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Deforesting the riverscape: the effects of wood on fish diversity in a Venezuelan piedmont stream

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Abstract

While deforestation of tropical ecosystems has been shown to have significant impacts on terrestrial habitats, its effects on aquatic habitats are poorly studied. Deforestation dramatically reduces the input of woody debris to streams, and given the importance of large woody debris to fish communities in temperate streams, this might be one mechanism by which logging could affect aquatic ecosystems in the tropics. To examine the effects of large woody debris on the diverse fish assemblage of a tropical stream, we surveyed pools with and without wood at Rio Las Marias, Venezuela. Pools containing wood contained greater numbers of individuals and more species of fish than pools without wood, and the two types of pools differed in their composition. To test whether these results were due to the presence of woody debris, we conducted an experimental wood addition. Pools to which wood was added showed marked increases in both fish abundance and species richness relative to wood-free pools, and the composition of the fish assemblage in experimental pools approached that of pools with naturally occurring woody debris. These results demonstrate that large woody debris plays a major role in structuring fish communities in tropical streams. As a consequence, logging practices that reduce the input of woody debris to tropical streams or directly remove wood from streams could have serious impacts on aquatic habitats, affecting both the diverse fish communities and local economies dependent on stream fisheries.

Keywords: Deforestation; Experiment; Fish diversity; Large woody debris; Tropical streams; Venezuela

1. Introduction

Land-use change associated with logging is one of the most serious threats to biological diversity in tropical ecosystems (Sala et al., 2000). Although the negative effects of logging on terrestrial ecosystems has been documented (e.g., Lovejoy et al., 1984), there has been relatively little consideration of the effects of deforestation on aquatic ecosystems (but see Bojsen and Barriga, 2002). One potentially important impact of deforestation on tropical streams is a dramatic reduction in the inputs of large woody debris.

Fallen logs are a conspicuous feature of many stream ecosystems (Maser and Sedell, 1994). Large woody debris has been shown to affect numerous aspects of stream ecosystems (Wallace et al., 1995), including channel morphology (Keller and Swanson, 1979), organic matter retention (Bilby, 1980), current velocity (Shirvell, 1990), invertebrate biomass (Benke et al., 1984), and predation risk (Everett and Ruiz, 1993). As a result, it is not surprising that a number of studies have shown a positive effect of large woody debris on fish densities and diversity (Angermeier and Karr, 1984; Shirvell, 1990; Everett and Ruiz, 1993; Reeves et al., 1993; Allouche and Gaudin, 2001).

Despite the interest in understanding how large woody debris affects fish communities in temperate streams, there has been relatively little work on the role of woody debris in tropical streams. Yet, large woody debris is a common feature of many tropical streams that are characterized by extreme flooding and bank erosion during the rainy season (e.g., Flecker and Feifarek, 1994). Furthermore, fish communities of tropical streams tend to have much higher diversity than temperate streams (Lowe-McConnell,

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1987) and include guilds such as wood and fruit-eating fishes that might be particularly influenced by woody debris. Understanding controls on fish abundance and diversity in tropical streams is particularly critical because these fisheries are extremely important to local communities. In some areas of the Neotropics, fish are a dominant source of the protein in human diets (Chapman, 1979; Bayley, 1981; Welcomme, 1985; Bayley, 1989; Novoa, 1989), and productive river fisheries can serve as a major component of local economies (Welcomme, 1979; Goulding et al., 1986; Zanetell, 2000).

This study examines the abundance of large woody debris, and the effect of woody debris on the abundance and diversity of fish in Rio Las Marias, a mid-sized stream located in the Andean piedmont region of Venezuela. Understanding the ecological role of woody debris is particularly relevant to the conservation and management of Andean piedmont streams, because large woody debris is often removed from stream channels by logging companies as a source of timber and by fishermen to improve access to fish sheltering therein (Flecker personal observation). Furthermore, logging and clearing of near-stream forests for cattle pasture and agriculture has occurred at high rates in the piedmont region; for example, Karwan et al. (2001) reported reductions in forest cover over the last half century of more than 50% in some piedmont watershed, and such forest loss can greatly reduce woody debris inputs into streams (Reeves et al., 1993).

We surveyed fish populations in pools with and without clumps of large woody debris and performed an experimental wood addition to: (1) estimate the effect of large woody debris on the abundance, and species richness of a diverse, tropical stream fish community, and (2) experimentally test whether differences observed in the survey were due to the presence of woody debris. Because large woody debris increases fish diversity and abundance in the temperate zone and because tropical fish assemblages contain guilds specializing on wood, we hypothesized that large woody debris would increase the abundance and diversity of the fish assemblage.

2. Methods

2.1. Site description

Rio Las Marias is a fourth-order stream of the Apure drainage of the Orinoco River system in Venezuela. The study site is located in the Andean piedmont region at about 225 m above sea level (9°10′N, 69°44′W, see description in Flecker, 1996). Stream bottom substrate is dominated by cobble and gravel, although some pools and runs are mostly sandy bottomed. Stream temperatures are warm and exhibit diel fluctuations from 25 to 32 °C. Typical of streams in the Andean piedmont, Rio Las Marias is distinctly seasonal with a single dry season generally occurring between December and April and a rainy season during the remainder of the year. During the rainy season, the channel of Rio Las Marias is extremely dynamic and floods large enough to cause major changes in channel morphology occur at the site on an annual basis (see Flecker and Feifarek, 1994). Channel-scouring floods result in large inputs of fallen logs, tree falls associated with bank collapses, and the redeposition of woody debris already in the channel. Dry season discharge is typically between 3 and 30 m^3/min.

Rio Las Marias has a diverse assemblage of fishes, composed largely of characiforms (tetras and allies) and siluriforms (catfishes). We have collected >75 fish species at the site and we continue to find additional fish species. Most years, the flannelmouth characin, *Prochilodus mariae* (Prochilodontidae), a migratory detritivore, is the dominant fish by biomass during the dry season months (Flecker, 1996).

2.2. Wood survey

In January 1998, we quantified the amount of woody debris in the wetted channel of a 2.7 km section of the Rio Las Marias. All pieces of large woody debris with a diameter greater than 10 cm and a length greater than 1 m were numbered, measured and converted to volumes. Angle relative to stream flow was also estimated. Live roots lying within the stream were counted, as were living trees.

We assumed tree trunks were roughly cylindrical and calculated volume by estimating the diameter of the cylinder as the average of the diameter at both ends of the piece. Root wads were measured by estimating a short, squat cylinder, or cone. Diameters were usually listed as half of the measurement of the base of the root wad, to account for the fact that root wads are not solid masses of wood, but tangles of smaller branches. Pieces were often partially decomposed, oddly shaped, or partially buried. Under those conditions, we estimated measurements that would most accurately express the total volume of the piece. Debris jams were more difficult to quantify; diameter, length, and width were approximated, along with an estimate of the total number of pieces of large woody debris.

2.3. Fish survey

In January 1999,we surveyed the fish communities in three pools containing large clumps of woody debris and in six pools without woody debris. All pools were located within a 4-km stretch of Rio Las Marias. Three of the pools without wood were randomly selected to receive an experimental addition of large woody debris after three weeks of observation (hereafter experimental pools) while the other three pools without wood served as references throughout the study (hereafter wood-free reference pools).

In each pool, we set up a standardized grid of 12 observation stations. To sample a pool, we entered the downstream station, waited 3 min, and performed three instantaneous point counts using mask and snorkel. All individuals visible at a station were counted and classified to species, with a 1-min interval between point counts. We then proceeded to the next sampling point upstream, waited 3 min and repeated the procedure. The 3 point counts from an individual station were averaged to estimate the number of individuals of each species present at each point in a pool.

Surveys were conducted in all 9 pools on 5 dates over the 6-week period of the experiment, three times prior to the wood addition, and twice afterwards. Pools were sampled in random order on each survey date to avoid biased results due to the time of day at which pools were sampled. No pools were surveyed for 2 weeks following the wood addition to allow the experimental pools to recover following the disturbance. Three pools (one in each treatment) were surveyed a sixth time, 8 weeks following the start of the experiment. Data from the final partial survey are not included in any of the analyses due to lack of replication, but are shown in the figures to illustrate longer-term trends.

At the beginning of the experiment, we measured the width of each pool along 6 transects and measured depth at 1-m intervals along each transect. These data were used to calculate mean pool depth and cross-sectional area (Hauer and Lamberti, 1996). We measured velocity at each of the 12 observation points in each pool using a Marsh–McBirney flowmeter (Flo-Mate Model 2000), and calculated mean velocities for each pool.

2.4. Experimental wood addition

To determine whether the presence of woody debris was responsible for differences in fish communities among pools with and without woody debris we added woody debris on Day 23 of the experiment to three experimental pools designated at the start of the experiment. All wood added to the pools was collected from the dry streambed and had likely been deposited during the previous rainy season. We selected the largest pieces of wood that could be moved into the streams, and arranged the woody debris in clumps, attempting to simulate the configurations and volumes of debris found in naturally occurring woody debris piles.

2.5. Data analysis

Data on the physical characteristics of the pools were analyzed using a single factor ANOVA model with the treatment consisting of three levels (Natural Wood, Wood-free Reference, and Experimental Pools). To compare the structure of fish communities in different pools, we calculated the mean number of fish observed at a sampling station (abundance) and the number of species present in each pool (richness) for each date. Because the number of species observed in a sample is in part a function of the number of individuals in the sample, we also calculated a rarefied estimate of species richness, i.e., the mean expected number of species observed given a fixed number of individuals (Gotelli and Colwell, 2001). For each pool at each date, we rarefied all samples to 26 individuals, the number of individuals observed in the least abundant pool, using EcoSim software (Gotelli and Entsminger, 2001).

To test for differences in the abundance, richness, and rarefied richness between wood pools and wood-free reference pools, we performed an ANOVA for a two-factor experiment with repeated measures (Ott, 1998). The wood treatment (Wood vs. Wood-free Reference) was considered a fixed effect, and pool was nested within treatment. The wood treatment was crossed with the five levels of time (i.e., the different survey dates). We ran this model using the GLM procedure.

To test for an effect of the wood addition, we performed two separate analyses using the model structure described above. The first analysis used the data from the three dates prior to the wood addition, and the second analysis used only the data from the two dates subsequent to the wood addition and compared the wood-free reference pools to the experimental pools. We hypothesized that prior to the experimental wood addition, wood-free reference pools would have similar fish diversity and abundance as the experimental pools, and that all pools would vary similarly through time. In contrast, a significant treatment effect following the wood addition would be consistent with our hypothesis that wood addition has a significant effect on fish community structure. We preferred this approach to a Before-After-Control-Impact (BACI) analysis (Underwood, 1992) due to the replication of "impacted" plots, the lack of replication within plots, and the unbalanced nature of our temporal replication before and after the experimental addition.

To examine differences in the community composition in pools with and without large woody debris, we conducted t tests (assuming unequal variance) to compare the mean abundance for each species, averaged across all dates, in wood and wood-free pools and in experimental pool before and after the wood addition. All statistical analyses were conducted using SYSTAT v7.0.

3. Results

3.1. Wood survey and physical characteristics of pools

In 1998, there was an average of 18.5 pieces of woody debris per km stream length, with an average total volume of 24.2 m^3/km stream length. The volumes of

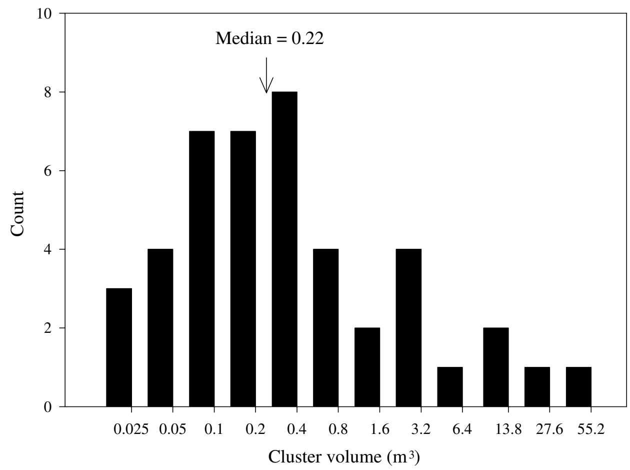

Fig. 1. Distribution of the volume of wood contained in clumps of large woody debris present in the active channel of the Rio Las Marias.

individual clumps of woody debris were distributed roughly log-normally, with the median clump containing 0.22 m^3 of woody debris (Fig. 1). Most (68.1%) of the pieces of wood in the stream were oriented parallel to the direction of flow, while only 12.8% of the pieces were oriented perpendicular to flow.

Pools selected for the different treatments were similar in their dimensions as neither their mean depth ($F_{2,6} = 0.07$, $p = 0.93$) nor their mean cross-sectional area ($F_{2,6} = 0.15$, $p = 0.87$) differed between treatments. Mean velocity was slightly higher for the wood-free reference pools (7.2 cm/s) than in the experimental (6.1 cm/s) or wood (4.6 cm/s) pools, but these differences were not significant ($F_{2,6} = 0.38$, $p = 0.70$).

3.2. Survey of wood and wood-free reference pools

At each survey date,the mean number of individual fish observed per station was significantly higher in pools with wood than in the wood-free reference pools (Fig. 2(a); $F_{1,16} = 121.88$, 0.01). Pools with wood also contained significantly more species than the wood-free pools at every survey date (Fig. 2(b)) ($F_{1,16} = 196.11$, $p < 0.01$), although richness did not vary significantly over time ($F_{4,16} = 2.50$, $p = 0.08$). Rarefied estimates of richness were higher on all but one of the sampling dates (Fig. 2(c)) and were significantly different over all ($F_{1,16} = 21.95$, $p < 0.01$), indicating that differences in species richness were not simply due to the presence of more individuals in pools with wood.

Pools with wood contained a distinct assemblage of fish species relative to pools without woody debris. Of the thirty species of fish observed in this study, 26 were more abundant in pools with wood, with at least a marginally significant increase in abundance for 19 ($p < 0.1$; Table 1). The presence of large woody debris in a pool increased the abundance of species belonging to many functional groups and across size classes. Furthermore, rare species, defined as those species with a mean abundance of less than 0.2 individuals per pool, were more prevalent in pools with woody debris (34% of the total species list) than in pools without woody debris (9.5% of the total species list).

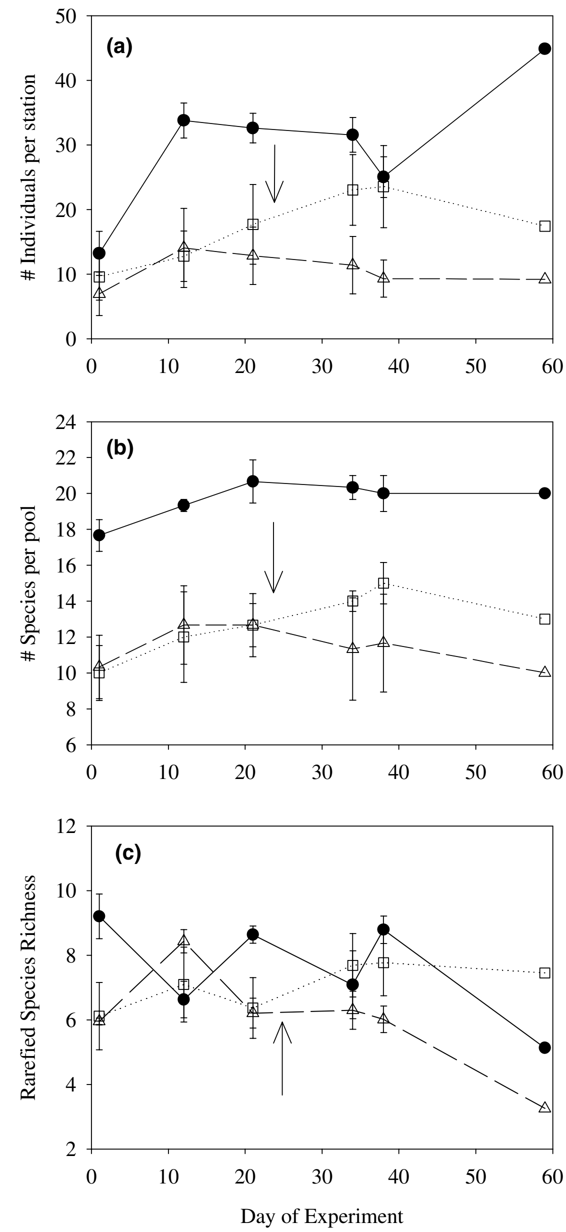

Fig. 2. (a) Mean number of fish of all species observed at a sampling station (±1 SE), (b) mean number of species observed in pools (±1 SE), and (c) Rarefied species richness in pools (±1 SE) over time in pools with naturally occurring wood (filled circles), wood-free pools (open triangles), and experimental pools (open squares). The date of the wood addition to the experimental pools is indicated by the arrow. Only one pool in each treatment was sampled on the final sampling date.

3.3. Experimental wood addition

Prior to the wood addition, experimental and wood-free reference pools did not differ significantly in abun-

Table 1
Average number of individuals observed at an observation station, averaged across all pools and all dates for wood-free pools, pools with naturally occurring wood, and experimental pools both before and after the wood addition for all species observed during the experiment

Species	Size (mm)	Wood-free	Wood	Pre-addition	Post-addition
Mid-water feeders					
Invertivores					
Cheirodontops geayi	35	0.04 (0.04)	0.05 (0.05)	0.31 (0.28)	–
Gephyrocharax valencia	35	–	**1.19 (0.27)**†	–	**0.28 (0.11)****
Omnivores					
Leporinus friderici	300	–	**0.02 (0.01)***	–	–
Brycon whitei	250	0.37 (0.10)	0.57 (0.14)	0.45 (0.14)	0.40 (0.17)
Leporellus vittatus	150	**0.03 (0.01)**	**0.08 (0.02)***	0.11 (0.07)	0.16 (0.09)
Astyanax integer	120	**0.12 (0.09)**	**1.01 (0.30)****	0.37 (0.20)	0.19 (0.10)
Leporinus striatus	100	**0.03 (0.02)**	**0.45 (0.07)**†	0.19 (0.17)	0.04 (0.03)
Astyanax metae	90	0.02 (0.01)	0.01 (0.01)	0.02 (0.01)	0.10 (0.06)
Astyanax bimaculatus	55	–	**0.07 (0.02)****	–	–
Roeboides dayi	50	**0.06 (0.00)**	**0.23 (0.07)***	–	0.02 (0.02)
Hemigrammus marginatus	45	–	**0.63** (*0.15*)†	–	–
Bryconamericus deuterodenoides	35	**3.71 (0.87)**	**9.77 (0.88)**†	**5.21 (1.54)**	**9.55 (2.10)***
Cheirodon pulcher	30	**0.64 (0.19)**	**4.49 (1.76)****	**0.40 (0.26)**	**2.19 (0.71)****
Creagrutus melasmus	30	**0.11 (0.05)**	**0.23 (0.05)***	0.20 (0.12)	0.26 (0.11)
Poecilia reticulata	25	0.06 (0.03)	0.01 (0.01)	0.08 (0.07)	0.04 (0.04)
Piscivores					
Salminus hilarii	450	0.21 (0.08)	0.11 (0.02)	0.12 (0.04)	0.07 (0.03)
Xenagoniates bondi	50	–	0.01 (0.01)	–	–
Benthic feeders					
Detritovores					
Prochilodus mariae	200	**1.50 (0.35)**	**4.73 (0.85)**†	**1.07 (0.24)**	**1.96 (0.47)***
Herbivores					
Farlowella vittata	200	–	**0.02 (0.01)***	–	–
Schizidon isognathus	200	0.04 (0.03)	0.02 (0.01)	0.13 (0.07)	–
Parodon apolinari	125	0.92 (0.32)	0.95 (0.11)	1.24 (0.47)	1.74 (0.62)
Ancistrus triradiatus	50	–	0.01 (0.00)	0.01 (0.01)	–
Chaetostoma milesi	50	–	0.02 (0.02)	0.02 (0.01)	0.11 (0.11)
Lasiancistrus sp.	50	**0.03 (0.01)**	**0.22 (0.04)**†	0.03 (0.02)	0.21 (0.10)
Rineloricaria sp.	75	–	–	0.01 (0.01)	–
Hypostomus sp.	50	–	–	0.01 (0.01)	–
Panaque maccus	15	–	0.01 (0.00)	–	–
Inveritvores					
Crenicichla sp.	120	**0.41 (0.17)**	**0.79 (0.15)***	**0.32 (0.09)**	**0.63 (0.13)***
Spatuloricaria gymnogaster	75	–	0.01 (0.01)	–	**0.01 (0.01)**
Characidium zebra	50	**0.01 (0.01)**	**0.12 (0.03)**†	–	**0.07 (0.02)**†
Aequidens pulcher	40	**0.09 (0.05)**	**0.41 (0.07)**†	**0.06 (0.04)**	**0.87 (0.21)**†
Characidium boavistae	40	**0.07 (0.02)**	**0.37 (0.09)**†	**0.06 (0.03)**	**0.35 (0.16)***
Omnivores					
Creagrutus cf beni	40	1.05 (0.52)	1.73 (0.38)	2.94 (1.21)	3.20 (0.86)
Ambush predator					
Hoplias malabaricus	175	–	**0.02 (0.01)***	–	0.02 (0.01)

Size is mean standard length as reported in (Taphorn, 1992). Standard error around each mean is shown in parentheses. Comparisons between wood-free and wood pools and pre-addition and post-addition pools that are significantly different are indicated in bold (* $p < 0.1$; ** $p < 0.05$; † $p < 0.01$).

dance, richness or rarefied richness (Fig. 2) (Table 2). In contrast, following the wood addition, there was a significant treatment effect for all three variables, with the addition of wood causing an increase in abundance, richness, and rarefied richness (Table 2). Increases in rarefied species richness in experimental relative to wood-free reference pools suggest that higher richness was not simply due to greater abundance of individuals. This is further supported by the accumulation curves of species over time for wood and wood-free pools compared to the experimental pools (Fig. 3). For example, immediately preceding the experimental addition, we had already observed roughly 90% of the species observed by the conclusion of the study in the wood and wood-free pools, and new species were added relatively gradually in subsequent sampling events. In the experimental pools, only 75% of the total species list had been observed prior to the addition, and the sampling event immediately following the addition added a large number of species not previously seen in those pools.

Table 2
ANOVAs for the effects of experimental wood addition on abundance, richness and rarefied richness

Source	Pre-addition			Post-addition		
	df	*F*-ratio	*p*	df	*F*-ratio	*p*
Abundance						
Treatment	1	1.677	0.231	1	136.326	**<0.001**
Time	2	6.876	**0.018**	1	0.498	0.519
Treatment*time	2	1.255	0.336	1	1.378	0.306
Pool (treatment)	4	15.605	**0.001**	4	39.012	**0.002**
Richness						
Treatment	1	0.391	0.549	1	20.250	**0.011**
Time	2	8.652	**0.010**	1	1.000	0.374
Treatment*time	2	0.130	0.880	1	0.250	0.643
Pool (treatment)	4	22.783	**<0.001**	4	18.375	**0.008**
Rarefied richness						
Treatment	1	1.702	0.228	1	9.554	**0.037**
Time	2	17.139	**0.001**	1	0.041	0.849
Treatment*time	2	3.681	0.074	1	0.025	0.741
Pool (treatment)	4	15.998	**0.001**	4	3.842	0.110

Pools are nested within treatments (i.e., pools assigned for wood addition or wood-free reference pools) and data from before and after the addition were analyzed separately. Significant results are highlighted in bold.

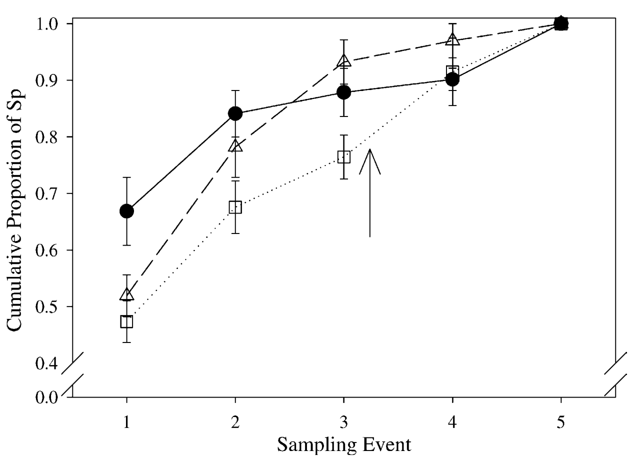

Fig. 3. Cumulative proportion of species observed over time (±1 SE) in pools with naturally occurring wood (filled circles), wood-free pools (open triangles), and experimental pools (open squares). The date of the wood addition to the experimental pools is indicated by the arrow.

The composition of the fish assemblage in experimental pools prior to the wood addition was generally consistent with the composition of the wood-free pools (Table 1). Of the 19 species of fish that were more abundant in wood pools than wood-free pools in the survey, 13 increased in abundance following the wood addition, with 8 of these increases being at least marginally statistically significant ($p < 0.1$). Only *Astyanax integer* and *Leporinus striatus*, two mid-water omnivores, decreased in abundance following the wood addition, and neither change was statistically significant.

4. Discussion

The deposition of large woody debris by rainy season floods has a striking effect on dry season fish communities of Rio Las Marias. The survey of pools with and without wood demonstrates that, despite similar physical characteristics, pools with wood have many more individuals and species of fish than pools without wood, and contain a much higher number of rare species. Furthermore, the experimental addition of large woody debris to previously wood-free pools resulted in an increase in abundance and species richness, and a shift in composition towards that typical of pools with naturally occurring wood.

This experiment took place during the end of the dry season, and by the time of the addition, riffles connecting pools with and without wood had dried up significantly. Given this, we were surprised to see such a dramatic shift in community structure and composition following the addition of large woody debris. While our sampling scheme was not designed to track individual fish, the large increase in both the number of fish and the number of species not previously observed in the experimental pools, relative to the changes in wood-free reference and wood pools, suggests that new individuals were moving into the experimental pools in response to the addition of wood. The fact that significant differences appear following wood addition despite extremely high between-pool variability suggests that these results are quite robust.

Although we have demonstrated the presence of wood in pools results in increased abundance and richness of the fish communities, the proximate mechanism for these changes is unclear. One possibility is that the woody debris serves either as a food resource or a substrate colonized by other resources, such as algae or heterotrophic microbes (Shearer, 1972; Triska et al., 1984) or invertebrates (Benke et al., 1984). Angermeier and Karr (1984) found increased fish abundance and species richness in reaches where woody debris had been artificially supplemented relative to reaches where all woody debris had been removed from an Illinois stream. They attributed these changes, in part, to increases in abundance of trichopterans and ephemeropterans, preferred prey items for insectivorous fish. This hypothesis is likely to explain why, in this study, species such as *Farlowella vittata*, which morphologically resembles twigs and is adapted to consume periphyton growing on logs and branches of woody debris, and *Panaque maccus*, which actually feeds on wood (Nelson et al., 1999) were found exclusively in pools with woody debris. However, the increase in fish abundance in the presence of woody debris was not restricted to herbivorous, detritivorous, and insectivorous species. Indeed, every feeding group other than mid-water piscivores contained species that were more abundant in pools with large woody debris.

Alternatively, woody debris might provide protection from predation either from birds (Power, 1984; Allouche and Gaudin, 2001) or piscivorous fish (Everett and Ruiz, 1993).Large clumps of woody debris, which typically extend in a tangled mass above the surface of the water, undoubtedly provide cover from avian predation. In Rio Las Marias, large schools of *Prochilodus mariae* and the less abundant *Brycon whiteii* were commonly observed feeding in the open water downstream of clumps of large woody debris. These schools would typically swim into the woody debris when disturbed (Wright, pers obs). Furthermore, the largest piscivore, *Salminus hilarii*, was one of the only species that was more abundant in pools without wood, although these differences were not significant. However, *Hoplias malabaricus*, a large ambush predator, was only observed within clumps of woody debris, indicating that the habitat is not devoid of predation risk.

Finally, it is possible that the large woody debris provides an environment that is more energetically favorable by decreasing water velocities (Bisson et al., 1987). Coho salmon fry were found to increase their use of mid-stream areas 3200% following the addition of artificial root wads, and used these habitats more frequently during high flow events (Shirvell, 1990). Thevenet and Statzner (1999), observed higher species richness in pools with large woody debris, and found that local flow heterogeneity explained much of the variability in fish abundance, suggesting that the flow altering effects of the woody debris were most important. In Rio Las Marias, many of the species abundant in the clumps of woody debris are small (<50 mm long) tetras (Characidae) that would presumably find it particularly costly to swim against the high velocities of unobstructed flow. Average velocity tended to be slower in pools with wood,although these differences were not significant.

Most likely, some combination of these mechanisms is responsible for the increase in abundance and species richness of fish in pools with clumps of large woody debris. Regardless of the exact mechanisms, most species of fish observed in this experiment respond positively to the presence of woody debris. This is generally consistent with a large number of studies that have taken place in temperate zone streams which have shown abundance (Angermeier and Karr, 1984; Shirvell, 1990; Everett and Ruiz, 1993; Lehtinen and Mundahl, 1997; Allouche and Gaudin, 2001) and diversity (Angermeier and Karr, 1984; Reeves et al., 1993) of fishes to increase in the presence of large woody debris (Murphey and Hall, 1981). Despite important differences in stream ecosystems and fish communities between the tropics and temperate zones, the provision of food resources, predator-free space,and refuge from current by large woody debris appears to affect fish in a similar manner.

5. Implications

This study represents one of the first attempts to demonstrate experimentally that the negative effects of deforestation on diversity in tropical ecosystems might extend beyond terrestrial ecosystems and into aquatic habitats. The removal of large woody debris from tropical streams, whether by fishers attempting to increase their efficiency or for lumber purposes, and the logging of riparian zone forests, which decreases inputs of woody debris to streams (Reeves et al., 1993) can have serious impact on fish diversity. This deforestation of the riverscape is a common practice in small to mid-sized streams of the Andean piedmont. In Rio Las Marias, we have observed wood removal operations during three of the last ten years, where virtually every sizeable log is removed from the riverbed (A.S. Flecker, personal observation). Timber companies exploit fallen trees in riverbeds not only as a source of wood, but also to obtain permits that can be used as cover for poaching live standing trees. Thus, timber companies illegally log gallery forest trees around streams at the same time that woody debris is harvested from the riverbed, and it is difficult for law enforcement officials to determine the initial source of this timber. Ultimately, extraction of timber from riverbeds results in both the immediate loss of woody debris as aquatic habitat as well as the loss of forested riparian zones. As forested lands dwindle in the Andean piedmont region (Karwan et al., 2001; Allan et al., 2002), the practice of wood removal is likely to increase further.

In addition to effects of deforestation on aquatic diversity, decreased inputs of woody debris to streams could potentially have serious economic costs. Most of fish species that were more abundant in pools with woody debris in this study are relatively small in size or rare, and are therefore not commercially important. However, even large fish, such as *Prochilodus mariae*, the most important commercial fish in the Apure drainage of Venezuela (Taphorn, 1992), showed greater abundance in pools with clusters of large woody debris. Furthermore, if large woody debris acts as a refuge from predation during dry season low flows when the magnitude of predation is increased (Lowe-McConnell, 1987), the removal of woody debris might restrict species to the limited deep pool refugia. This could potentially lead to resource and growth limitation in the commercially important fish species (Allouche and Gaudin, 2001). Thus removal of woody debris is likely to have economic and social costs.

Furthermore, in the large and complex food webs typical of tropical streams, the probability of unexpected indirect effects resulting from eliminating many species from many functional groups is high. Flecker (1996) showed that removing a single species, *Prochilodus mariae*, from the fish community resulted in radical changes in sedimentation rates. While not all species are likely to have as strong effects as *Prochilodus mariae*, the loss of diversity resulting from the removal of large woody debris from tropical streams is likely to have serious impacts from the conservation, ecosystem and economic standpoints.

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