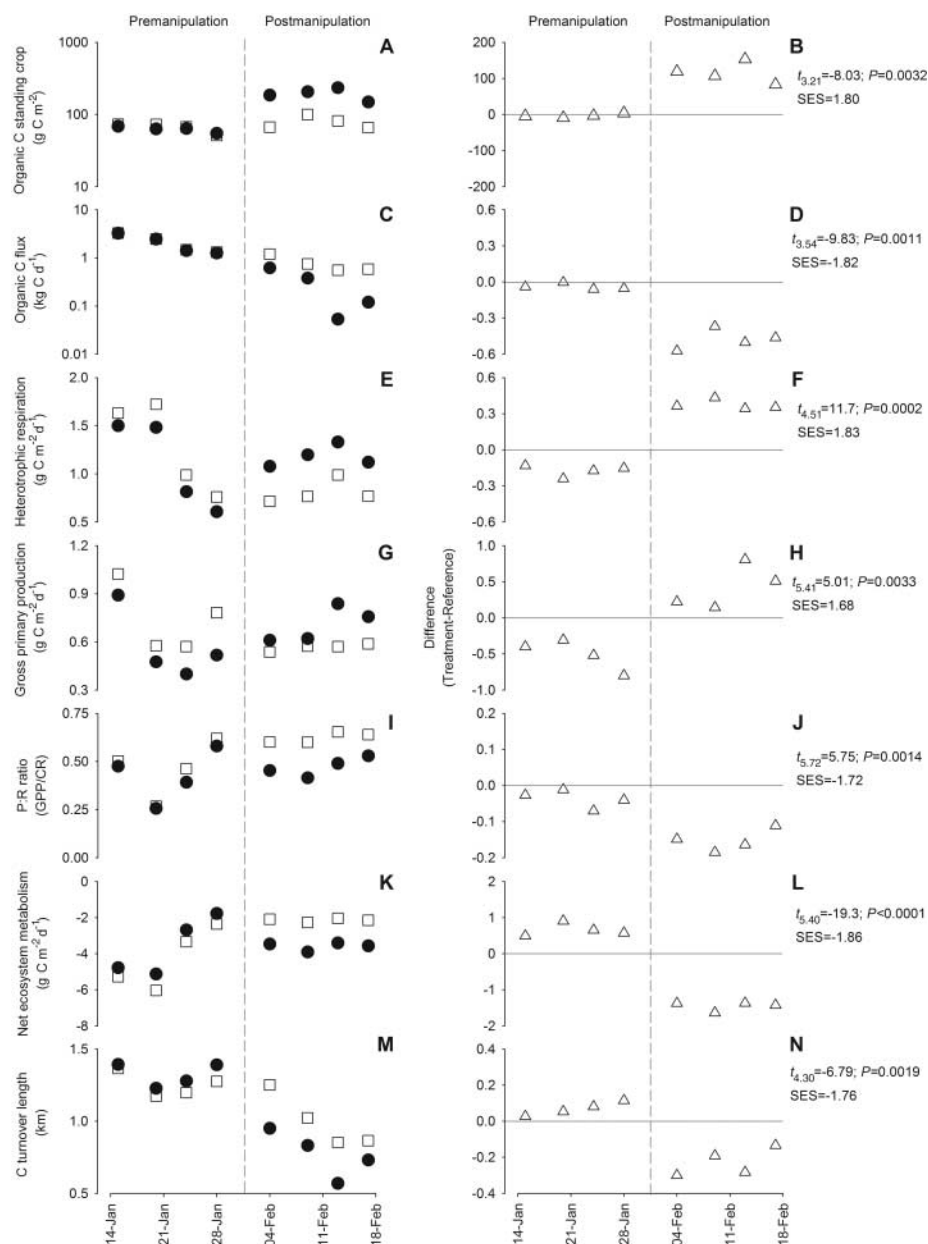

Fig. 2. Photographs of the split-stream removal experiment. (**Top**) The plastic divider and 210 m section of Rio Las Marías. (**Bottom**) Visual differences in benthic particulate matter after removing *P. mariae* (right) compared with the intact fish assemblage (left).

Fig. 1. Interannual variation in organic carbon flux. Whole-stream flux of suspended particulate organic carbon increased as a function of *Prochilodus* biomass (as wet mass). Y97 indicates 1997 data; Y98, 1998 data; etc. Y2K, 2000 data.

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]. The time it takes POC to travel a given distance downstream is a measure of its retention. Before the manipulation, the residence time of POC per longitudinal meter of river (*16*, *17*) was similar between the reference (mean ± 1 SD = 0.43 ± 0.09 day m^{-1}) and the treatment (mean ± 1 SD = 1.5 ± 0.54 day m^{-1}) but increased by an order of magnitude, 0.8 ± 0.19 day m^{-1} in the reference compared with 10.91 ± 3.67 day m^{-1} in the treatment, after removing *Prochilodus* ($t_{3.01} = 5.27$, $P = 0.01$). Thus, during the dry season when floods are small and infrequent, *Prochilodus* enhances the transport of POC, which is a source of energy to downstream communities and a key biogeochemical function of rivers (*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 treatment 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 $19 \pm 9.1\%$ per year ($t_{22} = -1.80$, $P = 0.03$). The current mean maximum body mass of 201 ± 81 g ($t_{22} = 2.50$, $P = 0.01$) 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*, *3*).
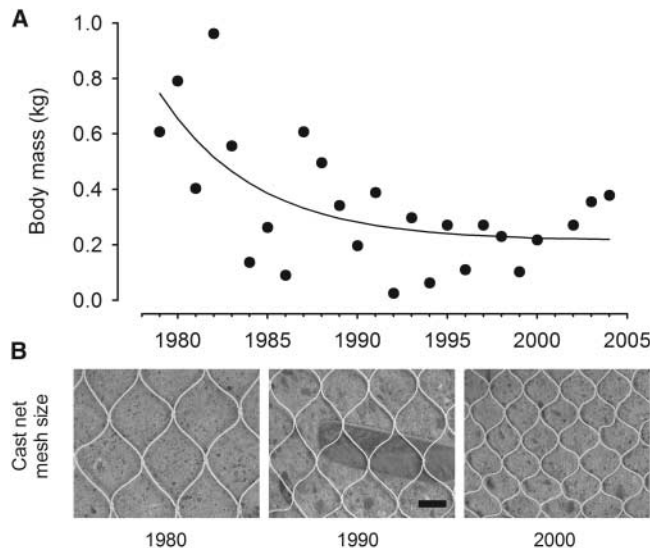
These results have several implications for conservation management and our understanding of ecosystem function. First, the results show low functional redundancy in a diverse ecosystem for a single detritivorous fish species that regulates fundamental ecosystem processes, synthesis and degradation of 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 (*5*). 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*).

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Fig. 4. Time trends of body mass for the migratory fish *P. mariae*. (**A**) Mean maximum body mass of individuals in the upper quartile for specimens collected throughout the Orinoco basin. The equation is *Prochilodus* mean maximum body wet mass (g) = $0.214 + e^{-0.19t}(0.856 - 0.214)$, which fit better ($F_{1,22} = 5.359$, $P = 0.03$) than a simpler, semi-log-linear model (lack-of-fit test: $F_{1,22} = 66.596$, $P < 0.0001$). (**B**) Photographs of cast nets made over the past 3 decades by a fisherman in the community near the study site. Scale bar indicates 2.5 cm.