

APPLIED ISSUES

Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams

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SUMMARY

1. Few studies have evaluated the effectiveness of riparian buffers in the tropics, despite their potential to reduce the impacts of deforestation on stream communities. We examined macroinvertebrate assemblages and stream habitat characteristics in small lowland streams in southeastern Costa Rica to assess the impacts of deforestation on benthic communities and the influence of riparian forest buffers on these effects. Three different stream reach types were compared in the study: (i) forested reference reaches, (ii) stream reaches adjacent to pasture with a riparian forest buffer at least 15 m in width on both banks and (iii) stream reaches adjacent to pasture without a riparian forest buffer.
2. Comparisons between forest and pasture reaches suggest that deforestation, even at a very local scale, can alter the taxonomic composition of benthic macroinvertebrate assemblages, reduce macroinvertebrate diversity and eliminate the most sensitive taxa. The presence of a riparian forest buffer appeared to significantly reduce the effects of deforestation on benthic communities, as macroinvertebrate diversity and assemblage structure in forest buffer reaches were generally very similar to those in forested reference reaches. One forest buffer reach was clearly an exception to this pattern, despite the presence of a wide riparian buffer.
3. The taxonomic structure of macroinvertebrate assemblages differed between pool and riffle habitats, but contrasts among the three reach types in our study were consistent across the two habitats. Differences among reach types also persisted across three sampling periods during our 15-month study.
4. Among the environmental variables we measured, only stream water temperature varied significantly among reach types, but trends in periphyton abundance and stream sedimentation may have contributed to observed differences in macroinvertebrate assemblage structure.
5. Forest cover was high in all of our study catchments, and more research is needed to determine whether riparian forest buffers will sustain similar functions in more extensively deforested landscapes. Nevertheless, our results provide support for Costa Rican regulations protecting riparian forests and suggest that proper riparian management could significantly reduce the impacts of deforestation on benthic communities in tropical streams.

Keywords: benthic macroinvertebrates, Costa Rica, deforestation, riparian buffers, tropical streams

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Introduction

Widespread clearing of tropical forests for agriculture has transformed landscapes throughout the tropics in recent decades (Laurance, 1999), and continues to affect millions of hectares annually (Achard *et al.*, 2002). Although the effects of deforestation on tropical stream ecosystems have received relatively little research attention, there is increasing evidence that conversion of forests to agricultural land uses has pervasive impacts on benthic communities in tropical streams. In particular, deforestation can degrade stream habitats (Iwata, Nakano & Inoue, 2003; Wantzen, 2006), change water temperature regimes and alter the abundance and diversity of basal food resources (Henry *et al.*, 1994; Benstead, Douglas & Pringle, 2003; Bojsen & Jacobsen, 2003; Benstead & Pringle, 2004), leading to major shifts in benthic community structure and declines in macroinvertebrate diversity (Benstead *et al.*, 2003; Bojsen & Jacobsen, 2003; Iwata *et al.*, 2003; Dudgeon, 2006; Wantzen, 2006).

Many of the effects of deforestation, including disruption of allochthonous resource subsidies, decreased stream shading and increased sedimentation, are directly linked to processes occurring at terrestrial-aquatic interfaces (Gregory *et al.*, 1991; Naiman & Décamps, 1997), suggesting that forested riparian buffer zones could significantly reduce the impacts of deforestation on tropical streams (Pringle & Scatena, 1999; Benstead *et al.*, 2003). In fact, studies in temperate systems have demonstrated that riparian forest buffers can filter sediment and nutrients from agricultural runoff, stabilize stream banks and provide shade that moderates stream temperatures and regulates instream primary production (Karr & Schlosser, 1978; Peterjohn & Correll, 1984; Osborne & Kovacic, 1993; Sweeney, 1993). Streamside forests also contribute leaf litter and other particulate organic matter that provides food and habitat for macroinvertebrates (Cummins *et al.*, 1989; Sweeney, 1993), often serving as the most important energy source for invertebrate production in headwater streams (Vannote *et al.*, 1980; Wallace *et al.*, 1997; Hall, Likens & Malcom, 2001).

Although riparian forest buffers are expected to provide similar functions in tropical systems, studies documenting relationships between forest buffers and lotic communities in the tropics are conspicuously

lacking. Recent studies have shown that riparian vegetation affects hydrological processes and sediment transport in humid tropical ecosystems (McKergow *et al.*, 2004; Gomi *et al.*, 2006) and is linked to physicochemical conditions in streams (Heartsill-Scalley & Aide, 2003). However, information on how these factors ultimately affect aquatic communities is scarce. Importantly, this limits our ability to develop meaningful riparian buffer strategies and predict how riparian management will influence biodiversity in tropical streams.

In this study, we investigated the extent to which riparian forest buffers moderate the effects of deforestation on benthic macroinvertebrate assemblages in small, lowland streams in southeastern Costa Rica. Costa Rica has historically had very high rates of deforestation (Sader & Joyce, 1988; Sánchez-Azofeifa, Harriss & Skole, 2001), but riparian forests are often maintained in agricultural areas. These forests are formally protected by the Costa Rican national forestry law (no. 7575), which prohibits cutting or clearing of trees in riparian protection zones that vary in width depending on the slope of surrounding terrain. We selected a study area in Costa Rica where large blocks of forest have been converted to pasture, but which retains relatively high forest cover overall. These conditions allowed us to compare sites affected by deforestation with nearby forested stream reaches, while controlling to a large extent for catchment-scale land cover.

We hypothesized that riparian forest buffers would maintain habitat and trophic conditions similar to those found in forest streams, and thus reduce the impact of deforestation on macroinvertebrate assemblages. In order to test this hypothesis, we compared macroinvertebrate assemblages and a set of stream environmental variables among three stream reach types: (i) forested reference reaches, (ii) stream reaches adjacent to pasture with a riparian forest buffer at least 15 m in width on both banks and (iii) stream reaches adjacent to pasture that lacked a forest buffer. The effects of land use change and other anthropogenic impacts on stream macroinvertebrates can vary considerably between different stream habitats (Kerans, Karr & Ahlstedt, 1992; Roy *et al.*, 2003), and so we also investigated whether relationships to deforestation and riparian forest buffers varied between pool and riffle habitats within our study reaches.

Methods

Study site

The study was conducted in Limón Province on the southern Caribbean slope of Costa Rica (9°35'N, 82°40'W). The study streams drain the hills between the Sixaola River Valley and the Caribbean coast, and are tributaries of either the Sixaola River or the Gandoca stream system (Fig. 1). The study area falls within the moist tropical forest life zone of Holdridge (1967), with mean annual temperatures around 26 °C and mean annual precipitation of approximately

2500 mm (WorldClim, Hijmans *et al.*, 2005). The area has a short dry season that generally falls between February and April. However, precipitation in the area is highly variable and does not exhibit strong seasonality, as illustrated by rainfall during our study at the nearest weather station with complete data (Fig. 2).

Twelve sampling reaches in lowland streams representing three different stream reach types (i.e. treatments) were selected for this study (Fig. 1) and concurrent research on stream fishes described in Lorion & Kennedy (In Press). Forest reaches were

Fig. 1 Map of study area in southeastern Costa Rica, with locations of the 12 sampling reaches.

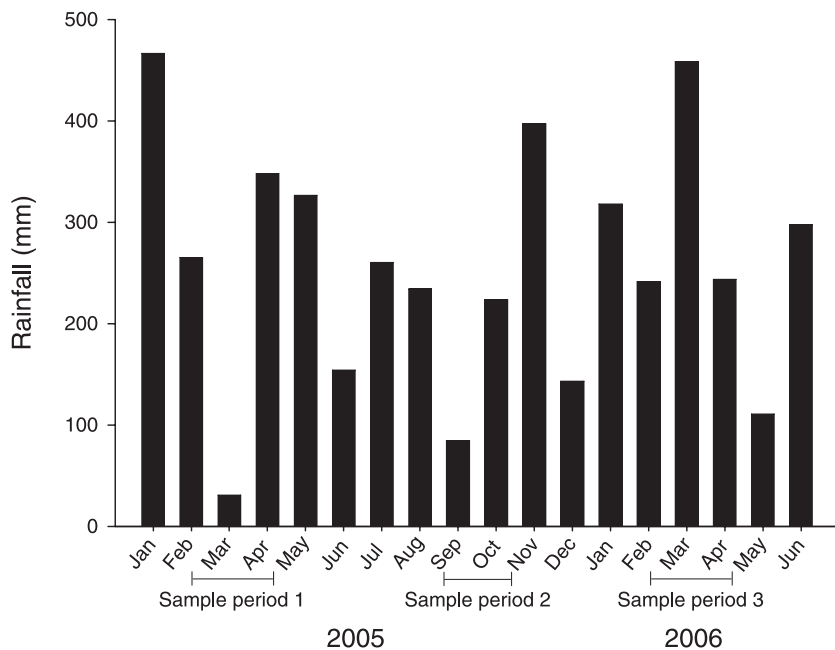
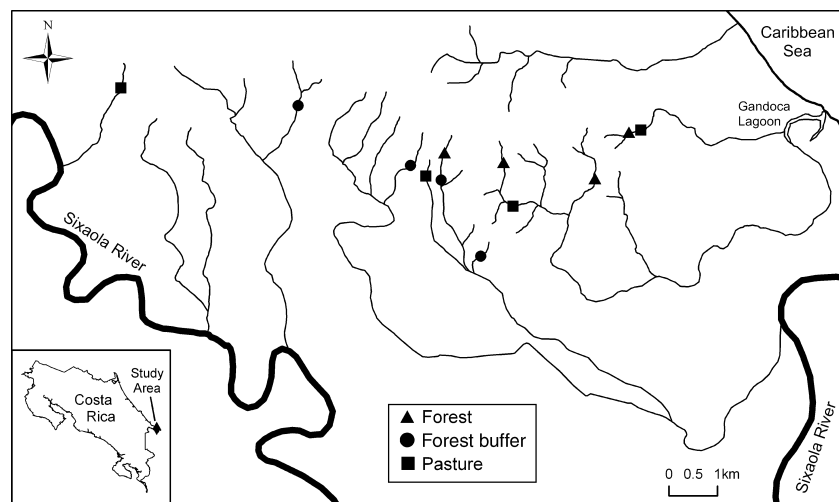


Fig. 2 Monthly rainfall at Puerto Vargas, Costa Rica, January 2005–June 2006. Puerto Vargas is located approximately 25 km northwest of the study area. Data courtesy of the National Meteorological Institute (IMN), San José, Costa Rica.

selected as reference sites and were located in forested catchments with little or no evidence of past anthropogenic disturbance in near-stream areas. Forest buffer and pasture reaches, in contrast, had all been directly affected by deforestation and were adjacent to actively grazed pastures. In forest buffer reaches, streams were separated from adjacent pastures by a riparian forest buffer averaging at least 15 m in width on both banks, in accordance with Costa Rican law for rural streams in flat terrain. Mean buffer width in these reaches, averaging measurements on both banks, ranged from 26 to 45 m. Forest buffers were typically wider on one bank than the other, however, and buffer width on the bank with the narrower buffer averaged approximately 20 m across the four reaches. Pasture reaches lacked a riparian forest buffer, but still had relatively high canopy cover (Table 1) due to the presence of a single row of remnant and planted trees along the stream channel. There was a nearly complete lack of understory trees and shrubs in pasture sites, and closely cropped grasses and herbaceous plants extended to the edge of the stream channel.

In addition to the riparian vegetation conditions discussed above, study sites were selected based on stream size and channel gradient (Table 1). Recognizing the potential importance of catchment-scale effects on the study streams, we also restricted our site

selection to streams with similar levels of forest cover at the catchment scale (Table 1). In each site, we established a sampling reach that was approximately 40 times the average wetted channel width, starting at a randomly selected point in the middle of a longer reach with similar riparian conditions. All study reaches had pool-riffle channels (Montgomery & Buffington, 1997), with pools generally occupying over 70% of the channel area. Riffles tended to be very shallow (average depth <5 cm), and were also distinguished from pools by having higher current velocities (Hawkins *et al.*, 1993).

Environmental variables

Stream habitat conditions in the study reaches were assessed once in each of following periods: February–April 2005 (sample period 1), September–October 2005 (sample period 2) and February–April 2006 (sample period 3). This sampling schedule was intended to capture dry and wet season conditions in 2005 and dry season conditions in 2006. However, precipitation did not vary in a predictable seasonal pattern during the study (Fig. 2). Furthermore, discharge in the small study streams responded rapidly to rainfall events, and then quickly returned to base flow conditions when rains ceased. Therefore, sampling always took place when streams were near base

	Forest	Forest buffer	Pasture
Altitude (m a.s.l.)	41 (25–55)	35 (30–38)	30 (20–37)
Catchment area (ha)	46 (26–79)	53 (15–103)	60 (15–130)
Catchment % forest	97 (93–100)	83 (72–92)	81 (60–91)
Channel width (m)	2.0 (1.7–2.5)	1.7 (1.3–2.2)	1.8 (1.4–2.3)
Mean depth (cm)	11 (8–16)	12 (8–18)	17 (11–22)
Substratum coarseness	2.8 (2.4–3.4)	2.5 (1.9–3.0)	2.6 (1.8–3.1)
Embeddedness (%)	36 (27–45)	46 (39–66)	56 (40–79)
Riffle area (%)	28 (19–41)	26 (10–49)	17 (9–23)
Channel gradient (%)	0.8 (0.6–1.1)	0.7 (0.4–0.8)	0.8 (0.5–0.9)
Canopy cover (%)	93 (91–95)	94 (93–95)	78 (44–93)
Temperature (°C)	24.6 (23.0–25.9)	25.2 (24.0–27.2)	26.3 (22.9–30.5)
Conductivity ($\mu\text{S cm}^{-1}$)	300 (239–403)	352 (160–442)	241 (210–286)
pH	7.9 (7.7–8.2)	8.0 (7.5–8.3)	7.6 (7.5–7.8)
NO ₃ -N (mg L ⁻¹)	0.06 (0.04–0.09)	0.08 (0.03–0.19)	0.03 (0.0–0.07)
NH ₄ -N (mg L ⁻¹)	0.05 (0.04–0.05)	0.04 (0.03–0.06)	0.02 (0.0–0.04)
PO ₄ -P (mg L ⁻¹)	0.09 (0.05–0.12)	0.11 (0.05–0.18)	0.08 (0.05–0.17)
Leaf litter (g AFDM m ⁻²)	35.1 (23.8–40.5)	31.7 (18.4–42.0)	48.2 (19.5–90.4)
Chlorophyll- <i>a</i> (mg m ⁻²)	5.0 (0.7–14.5)	6.4 (0.7–17.8)	62.2 (0.6–165.6)

Table 1 Mean values (range) of environmental variables in forest, forest buffer and pasture study reaches in southeastern Costa Rica ($n = 4$ for each reach type)

Leaf litter and chlorophyll-*a* standing crop means are based on habitat-weighted estimates for the study reaches for three sample periods (leaf litter) or two sample periods (chlorophyll-*a*).

flow and the three sampling periods are referred to by their sequential order instead of by season.

In each study reach, we established 20 equally spaced transects perpendicular to the stream flow to quantify channel depth and substrate characteristics following methods adapted from Iwata *et al.* (2003). Stream depth was measured at five equally spaced points along each transect. The dominant substrate in a 10 × 10 cm area surrounding each depth sampling point was classified as sand or silt (particle size <2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), boulder (>256 mm), or bedrock. These substrata were then coded as: 1, sand or silt; 2, gravel; 3, pebble; 4, cobble; 5, boulder and 6, bedrock, and the mean of the coded values for the reach was used as an index of substrate coarseness (Bain, Finn & Booke, 1985; Iwata *et al.*, 2003). In sample period 3, substratum embeddedness was measured by visually estimating the percentage of the surface area of individual substrata particles embedded in fine sediments (to the nearest 25%) at each depth sampling point.

To determine the relative abundance of pool and riffle habitats in the sampling reach, we estimated the surface area of each habitat unit based on total unit length and average width from three width measurements. Stream channel canopy cover was calculated based on 20 measurements with a spherical densiometer. Canopy cover measurements were made in mid-channel facing upstream, downstream and towards both banks at the top and bottom of the sampling reach and at three equally spaced points between. At forest buffer sites, buffer width on each bank was measured at the same five points. Buffer width was only measured on one date because we did not observe changes in riparian vegetation at buffer sites during the study.

Measurements of stream water temperature, conductivity and pH were taken at each site between 12:00 and 13:00 hours using a multi-sensor probe (YSI 556 MPS, Yellow Springs Instruments, Inc., Yellow Springs, OH, U.S.A.) on the day that habitat measurements were made. Two replicate water samples were also collected from all study reaches for water chemistry analysis on 1 May 2006, when streams were at base flow. Samples were placed on ice and transported to the laboratory, where they were analysed for pH, conductivity and concentrations of NO₃-N, NH₄-N and PO₄-P using standard

methods [American Public Health Association (APHA), 1995].

The abundance of epilithic algae in the study reaches was estimated in the latter two sample periods by measuring chlorophyll concentrations on natural stream substrata. At each site, one or more small stones were collected at 10 randomly selected sampling points in the study reach. Sampling points were stratified so that five samples were collected in pools and riffles, respectively. In the laboratory, chlorophyll was extracted by immersing stones in 96% ethanol for 24 h at room temperature. Chlorophyll-*a* concentration in the extract was determined spectrophotometrically, without phaeophytin correction, using the equation of Wintermans & De Mots (1965). Stone surface area was calculated using the equation of Dall (1979), and one-half of the stone area was used to estimate chlorophyll-*a* standing crop at each sampling point. Mean values from the five sampling points in each habitat type were used to estimate chlorophyll-*a* standing crops in pools and riffles, respectively. Estimates of leaf litter standing crops in pools and riffles were made using coarse benthic organic matter collected in Surber samples (see below). Leaf litter was sorted from woody material, dried at 60 °C for 48 h, subsampled and then ashed at 500 °C for 2 h to determine ash-free dry mass.

Macroinvertebrate sampling

Benthic macroinvertebrates were sampled on the same day that habitat measurements were made in all three sample periods. At each site, 10 Surber samples (0.093 m², 1000 µm mesh) were collected from randomly selected locations within the study reach. Sampling locations were stratified by habitat type so that five samples were collected from pools and riffles, respectively. Substrata within the sampling area were disturbed to a depth of approximately 10 cm and larger stones were scrubbed by hand to remove all attached invertebrates. Material captured in Surber samples was preserved in the field in 95% ethanol, and invertebrates were later separated from other material using a dissecting microscope.

All macroinvertebrates collected were identified to the lowest feasible taxonomic level (genus or family for aquatic insects) using Merritt & Cummins (1996), Roldán (1996) and M. Springer & P. Hanson (unpubl.

data). Fisher's alpha diversity index was then calculated for each site, and was used for macroinvertebrate diversity comparisons because it is not heavily influenced by sample size (Magurran, 1988). The number of taxa in the orders Ephemeroptera, Plecoptera and Trichoptera (EPT richness) in pools and riffles at each site was also determined because this metric is often used as an indicator of water quality (Rosenberg & Resh, 1993). We measured the body length of macroinvertebrates to the nearest 1 mm, and estimated aquatic insect biomass using published length-mass equations (Benke *et al.*, 1999) for taxa in the same genus or family, or with a similar body shape. We did not attempt to estimate biomass for other invertebrates because we lacked length-mass equations for many common non-insect taxa. Macroinvertebrates were assigned to functional feeding groups based on Merritt & Cummins (1996) and Tomanova, Goitia & Helesic (2006) when taxonomic resolution permitted.

Data analysis

Environmental variables and macroinvertebrate abundance and diversity measures were compared among reach types (forest, forest buffer or pasture) and sample periods with repeated measures ANOVAS using PROC MIXED in the program SAS (SAS Institute Inc, 2002). Akaike Information Criterion values for small samples (AIC_c) were used to select the most appropriate covariance structure for within-subject variation in the models. For environmental variables that were only measured in one sample period, one-way ANOVAS or Kruskal-Wallis tests were used to test for significant differences among reach types, depending on whether or not distributional assumptions for a parametric test were met. For variables measured in pool and riffle habitats separately, including all macroinvertebrate variables, repeated measures ANOVA models were used to test for differences among reach types, sample periods and habitat types (pools or riffles). Variables were log-transformed to meet distributional assumptions when necessary. Chlorophyll-*a* abundance in pool samples from one forest reach were below the detection limits of our measurement method, and so an estimate based on these detection limits was used as a conservative replacement for this value. When ANOVA models indicated a significant effect of reach

type for any variable, pairwise comparisons of the three reach types were made. *P*-values were not adjusted for multiple comparisons in these tests or in the tests described below because *F*-tests provide adequate protection against type I error for three or fewer pairwise comparisons (Toothaker, 1993).

To investigate the effects of reach type, habitat type and sampling period on the taxonomic composition of macroinvertebrate assemblages, we used two multivariate techniques, permutational multivariate analysis of variance (PERMANOVA) and non-metric multidimensional scaling (NMS). Both techniques are robust to departures from the distributional assumptions of parametric tests, and are therefore appropriate for the analysis of community data (McCune & Grace, 2002). Prior to analysis, macroinvertebrate abundance data were $\log_{10}(x + 1)$ transformed and rare taxa, defined as taxa represented by a single individual across all sampling sites and periods, were removed from the data set. This resulted in the removal of 12 of the 105 taxa collected in the study. Bray-Curtis dissimilarity (Bray & Curtis, 1957) was used as the distance measure for PERMANOVA tests and NMS ordinations.

PERMANOVA tests were based on the methods of Anderson (2001) and McArdle & Anderson (2001), and were conducted using the program PERMANOVA (Anderson, 2005). Data from all three sample periods were analysed together, with sample period, reach type and habitat type as fixed factors. *P*-values for the test statistic (pseudo *F*-value) were based on 10 000 permutations of raw data. When three-way PERMANOVA tests indicated a significant effect of reach type, pairwise comparisons of reach types were made, also based on 10 000 permutations.

PERMANOVA tests may have overestimated differences among reach types and habitat types because we used a repeated measures study design. Therefore, NMS ordination was used to investigate how consistently samples from different habitat types and reach types were segregated in multivariate space. NMS ordination was conducted using the program PC-ORD (McCune & Mefford, 1999), and the final ordination was based on the best configuration from 250 runs with random starting points. Appropriate dimensionality for the ordination was determined using a scree plot and significance tests of stress values based on 250 Monte Carlo randomizations. The contributions of individual taxa to differences

between reach types and habitats were determined using the two-way crossed SIMPER routine in the program PRIMER 6 (PRIMER-E Ltd, 2006).

Results

Environmental variables

Stream habitat conditions varied considerably among the study reaches (Table 1), yet no statistically significant differences among reach types were observed for mean depth, substratum coarseness or the proportion of riffle habitat (results not shown). Substratum embeddedness tended to be lower in forest reaches than in the other reach types (Table 1), but differences among reach types were not statistically significant ($P = 0.147$, Kruskal–Wallis test). Among the measured physicochemical variables, only stream water temperature differed significantly among reach types ($F_{2,9} = 4.29$, $P = 0.049$, data log-transformed for analysis), with pasture reaches having higher water temperatures than forest reaches. Forest buffer reaches had intermediate water temperatures and did not differ from the other two reach types. Stream temperatures also varied significantly among sample periods ($F_{2,9} = 28.13$, $P < 0.001$), and were lowest in the third sample period, when rainfall was highest. All streams had relatively high conductivity and slightly basic pH and nutrient concentrations did not show any consistent differences among reach types (Table 1).

Leaf litter standing crops also showed no consistent differences among reach types (Table 1). In the repeated measures ANOVA, only sample period had a significant effect on leaf litter standing crop ($F_{2,36} = 6.27$, $P = 0.005$). The ANOVA for log-transformed chlorophyll-*a* standing crop showed marginally significant effects of reach type ($F_{2,18} = 3.13$, $P = 0.068$) and sample period ($F_{1,18} = 4.10$, $P = 0.058$), as well as a significant interaction between these factors ($F_{2,18} = 3.61$, $P = 0.048$). Chlorophyll-*a* standing crops tended to be greater in pasture reaches than in forest and forest buffer reaches, but there was high variability within reach types (Table 1).

Macroinvertebrate abundance and diversity

No significant differences in macroinvertebrate density were observed among reach types or sample

Table 2 Results of repeated measures ANOVA models for macroinvertebrate density, biomass and diversity in the study reaches, with reach type (forest, forest buffer or pasture), sample period and habitat type (pool or riffle) as fixed effects ($n = 4$ for each reach type)

	Reach type		Sample period		Habitat type	
	$F_{2,18}$	P	$F_{2,36}$	P	$F_{1,18}$	P
Density (individuals per m ²)*	0.39	0.680	2.36	0.109	6.37	0.021
Biomass (mg AFDM m ⁻²)*	0.58	0.569	1.13	0.336	7.47	0.014
Fisher's alpha	3.73	0.044	0.08	0.925	3.46	0.079
EPT taxa richness	4.20	0.032	0.70	0.505	2.24	0.152

Results in bold are significant at $P < 0.05$. Biomass comparisons are based on aquatic insects only. Interaction terms were not significant for any of the models.

*log₁₀(*x*) transformed for analysis.

periods (Table 2). However, we did observe a significant difference between habitat types (Table 2), with riffles having higher macroinvertebrate densities than pools (Table 3). Very similar patterns were observed for aquatic insect biomass, which did not differ among reach types or sample periods (Table 2), but was significantly higher in riffles than in pools (Table 3).

A total of 105 macroinvertebrate taxa were identified in the study streams, including 91 aquatic insect taxa representing 56 families (Appendix S1). Taxa richness in individual sample sites ranged from 21 to

Table 3 Mean ± 1SE of macroinvertebrate density, aquatic insect biomass and Fisher's alpha diversity index in the three study reach types and in riffle and pool habitats within the study reaches

	Density* (ind. m ⁻²)	Biomass* (mg AFDM m ⁻²)	Fisher's alpha
Reach type			
Forest	1078 ± 136	227 ± 30	8.0 ± 0.4 ^a
Forest buffer	1289 ± 304	203 ± 33	7.6 ± 0.3 ^{ab}
Pasture	913 ± 187	179 ± 64	6.6 ± 0.4 ^b
Habitat type			
Riffle	1396 ± 144 ^a	281 ± 41 ^a	7.8 ± 0.3
Pool	790 ± 129 ^b	125 ± 17 ^b	7.0 ± 0.3

Different superscript letters indicate significant differences among reach types or habitat types based on repeated measures ANOVA models (see Table 2).

*Statistical comparisons were based on log-transformed data.

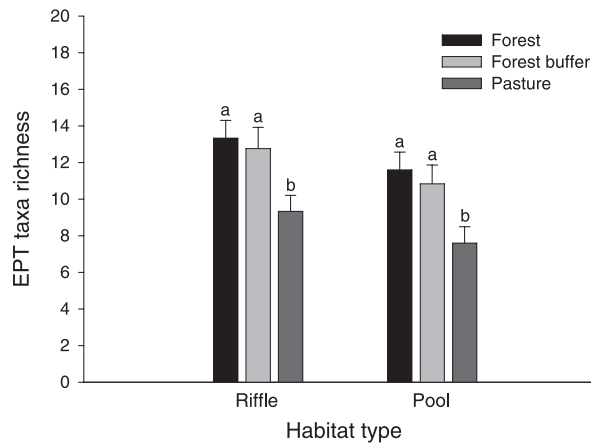


Fig. 3 Plots of mean (+SE) EPT taxa richness in riffle and pool habitats in the three study reach types. Different letters indicate significant differences among reach types based on a repeated measures ANOVA model (see Table 2).

52 taxa for a single sample date and from 45 to 67 taxa over the course of the study. Macroinvertebrate diversity, measured by Fisher's alpha diversity index, differed significantly among reach types (Table 2), and was higher in forest reaches than in pasture reaches (Table 3). Alpha diversity in forest buffer reaches was intermediate and did not differ from the other two reach types. The difference in alpha diversity between habitat types was only marginally significant (Table 2), but riffles tended to have higher diversity than pools (Table 3). EPT taxa richness also differed among reach types (Table 2), with forest and forest buffer reaches both having significantly higher EPT richness than pasture reaches (Fig. 3). No significant differences in EPT richness were observed among sample periods or habitat types, although there was a trend toward higher EPT richness in riffles relative to pools (Fig. 3).

Macroinvertebrate assemblage structure

Macroinvertebrate assemblages in the study streams were numerically dominated by aquatic insects (Fig. 4a). Non-insect taxa, especially gastropods and oligochaete worms, were much more common in pasture reaches, but still made up less than 20% of all macroinvertebrates collected in these sites. Ephemeroptera accounted for over half of all individuals collected in forest and forest buffer sites, but were generally much less abundant in pasture sites. Diptera was also an important component of benthic commu-

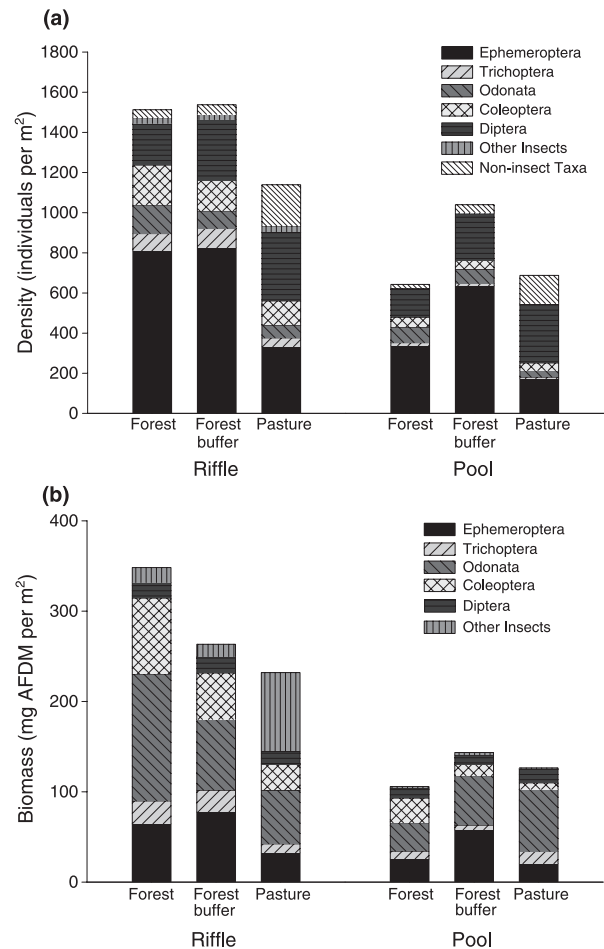


Fig. 4 Taxonomic composition of macroinvertebrate assemblages in riffle and pool habitats in forest, forest buffer and pasture reaches based on (a) density and (b) biomass. Density and biomass values are means across all three sample periods; biomass values were not calculated for non-insect taxa.

nities in all reach types, and tended to be most abundant in pasture sites (Fig. 4a). Ephemeroptera and Diptera were much less important in terms of total insect biomass, while Odonata and Coleoptera were more prominent, particularly in riffle habitats in the forest reaches (Fig. 4b). Insect biomass in riffle habitats in the pasture reaches was heavily influenced by a small number of very large individuals representing groups that were generally rare (e.g. Megaloptera).

Multivariate comparisons of macroinvertebrate assemblages based on our finest taxonomic resolution for all taxa (see Appendix S1) revealed strong patterns related to reach type and habitat type. PERMANOVA tests indicated that reach type, sample period and

Table 4 Results of three-way PERMANOVA test for the effects of reach type, sample period and habitat type on the taxonomic composition of macroinvertebrate assemblages in study reaches in southeastern Costa Rica

Source	d.f.	SS	MS	F	P
Reach type (R)	2	14 401	7201	6.1371	0.0001
Sample period (P)	2	4194	2097	1.7874	0.0342
Habitat type (H)	1	14 403	14 403	12.2758	0.0001
R × P	4	3035	759	0.6467	0.9587
P × H	2	653	326	0.2782	0.9999
R × H	2	1962	981	0.8363	0.6481
R × P × H	4	1824	456	0.3887	0.9999
Residual	54	63 358	1173		

Results in bold are significant at $P < 0.05$.

habitat all had significant effects on the composition of macroinvertebrate assemblages in the study reaches (Table 4). The effect of sampling period was relatively weak, while reach type and habitat type were both highly significant (Table 4). Pairwise comparisons among reach types showed significant differences in macroinvertebrate assemblages between forest and pasture reaches ($t = 2.91$, $P = 0.0001$) and between forest buffer and pasture reaches ($t = 2.35$, $P = 0.0001$). Differences between forest and forest buffer reaches were not as pronounced, but were also significant ($t = 1.51$, $P = 0.0344$).

Ordination of the sampling sites based on log-transformed macroinvertebrate abundance illustrated how consistently assemblage composition differed among reach types and between pool and riffle habitats. NMS ordination of samples from the 12 study reaches, organized by sample period and habitat type, produced a three-dimensional configuration with moderate stress (final stress = 12.06). Coefficients of determination between distances in the ordination space and Bray–Curtis distances in the original n -dimensional space indicated that the three ordination axes explained 89.7% of the total variation in assemblage structure. The plot of NMS axis 1 versus axis 3 supported the conclusion that macroinvertebrate assemblages varied significantly among reach types (Fig. 5a). Forest and pasture reaches showed nearly complete segregation in multivariate space, and three of the four forest buffer reaches grouped very closely with the forest reaches (Fig. 5a). One forest buffer reach, represented by six points in the ordination, consistently fell within the pasture group (Fig. 5a). Differences in the composition of

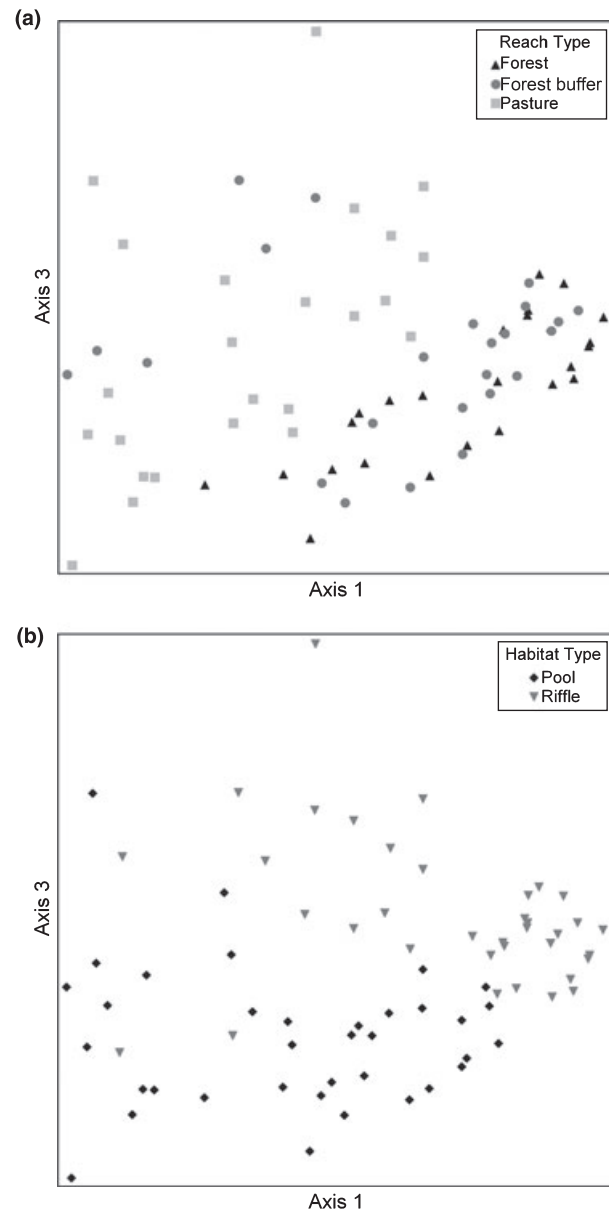


Fig. 5 Plot of axis 1 versus axis 3 of the three-dimensional NMS ordination of samples from the 12 study reaches, with samples identified by (a) reach type or (b) habitat type. Individual data points represent five pooled Surber samples. Each of the 12 study reaches is represented by six data points in the ordination, corresponding to riffle and pool samples collected in each of the three sample periods.

macroinvertebrate assemblages between pool and riffle habitats were also apparent with this combination of axes (Fig. 5b). Other combinations of axes showed similar differences between reach types and habitats, but patterns were not as strong as for the combination presented above. Differences among

sample periods, although significant in the PERMANOVA analysis, were not apparent in any two-dimensional combination of the ordination axes or in a three-dimensional view.

The SIMPER analysis indicated that taxa representing several different functional feeding groups contributed to differences between forest and pasture reaches. In particular, pasture reaches differed from forest reaches by generally having higher abundances of the scrapers Thiaridae and Hydrobiidae and the collector-gatherer Oligochaeta and lower abundances of the collector-gatherers *Farrodes*, *Thraulodes*, *Tricorythodes*, *Neoelmis* and *Terpides*, the shredder *Anchytarsus* and the predators *Heteragrion*, Gomphidae, Coenagrionidae and *Palaemnema* (Table 5). Insects of the families Chironomidae and Baetidae also tended to be more abundant in pasture reaches (Table 5). Many of the same taxa contributed to differences between forest buffer and pasture reaches (Table 5), consistent with the generally high similarity in assemblage structure between forest and forest buffer reaches. Some differences were also apparent, however, as *Tricorythodes* and Baetidae made

comparatively larger contributions to differences between pasture and forest buffer sites while *Anchytarsus* was much less important (Table 5). Taxa making important contributions to dissimilarity between pools and riffles included *Thraulodes*, *Neoelmis*, *Tricorythodes*, *Smicridea*, Thiaridae, *Allenhyphes*, *Farrodes* and Baetidae, all of which were generally more abundant in riffles, and *Caenis* and *Campsurus*, which were more abundant in pools.

Discussion

Deforestation and riparian forest buffers

Our results suggest that conversion of forests to pasture, particularly in riparian areas, can lead to significant changes in benthic macroinvertebrate diversity and assemblage structure in small, lowland Costa Rican streams. The differences we observed among our three study reach types are particularly noteworthy considering the small scale of deforestation in our study catchments and the fact that streamside trees had not been completely cleared in pasture reaches. Although we were not able to sample pasture and forest buffer reaches before deforestation occurred, the geographic proximity of our study sites and their similarity in channel size and geomorphology suggests that all sites had very similar benthic communities prior to forest clearing in the study area. Therefore, differences we observed among sites appear to be directly attributable to land use change.

The effects of forest clearing on macroinvertebrate assemblages in our study streams appeared to depend heavily on the presence or absence of a riparian forest buffer, providing support for our hypothesis that riparian forest buffers can reduce the effects of deforestation on stream biota. Macroinvertebrate assemblages in pasture reaches, which lacked a forest buffer, had lower diversity and significantly different taxonomic composition than those in our forested reference reaches. These differences were consistent with the effects of deforestation observed in other comparative studies of neotropical streams (Bojsen & Jacobsen, 2003; Couceiro *et al.*, 2007), as well as impacts associated with pastoral development in previously forested temperate catchments (Quinn, 2000). Reaches with a forest buffer, in contrast, generally supported macroinvertebrate assemblages that were very similar to those in forested reference

Table 5 List of taxa making the largest contributions to dissimilarity between forest and pasture reaches, and between forest buffer and pasture reaches, based on SIMPER analysis, in order of decreasing importance

Rank	Forest versus pasture	Forest buffer versus pasture
1	<i>Farrodes</i>	<i>Tricorythodes</i>
2	<i>Anchytarsus</i>	<i>Farrodes</i>
3	Thiaridae	Thiaridae
4	<i>Thraulodes</i>	<i>Thraulodes</i>
5	<i>Tricorythodes</i>	<i>Caenis</i>
6	<i>Caenis</i>	<i>Allenhyphes</i>
7	<i>Neoelmis</i>	<i>Neoelmis</i>
8	Oligochaeta	Baetidae
9	<i>Heteragrion</i>	<i>Campsurus</i>
10	Gomphidae	Chironomidae
11	<i>Terpides</i>	<i>Heteragrion</i>
12	Coenagrionidae	Coenagrionidae
13	Hydrobiidae	Oligochaeta
14	<i>Palaemnema</i>	Hydrobiidae
15	<i>Campsurus</i>	<i>Hexatoma</i>
16	Hexacylloepus	Hexacylloepus
17	Chironomidae	<i>Anchytarsus</i>
18	<i>Perigomphus</i>	<i>Terpides</i>
19	Baetidae	Gomphidae
20	<i>Hexatoma</i>	<i>Palaemnema</i>

Taxa in bold were generally more abundant in pasture reaches.

sites, both in terms of taxonomic composition and diversity. The contrast between pasture and forest buffer reaches was particularly evident for EPT taxa, a group commonly used as an indicator of stream degradation.

Our diversity comparisons should be interpreted with some caution because of the differences in taxonomic resolution among macroinvertebrate groups in our study. Comparisons of EPT taxa richness are more robust in this regard because most EPT taxa were identified to the genus level. The generally higher abundance of EPT taxa in forest and forest buffer reaches compared to pasture reaches likely had an influence on differences in EPT richness among reach types. However, we also noted that several of the EPT families that are considered especially sensitive to stream degradation in our study area (Mafla, 2005) were either very rare (e.g. Perlidae, Leptoceridae) or absent (e.g. Ecnomidae) in pasture reaches. These taxa also tended to be uncommon in forest and forest buffer reaches, but were present at many different sites.

Caveats concerning taxonomic resolution do not apply to the differences in taxonomic composition that we observed among reach types, which were evident even at the ordinal level and were consistent across habitat types and sample periods. These differences were driven by a variety of taxa representing several functional feeding groups, and in some cases links to the abundance of food resources were evident. In particular, pasture reaches tended to have higher densities of scraping taxa, especially the gastropods Thiariidae and Hydrobiidae. The families Baetidae and Chironomidae, which were most abundant in pasture sites, also include many scraper and collector-gatherer taxa that can exploit in-stream primary production. Patterns of abundance among reach types for these taxa were consistent with the trend toward higher periphyton abundance in pasture reaches.

Interestingly, we found that the most common shredder in the study streams, *Anchytarsus*, was generally much more abundant in forest reaches than in pasture reaches, with intermediate densities in forest buffer sites (Appendix S1). Shredder abundance is typically linked to the abundance of leaf litter (Cummins *et al.*, 1989), and the density of ptilodactylids has been shown elsewhere to have a significant positive association with the abundance of litter

detritus (Bojsen & Jacobsen, 2003). However, in our study streams, the abundance of *Anchytarsus* and other invertebrate shredders did not mirror patterns in leaf litter abundance, which showed no significant differences among reach types. Given the contrasts in riparian and upland vegetation among reach types, the lack of consistent differences in leaf litter standing crops was somewhat surprising. However, allochthonous subsidies from forested areas upstream may have masked local differences in leaf litter input. It remains an open question how differences in vegetation among our study sites might affect the quality of litter available to shredders. Despite heavy shading by riparian vegetation and abundant leaf litter in most of our streams, shredders always made up a very small component of the benthic fauna, consistent with a general pattern in tropical streams (Wantzen & Wagner, 2006).

Differences in thermal regimes among reach types may have also played a significant role in producing the patterns we observed in macroinvertebrate assemblages. Point measurements in our study streams indicated that pasture reaches had significantly higher stream temperatures than forest reaches, a pattern confirmed by continuous monitoring of stream temperatures in a subset of the study sites (C. Lorion, unpubl. data). Temperatures in forest buffer reaches tended to be intermediate, suggesting that riparian shading is an important factor. Although we know very little about the thermal ecology of benthic macroinvertebrates in our study streams, water temperature is known to have a significant influence on macroinvertebrate growth, fecundity and survival (Sweeney, 1993). The highest water temperatures observed in pasture reaches were 2–3 °C outside the range of temperatures recorded during months of continuous monitoring in forest reaches. Some EPT taxa may be especially sensitive to high water temperatures, and altered thermal regimes could help explain why the EPT group was generally less abundant and diverse in pasture reaches.

Total macroinvertebrate abundance has often been found to increase in streams where canopy cover has been reduced by forest clearing (e.g. Hawkins, Murphy & Anderson, 1982; Bojsen & Jacobsen, 2003), due in large part to increased primary production. Therefore, it was somewhat surprising that we did not see any consistent trends in macroinvertebrate density among the different reach types we compared.

However, a previous study in southeastern Costa Rica found that forested sites actually had higher macroinvertebrate densities than sites where forests had been cleared (Paaby, Ramírez & Pringle, 1998), suggesting that the negative impacts of deforestation can counteract potential subsidy effects associated with canopy removal. Overall, we surely underestimated macroinvertebrate abundance in our study streams by using a Surber sampler with relatively coarse mesh. Nevertheless, our estimates of macroinvertebrate density were, on average, over 10 times higher than a previous study of lowland streams in southeastern Costa Rica where macroinvertebrates were collected with a Surber sampler with the same mesh size (Paaby *et al.*, 1998).

Spatial and temporal variation within reaches

Pool and riffle habitats in our study reaches supported macroinvertebrate assemblages with very different taxonomic composition, consistent with previous work in neotropical streams (Buss *et al.*, 2004), including one of the few studies of stream macroinvertebrates in southeastern Costa Rica (Ramírez *et al.*, 1998). Despite these differences, the effects of deforestation, and the influence of riparian forest buffers, appeared to be consistent across pool and riffle habitats. We did not observe a significant interaction between reach type and habitat type for any of our comparisons of macroinvertebrate abundance, diversity or taxonomic composition. Results from extensive bioassessment surveys in North America have shown that anthropogenic impacts are generally consistent across stream habitats (Gerth & Herlihy, 2006). However, even when trends among habitats are similar, macroinvertebrate assemblages in different habitats may be responding to different stress gradients (Buss *et al.*, 2004). Whether or not benthic macroinvertebrates in pools and riffles were responding to the same factors in our study streams, our results suggest that deforestation has similar impacts in both habitats. It should also be noted that the Surber sampler is likely to be more effective in riffles than in pools because it depends on invertebrates being washed downstream into the collecting net. This difference in sampling efficiency may have contributed to observed differences in macroinvertebrate abundance and assemblage composition between habitat types.

Temporal dynamics appeared to have less influence on macroinvertebrate assemblages than riparian conditions or stream habitat type, despite the fact that we targeted our sampling to capture seasonal variation. There were no significant changes in macroinvertebrate abundance or diversity through time, and compositional changes in the benthic fauna between sampling periods were relatively weak compared with other factors. Seasonal changes in macroinvertebrate abundance and assemblage structure in neotropical streams are strongly linked to rainfall patterns and associated disturbance by floods (Flecker & Feifarek, 1994; Jacobsen & Encalada, 1998; Ramírez, Pringle & Douglas, 2006). Rainfall did not show any clear seasonality during our study, and so the lack of consistent temporal trends in macroinvertebrate assemblages is not particularly surprising. The fact that high rainfall variability during our study did not obscure differences in macroinvertebrate assemblages among reach types or habitat types is more surprising and suggests that these assemblages are largely structured by deterministic processes.

Forest buffers in tropical stream management and conservation

In our study, stream reaches with riparian forest buffers averaging at least 15 m in width generally maintained macroinvertebrate assemblages with similar diversity and taxonomic composition as forested reference sites, despite the fact that forests outside the riparian buffer zone had been converted to pasture. These results suggest that proper management of riparian areas could substantially reduce the negative effects of deforestation on benthic communities in tropical headwater streams and provide support for Costa Rican regulations mandating protection of riparian forests in this zone. Forest buffers around our study streams were often considerably wider than this minimum requirement, but were also highly variable and had some areas less than 15 m in width. Despite this variability, these areas appeared to promote stream biodiversity and maintain stream ecosystem conditions similar to those found in forested catchments.

One forest buffer reach was a clear exception to this pattern, and illustrates the limitations of riparian buffers. This reach, despite having a wide forest buffer, had been disturbed by foraging pigs, was

paralleled by a road that was subject to erosion during rain events, and had elevated nutrient concentrations that may have been influenced by domestic effluent from several nearby residences. Stream bank trampling by livestock and erosion from poorly maintained roads are both important sources of sediment pollution in streams (Waters, 1995), and benthic habitats in this site had clearly been affected by sedimentation. It is difficult to know whether water quality was also a factor, but this reach consistently had the lowest macroinvertebrate densities of any of our sites. Riparian forest buffers can only be expected to effectively mitigate impacts on streams when factors that bypass them or overwhelm their capacity to filter sediments and nutrients are reduced or eliminated (Osborne & Kovacic, 1993; Wenger, 1999).

Riparian buffer functions can also be expected to vary depending on catchment-scale patterns in land use (Allan, 2004). We focused on reach-scale effects in catchments with high forest cover in this study in order to eliminate many potentially confounding factors, and further research will be needed to determine whether riparian buffers will sustain similar functions in landscapes with more extensive deforestation. Although some studies in temperate streams have found that benthic communities are most strongly influenced by local riparian conditions (Lammert & Allan, 1999; Sponseller, Benfield & Valett, 2001), others have shown that catchment-scale land use is more important and can overwhelm local effects (Roth, Allan & Erickson, 1996; Harding *et al.*, 1998). Whichever spatial scale is most important, it appears that even in catchments with high forest cover, clearing of riparian vegetation can disrupt terrestrial-aquatic linkages in headwater streams (England & Rosemond, 2004).

Finally, the patterns we observed in macroinvertebrate assemblages complement research on stream fishes at the same study sites, which also revealed significant differences in assemblage structure between forest and pasture reaches (Lorion & Kennedy, In Press). Fishes in lowland Costa Rican streams have been shown to exert top-down effects on benthic communities (Pringle & Hamazaki, 1998), and so changes in fish abundance and species composition in deforested sites may well be another factor driving differences in macroinvertebrate assemblage structure among reach types. Whether

or not this is the case, we found that reaches with a riparian forest buffer generally supported fish and benthic macroinvertebrate assemblages that were very similar to those observed in forested reference sites. This concordance between the two assemblages, which represent multiple trophic levels and diverse habitat associations, suggests that our conclusions regarding forest buffer functions are robust. Riparian forest buffers are not a replacement for continuous forest, but can promote biodiversity and stream ecosystem integrity in tropical catchments affected by deforestation.

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Mean density (individuals per m²) of macroinvertebrate taxa collected in riffle and pool habitats in forest (F), forest buffer (FB), and pasture (P) reaches

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