RELATIONSHIPS OF STREAM INVERTEBRATE COMMUNITIES TO DEFORESTATION IN EASTERN MADAGASCAR

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Abstract. Madagascar has been recently identified as a global hotspot for freshwater biodiversity. Loss of most of its eastern rain forest, combined with a high incidence of micro-endemism and specialization to forest stream habitats, has likely led to extinction of many of the island's stream insect species. We compared habitat and macroinvertebrate community structure in three streams draining protected rain forest within Ranomafana National Park in eastern Madagascar and three agriculture streams draining the park's largely deforested peripheral zone. Multivariate analyses showed that macroinvertebrate communities differed between stream types. Forest streams were characterized by species-rich, diverse communities composed primarily of collector–gatherers and collector–filterers belonging to the orders Trichoptera, Ephemeroptera, Plecoptera, and Diptera. In contrast, relatively depauperate agriculture stream communities were dominated by generalist collector–gatherer taxa mostly belonging to the order Ephemeroptera. Agriculture streams had 0–14% canopy cover, significantly higher mean and maximum water temperatures, and significantly lower benthic organic matter storage than forest streams (71–83% canopy cover). We found no evidence for higher sedimentation rates or nutrient concentrations in agriculture streams. Differences in thermal regime may be important in the declines of certain taxa in agriculture streams (e.g., Plecoptera). However, our data support the hypothesis that differences in stream communities are caused mainly by differences among taxa in ability to track shifts in basal resources (i.e., terrestrial detritus vs. in situ algal production) caused by deforestation. Community simplification and loss of endemic specialist taxa will continue if projections of future deforestation are proved correct. We recommend that stream biodiversity be considered in future conservation planning and propose the creation and maintenance of multiuse riparian forests that could serve both ecological and economic functions. Given that more than 5×10^5 km of stream and river channel are affected by tropical deforestation annually, our results have potential applications in other tropical regions.

Key words: benthic communities; deforestation; freshwater biodiversity; hotspots; insects; macroinvertebrates; Madagascar; riparian zones; river conservation; tropical streams.

INTRODUCTION

Deforestation is a major component of global change that has affected $\sim 8 \times 10^6$ km^2 of the earth's surface (Williams 1990, Meyer and Turner 1994). While some temperate regions are undergoing net afforestation, rates of tropical forest loss currently exceed 1.25×10^5 km^2/yr (0.7%/yr; Food and Agriculture Organization of the United Nations [FAO] 1999). Modification of vegetation cover at this scale is associated with significant changes to the global carbon budget (Dixon et al. 1994) and major losses of terrestrial biodiversity (Pimm et al. 1995, Hughes et al. 1997).

Although stream ecosystems are tightly linked to catchment processes through vegetation (Ross 1963, Hynes 1975, Wallace et al. 1997), little information is available on rates of stream ecosystem transformation

by deforestation or its ecological effects, particularly in the tropics. Assuming a drainage density of 4 km stream channel/km^2 land area for the humid tropics (Gregory 1976, Knighton 1984), we estimate that $>5 \times 10^5$ km of stream and river channel are affected by tropical deforestation annually (Table 1). This estimate may be conservative for two reasons. First, the drainage density used may underestimate the length of low-order stream channels within catchments (Wang and Yin 1998, Meyer and Wallace 2001). Second, our estimates assume that deforestation is uniform across landscapes, i.e., not affected by the location of stream channels within a catchment. In some cases, this assumption may be erroneous. In eastern Madagascar, for example, "... hillsides along river and creek paths seem to be especially popular routes for expanding the agricultural frontier ..." (Ferraro 1994).

Deforestation has many consequences for stream ecosystems, including increased sediment delivery, higher insolation and water temperatures, enhanced nutrient loads, and changes in the relative availability of

TABLE 1. Recent estimated loss rates for global tropical forest types and for forest types on Madagascar, with respective estimates of stream channel length affected annually.

Region	Ecosystem type	Deforestation rate (km^2/yr)	Source	Estimated stream length affected (km/yr)
Global	all tropical forests	125 930	FAO (1999)	503 720
Global	rain forests†	46 000	FAO (1993)	184 000
Global	tropical hill and montane forests‡	25 000	FAO (1993)	100 000
Madagascar	all forests	1300	FAO (1999)	5200
Madagascar	eastern rain forests§	1110	Green and Sussman (1990)	4440

Note: A drainage density of 4 km/km^2 was assumed for all regions and ecosystem types (Gregory 1976, Knighton 1984).
† Evergreen and semi-evergreen forests in regions of >2000 mm mean annual rainfall and <800 m in altitude.
‡ Premontane to alpine forests (wet, moist, or dry) in areas >800 m in altitude.
§ Primary forest or closed-canopy secondary forest.

basal food resources (Likens et al. 1970, Webster et al. 1983, 1992). However, our understanding of its long-term consequences for the taxonomic structure of stream communities lags far behind that of its ecosystem-scale effects, particularly in the tropics. In particular, information on species declines and extinction remains anecdotal at best (Harding et al. 1998). This problem is compounded in the tropics by low levels of taxonomic knowledge and the paucity of long-term studies (Gibon 2000).

The island of Madagascar provides an illuminating case study of these problems. Madagascar is a global priority for conservation efforts because of the level of threat to its largely endemic biota (McNeeley et al. 1990). It has also recently been identified as a hotspot for freshwater biodiversity because of its unique assemblage of endemic fishes, crustaceans, and molluscs (Stiassny and DePinna 1994, Groombridge and Jenkins 1998). Madagascar's endangered biodiversity is concentrated along its eastern rain forest belt (Lees et al. 1999) and the freshwater representatives are no exception (Ganzhorn et al. 1997, Benstead et al. 2000). Clearance of Madagascar's eastern rain forest biomes has been estimated at 1110 km^2/yr (1.5%/yr) between 1950 and 1985 (Green and Sussman 1990). By employing the same drainage density and assumptions as above, ~154 000 km of stream channel were affected during this period by deforestation in Madagascar's eastern rain forest biome (Table 1). The resulting habitat alteration has been associated with declines and extinction of many endemic fishes and crustaceans (Hobbs 1987, Reinthal and Stiassny 1991, de Rham 1996, Stiassny 1996, Benstead et al. 2000).

Until recently, Madagascar's stream insect communities were very poorly understood. However, research by the Biodiversity and Biotypology of Malagasy Continental Waters Project, using light traps to sample adult insects, has discovered hundreds of new and endemic taxa, including 500 new caddisflies (Trichoptera) and 200 new mayflies (Ephemeroptera; Elouard and Gibon 2003). Madagascar is now thought to harbor 30–50% of Africa's species in major stream insect orders—in an area 50 times smaller than the mainland (Elouard

and Gibon 2003). More than 95% are endemic to the island (Gibon 2000). Thus, it appears that Madagascar's stream ecosystems support highly diverse and endemic insect communities. As has been found in temperate regions (Ross 1963), many of these new insect taxa appear to be restricted to native vegetation communities, particularly high-altitude primary forest (Gibon and Elouard 1996, Gibon et al. 1996, Gibon 2000). Many species are also restricted to narrow latitudinal and altitudinal limits along the eastern rain forest belt, giving rise to a high incidence of micro-endemism (Gibon 2000). Association of micro-endemic stream insects with native vegetation highlights the vulnerability of these taxa to deforestation. Given that Madagascar has lost at least 63% of its rain forest in recent centuries (Green and Sussman 1990), that there is a high degree of micro-endemism in stream insect groups (especially among Trichoptera, Plecoptera and Megaloptera), and that many of these taxa are restricted to rain forest streams (e.g., 75% of philopotamid Trichoptera; Gibon 2000), it is reasonable to assume that historic deforestation has led to the extinction of stream insect species (Gibon et al. 1996, Courtney 2003, Elouard and Gibon 2003).

Recent increases in knowledge of Madagascar's stream insects are based on an almost island-wide light-trapping survey of adult insects that has provided crucial information about species richness, distributions, and systematics (e.g., Gibon and Elouard 1996, Gibon et al. 1996, Sartori et al. 2000). However, until recently, no long-term studies of stream ecosystems had been conducted on the island. Information about the mechanisms driving species declines and extinction in streams affected by forest clearance is consequently lacking. In this study, we report the results of research on three streams draining protected rain forest within Ranomafana National Park in eastern Madagascar and three streams draining the park's largely deforested peripheral zone. We use results from the 4-yr study to ask the following questions: (1) What are the consequences of deforestation for macroinvertebrate community structure and stream habitat in eastern Madagascar? (2) What are the potential mechanisms driving
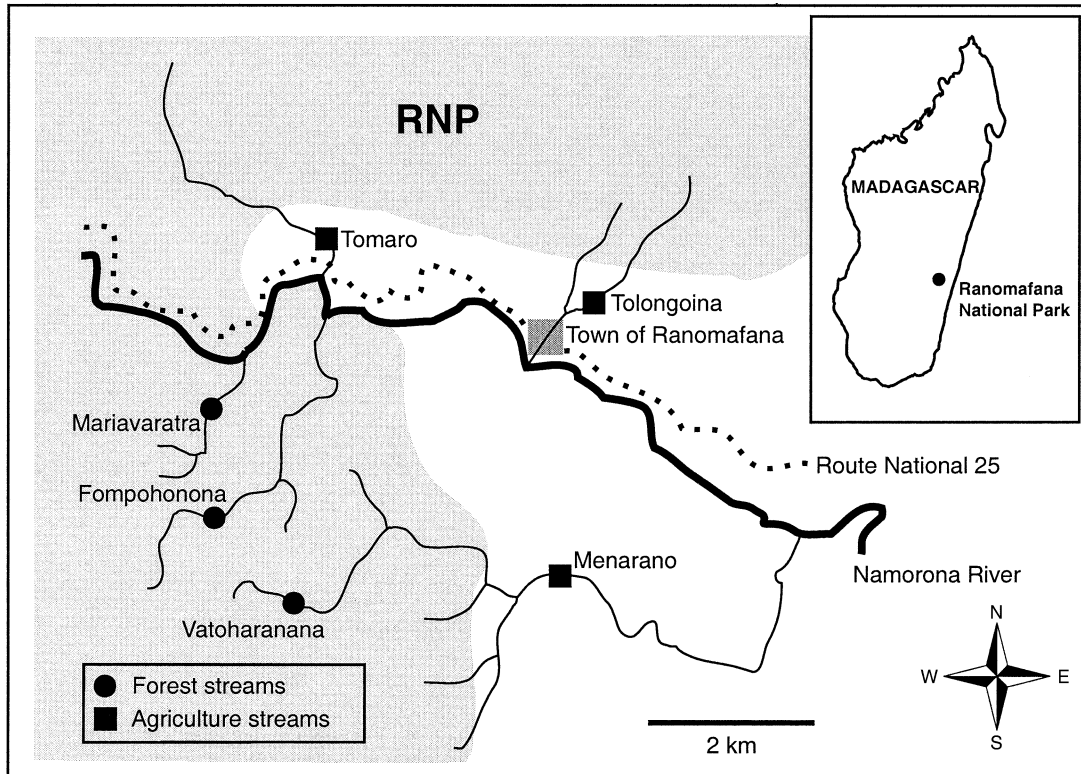
FIG. 1. Map showing location of Ranomafana National Park and the six streams included in this study. Only part of the park is shown (shaded region); the peripheral zone extends 3 km from the park boundary.

changes in community structure? and (3) How might the stream communities of eastern Madagascar (and similar areas) be conserved?

STUDY SITE AND NATURAL HISTORY

This study was conducted within Ranomafana National Park (RNP; 21°15′ S, 47° 27′ E) and in the vicinity of its peripheral zone (Fig. 1). RNP is a 41 300-ha reserve located in eastern Madagascar. The park spans elevations of 400–1500 m and its vegetation consists of primary and secondary lowland and premontane tropical rain forest. The peripheral zone is a buffer area, extending 3 km from the park boundary, in which land use consists of swidden (slash-and-burn) agriculture, secondary (fallow) vegetation, riparian rice paddies, and remnant forest patches. Important crops include hill and paddy rice, manioc, bananas, coffee, and leafy vegetables. Mean monthly precipitation in the region varies seasonally, peaks during December through March, and can be extremely high (e.g., 14–1171 mm, September 1992–June 1994; Balko 1998).

Six study streams were used in the study (Fig. 1 and Table 2); three were within the forest protected by RNP while three were located in deforested areas within or near the peripheral zone (hereafter referred to as agriculture streams). Areas adjacent to forest streams have been subjected to differing levels of low-impact selective logging over the last 50 yr (Balko 1998; see

Table 2). The study streams were small (5.3–13.7 m mean width), located at 700–1100 m above sea level, and fast flowing with gravel, cobble, and boulder substrata. All study streams flow into the Namorona River (fifth order), which experiences seasonal flows that peak in February or March (Chaperon et al. 1993). Canopy cover ranged from 71–83% in the three forest streams, and was 0–14% in the peripheral zone streams (Table 2).

Exact timing of forest loss in areas adjacent to agriculture streams is difficult to assess. Colonization of the Ranomafana region began ~200 yr BP and large-scale immigration into the area began with construction of the main road to the coast (Route National 25) in the late 1940s (Ferraro 1994). Thus, we conclude that deforestation in areas adjacent to agriculture streams began at least 50 yr ago.

Benthic communities of forest and agriculture streams are dominated by aquatic insect larvae. Larval anurans are abundant in all streams. Freshwater crabs (Potamonautidae) and crayfishes (*Astacoides granulimanus*) are present in most streams but appear less abundant in agriculture streams, possibly because of collection for food by local villagers. Atyid shrimp (*Caridina* spp.) are found at very low densities in at least two of the streams. No fishes have been observed in forest streams, although the eel *Anguilla mossambica* may be present (Ferraro 1994). Introduced tilapia (*Ti-*

TABLE 2. Physical description of stream reaches sampled in Ranomafana National Park and peripheral zone, eastern Madagascar, 1996–1999.

Stream	Mean width (m)	Mean maximum depth (m)	Mean temperature (°C)	Mean conductivity (μS/cm)	Substratum	Mean canopy cover (%)	Land use
Forest							
Mariavaratra	6.0	0.31	17.0	14.7	cobble with boulders and gravel/sand	71	selectively logged during mid-1980s
Fompohonona	5.3	0.38	17.0	20.5	cobble with sand and boulders	74	primary forest; some human disturbance
Vatoharanana	9.6	0.51	17.0	15.3	boulders, cobble, and sand	83	primary forest; some human disturbance
Agriculture							
Tomaro	13.7	0.72	18.5	12.6	cobble	0	rice agriculture
Tolongoina	7.2	0.56	17.3	13.6	boulders, cobble, gravel, and sand	14	rice and sugar cane agriculture
Menarano	9.7	0.48	17.5	13.6	cobble and sand	0	rice and cassava agriculture

lapia zillii) and green swordtail (*Xiphophorus helleri*) are present at very low densities in all three agriculture streams. A native, undescribed, Madagascar rainbowfish (*Bedotia* sp.) is also present at low densities at one of the agriculture streams (Menarano; M. L. J. Stiassny, *personal communication*). The top predator in all the study streams is the aquatic tenrec *Limnogale mergulus* (Afrotheria: Tenrecidae). This small (80–100 g) nocturnal mammal feeds almost exclusively on tadpoles and aquatic macroinvertebrates (Benstead et al. 2001).

METHODS

Macroinvertebrate community structure

We collected macroinvertebrates from the study streams in April–May 1996 and April–August 1998. One of the agriculture streams (Tolongoina; TOL) was not sampled in 1996. On each occasion, we took 10 Surber samples (0.093 m²; mesh 600 μm) from shallow riffles. Large cobbles within the sample area were thoroughly scrubbed by hand and the substratum disturbed as deep as possible (5–10 cm) for a period of 1 min. Samples were transported to the laboratory in stream water and placed in a nearby stream in bags pricked with a pin to prolong survival until processing. All macroscopically visible invertebrates (>0.5 mm) were picked from samples within 12–18 h and preserved in 70% ethyl alcohol for transportation to the University of Georgia.

No keys and few descriptions are available for the largely endemic stream insect fauna of Madagascar. We sorted all insects and other invertebrates to morphospecies and sent representative specimens in most major orders to expert taxonomists familiar with material from the Afrotropical region (see *Acknowledgments*). In many cases, identification to genus was possible. We used mouthpart morphology and Merritt and Cummins (1996) to assign taxa to functional feeding groups.

We calculated biomass of macroinvertebrates from the samples collected in 1998. Lengths of invertebrates were measured to the nearest 1 mm under a stereomicroscope fitted with an eyepiece micrometer. Biomass was calculated using published length–mass regressions (Benke et al. 1999) for invertebrates in the same genera, family, or order.

To examine possible differences in macroinvertebrate communities between stream types (forest and agriculture) and the two years (1996 and 1998) we used three multivariate techniques: analysis of similarities (ANOSIM), similarity percentages (SIMPER), and ordination. First, a dissimilarity matrix was generated by comparing the entire faunal composition of all sample pairs. Inter-sample compositional similarities were computed using the Bray-Curtis coefficient (Bray and Curtis 1952) which, compared with several commonly used dissimilarity coefficients, has been shown to have the most robust relationship with ecological distance (Faith et al. 1987). We used the two-way crossed ANOSIM routine of the computer program PRIMER (Version 5.2, Plymouth Marine Labs, Plymouth, UK; see Clarke and Warwick 1994) to compare the average rank similarities of samples from the different stream types and years. ANOSIM calculates a test statistic, R, which usually varies between 0 and 1, with high values indicating differences between treatments. A test of the significance of R is obtained by comparing its value to a distribution of values expected under the null hypothesis of no difference between treatments (see Clarke and Warwick 1994 for more details). This nonparametric permutation test was used in preference to comparable parametric tests such as multivariate analysis of variance (MANOVA) because the latter is based on assumptions that are unlikely to be satisfied for most multi-species data sets (Clarke and Warwick 1994). Streams were replicates in this design, so abundance data were averaged across the 10 samples from each stream in each year. It was not possible to test for an interaction between these factors because of the different number of replicate agriculture streams in each

year (Anderson 2001) and because the low number of replicate streams precluded the use of separate pairwise comparisons of stream types for each year. To distinguish between influence of abundance and compositional differences in community structure, ANOSIM was done on both untransformed and presence/absence-transformed data.

Second, the percentage contributions of each taxon to the overall dissimilarity ($\bar{D}i$) between stream type for each year and between years for each stream type were quantified by the SIMPER routine in PRIMER (Clarke and Warwick 1994). This procedure also calculates the ratio of the mean $\bar{D}i$ for all sample pairs between groups to the standard deviation (mean $\bar{D}i$/sD($\bar{D}i$)). This ratio indicates how consistently a taxon contributes to mean dissimilarity across all pairs within a group and is a measure of the importance of each taxon in discriminating communities between groups (Clarke and Warwick 1994).

Finally, we used the ordination technique of semi-strong hybrid (SSH) multidimensional scaling (Belbin 1991) using the computer program PATN, (CSIRO Wildlife and Ecology, Australia; see Belbin 1993) and the dissimilarity matrices described above. We used this ordination technique because it is considered to be one of the most robust available and suitable for the typical situation in which faunal responses to underlying gradients are unimodal, noisy, or skewed (Faith et al. 1987, Marchant et al. 1994). To assist in interpreting differences in community structure between stream types, separate ordinations were done on the untransformed data from each year. Principal axis correlations (PCC; Belbin 1993) were then carried out to show the direction of maximum correlation in ordination space for those taxa that accounted for 90% of overall dissimilarity between stream types in each year. PCC was also done for total richness, total abundance, richness, and abundance of taxa in seven insect orders, and richness and abundance of taxa in five functional feeding groups. Monte Carlo simulations were performed to test the significance of the correlations (r values) using 1000 simulations (Belbin 1993). Only variables with $r > 0.9$ were plotted.

Stream habitat characteristics

Physical and chemical data.—In order to examine differences in thermal regime between forest and agriculture streams, we obtained water temperature data from all six streams using submerged data loggers (Optic StowAway, Onset Computer, Pocasset, Massachusetts, USA) during April through May 1999. Loggers were programmed to record water temperature every 30 min. Only three data loggers were available. Consequently, we maintained at least one logger in a stream of each type (forest and agriculture), while recording temperature data in each stream for a period of 5–13 d. We analyzed the data by calculating 24 h mean, maximum, and minimum temperatures from forest and

agriculture streams. When temperature data were available from more than one stream within a stream type (forest or agriculture) we used the mean of the two values to calculate these 24-h variables. Means, maxima, and minima for 24-h periods were then compared between forest and agriculture streams using a Student's *t* test. (JMP; SAS Institute Inc. 1994). Mean percent canopy cover was measured in each stream using a canopy densiometer in the middle of the channel at 10 equidistant points along 300-m reaches.

We collected water samples for nutrient chemistry analysis from each of the six streams from December 1997 to January 1998, from May 1998 to September 1998, and during May 1999. At least two replicate filtered (0.45 μm Millipore) samples were collected from streams during each period. We could not freeze samples, so they were preserved by acidification (pH <3 with concentrated HCl; APHA 1985) in the field. Once transported to the University of Georgia, samples were analyzed for $NO_3 + NO_2$ (cadmium reduction method), NH_4 (phenate method), and soluble reactive phosphorus (SRP; ascorbic acid method) using an Alpkem RFA 300 automated analyzer (Alpkem, College Station, Texas, USA) (American Public Health Association [APHA] 1985). Samples collected in 1999 were not analyzed for SRP. Mean concentrations of $NO_3 + NO_2$, NH_4 and soluble reactive phosphorus were compared between stream types (forest and agriculture) using nested analysis of variance (ANOVA) with random effects.

Benthic substrata.—Particle size distributions in substrata of the six streams were compared using pebble counts (Kondolf 1997). In each stream, more than 100 particles >1 m apart were measured; we restricted pebble counts to the geomorphic units that were sampled for macroinvertebrates (i.e., shallow riffles). Particles were selected by blindly lowering the index finger to the streambed until a particle was touched. Before picking up each particle, we first visually estimated its percentage of sediment cover and percentage embeddedness (nearest 5%). Particles were subsequently measured along their intermediate axis and sorted into half-phi size classes. Substrate data are presented as cumulative percentage size frequency curves, and mean percentage of sediment cover and embeddedness. Mean percentage of sediment cover and embeddedness were compared in forest and agriculture streams using nested ANOVA with random effects. Data were arcsin square-root transformed before analysis.

Basal resources.—Storage of coarse benthic organic matter (CBOM) was measured in all six streams during December 1997 and January 1998. CBOM was collected in a series of adjoining Surber samples (0.093 m², mesh 600 μm) along 10 streambed transects (bank to bank; width 30 cm) spaced ~30 m apart along 300-m reaches in each stream. We did not collect large pieces of wood (>30 cm in length) or estimate storage of coarse woody debris accumulations. For this reason,

and because we collected CBOM only from the surface of the streambed, our measurements of CBOM are likely to be low estimates of actual storage. However, our estimates serve as a relative measure of CBOM availability in forest and agriculture streams. We measured CBOM storage only once; <5% of tree species in the region are deciduous (D. Turk, *personal communication*), making seasonal variation in direct inputs unlikely. Although CBOM storage is also affected strongly by seasonal discharge patterns, differences in canopy cover and riparian vegetation between forest and agriculture streams suggest that our CBOM data provide a reasonable approximation of the relative availability of terrestrial organic matter for macroinvertebrates in the two stream types.

CBOM was dried and transported to the University of Georgia where it was sorted into leaf litter and wood categories, redried at 60°C for 72 h, cooled in a desiccator, weighed, subsampled, ashed at 500°C for 1 h, cooled in a desiccator and reweighed to obtain ash-free dry mass (AFDM). We expressed CBOM storage as g AFDM/m^2 of leaf litter only and total CBOM. Differences between individual streams were tested using nested ANOVAs with random effects, followed by Tukey-Kramer tests if differences between streams were significant ($P < 0.05$).

Standing crop of epilithon was measured in each stream during August 1998 and April–May 1999. Cobbles (1998, $n = 5$; 1999, $n = 8$) collected from riffles were scrubbed with a stiff toothbrush and rinsed using a wash bottle. We quantified surface area of cobbles using aluminum foil and a mass–area regression. Measured subsamples of epilithon slurries were filtered onto preashed, preweighed glass fiber filters (0.7-μm nominal pore size) that were then dried at 50°C for 72 h and transported back to the University of Georgia. Filters were redried, cooled in a desiccator, weighed, ashed at 500°C for 1 h, cooled in a desiccator and reweighed to obtain ash-free dry mass (AFDM). Standing crop of biofilm was expressed as g AFDM/m^2 cobble surface and compared between stream types and streams using the same tests as for CBOM above.

RESULTS

Macroinvertebrate community structure

There were no significant differences between stream types (forest and agriculture) in mean total macroinvertebrate density (1996 and 1998) or mean total macroinvertebrate biomass (1998). Macroinvertebrate community structure was significantly different between stream types ($R = 0.44$, $P = 0.01$) and between years ($R = 0.59$; $P = 0.04$) for the untransformed data. The ordination plot (Fig. 2a) suggests that the difference between stream types was consistent across years, with no interspersion of forest and agriculture streams in either year and no overlap of samples from the two years. The difference between these factors was not

simply due to changes in abundance as the presence/absence data also showed significant differences between streams types ($R = 0.42$, $P = 0.02$) and years ($R = 0.36$; $P = 0.03$). The presence/absence data still separated forest and agriculture streams in both years, but within a stream type there was less separation between years (Fig. 2b), indicating temporal changes in abundance. The greater spread of points among agriculture streams, particularly the Menarano (MEN), indicated more variable community structure in this stream type than in forest streams (Fig. 2).

Differences between stream types were apparent for broad taxonomic groupings and functional feeding groups. In both years, abundance of Ephemeroptera and collector–gatherers was positively correlated with agriculture streams, whereas richness and abundance of Diptera, and abundance of Trichoptera and collector–filterers, were positively correlated with forest streams (Figs. 3a and 3b, 4a and 4b). In 1996, total abundance was positively correlated with agriculture streams, but richness and abundance of Plecoptera were positively correlated with forest streams (Figs. 3a and 3b). In 1998 total richness and richness of collector-gatherers and collector-filterers were positively correlated with forest streams (Fig. 4a and 4b).

In 1996, samples from the agriculture streams were dominated by *Afroptilum* spp. (Ephemeroptera), whereas forest streams were dominated by *Afroptilum* spp. and *Tricorythus* F (Ephemeroptera), the caddisflies *Leptonema*, *Gyrocarisa*, and Hydropsychid L (Trichoptera), and Chironomidae (Table 3). In 1998, most taxa occurred in far higher abundance than in 1996 and *Afroptilum* spp., Hydropsychid L, *Tricorythus* F, Chironomidae, and *Gyrocarisa* were the most abundant taxa in both stream types (Table 3).

For the untransformed data, average similarity of forest streams was ~15% higher than that of agriculture streams (56% vs. 41% in 1996, 68% vs. 54% in 1998) and average similarity was higher in 1998 than in 1996 for both stream types. Dissimilarity between stream types was almost 20% higher in 1996 than in 1998 (61% vs. 44%). In 1996, 18 taxa accounted for a total of 90% of the overall dissimilarity between agriculture and forest streams, with the mayflies *Afroptilum* spp. and Ephem U together accounting for 48% of between-group dissimilarity (Table 3). Both these taxa, along with Hydropsychid L and Ephem V occurred in higher abundance in agriculture streams (Fig. 3a and 3c). Of the overall dissimilarity between forest and agriculture streams in 1998, 90% was accounted for by 19 taxa, with 50% accounted for by four taxa: *Afroptilum* spp., *Tricorythus* F, Hydropsychid L, and *Gyrocarisa* (Table 3). Most (13 of 19) taxa were more abundant in forest streams than in agriculture streams (Fig. 4a and 4c). In both years, relatively few of the important contributors to differences between stream types were good discriminators between these two groups and no taxa were considered good discriminators between stream
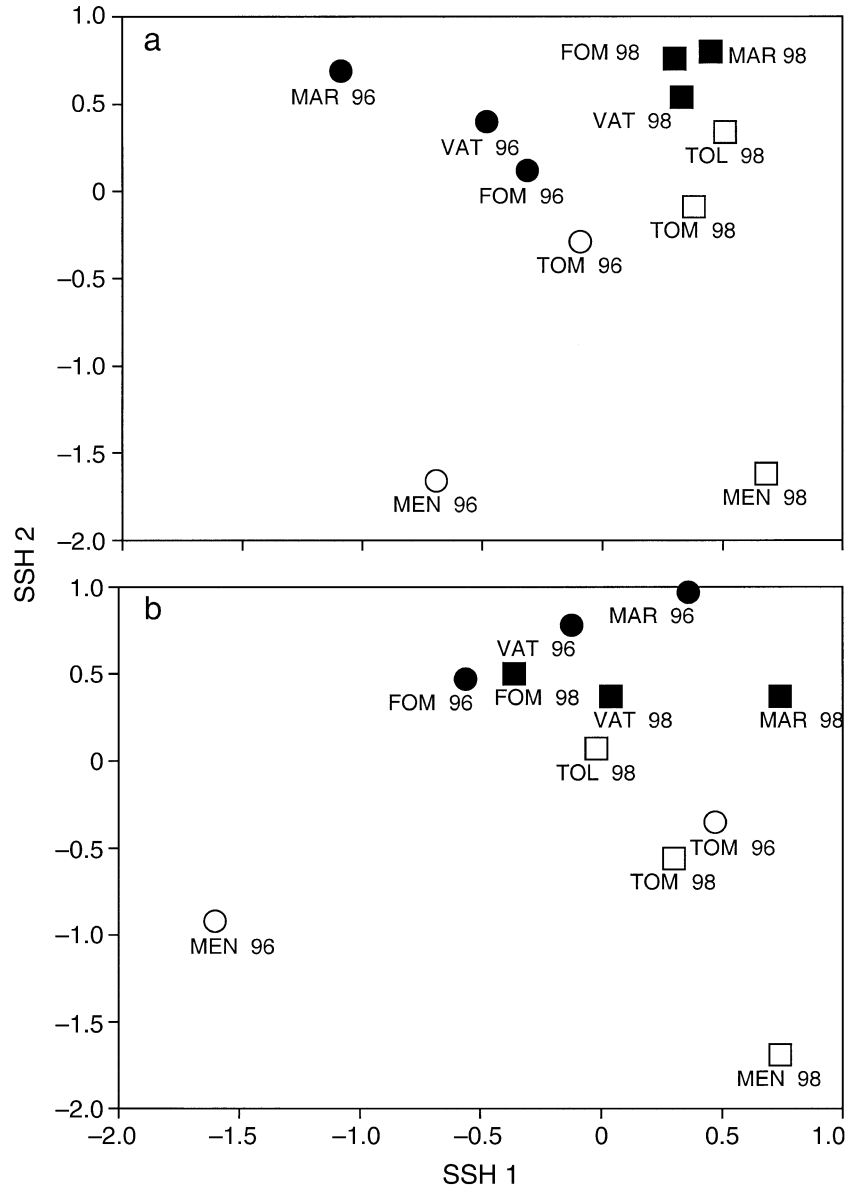
FIG. 2. Semi-strong hybrid multidimensional scaling (SSH) ordination plot of macroinvertebrate communities from forest and agriculture streams in eastern Madagascar based on Bray-Curtis dissimilarities: (a) untransformed abundance data, stress = 0.07; (b) presence/absence-transformed data, stress = 0.11. Solid symbols are forest streams; open symbols are agriculture streams. Circles are 1996 samples; squares are 1998 samples.

types in both years (Table 3). Many taxa, particularly the most abundant, showed a high degree of stream-scale patchiness, often occurring in only one of the replicate streams. This is evident from the vectors for many of the abundant taxa, which show clear correlation with particular streams within a treatment (Figs. 3a and 3c, 4a and 4c).

For forest streams, 13 taxa accounted for 90% of the overall dissimilarity between years, with *Afroptilum* spp. and Hydropsychid L accounting for over 40% (Table 3). All taxa except *Leptonema* were more abundant in 1998 and most occurred consistently enough among

replicate streams to be good discriminators between years. In agriculture streams, 18 species accounted for 90% of total dissimilarity between years with two taxa—*Afroptilum* spp. and *Tricorythus* F—accounting for almost 40% (Table 3). All of these taxa were more abundant in the second year except Ephem U and Ephem V, which were only found in 1996. In contrast to forest streams, few taxa were consistently good discriminators between years in the agriculture streams.

Stream habitat

Canopy cover was zero along 300-m reaches in two of the agriculture streams and averaged 14% in the third
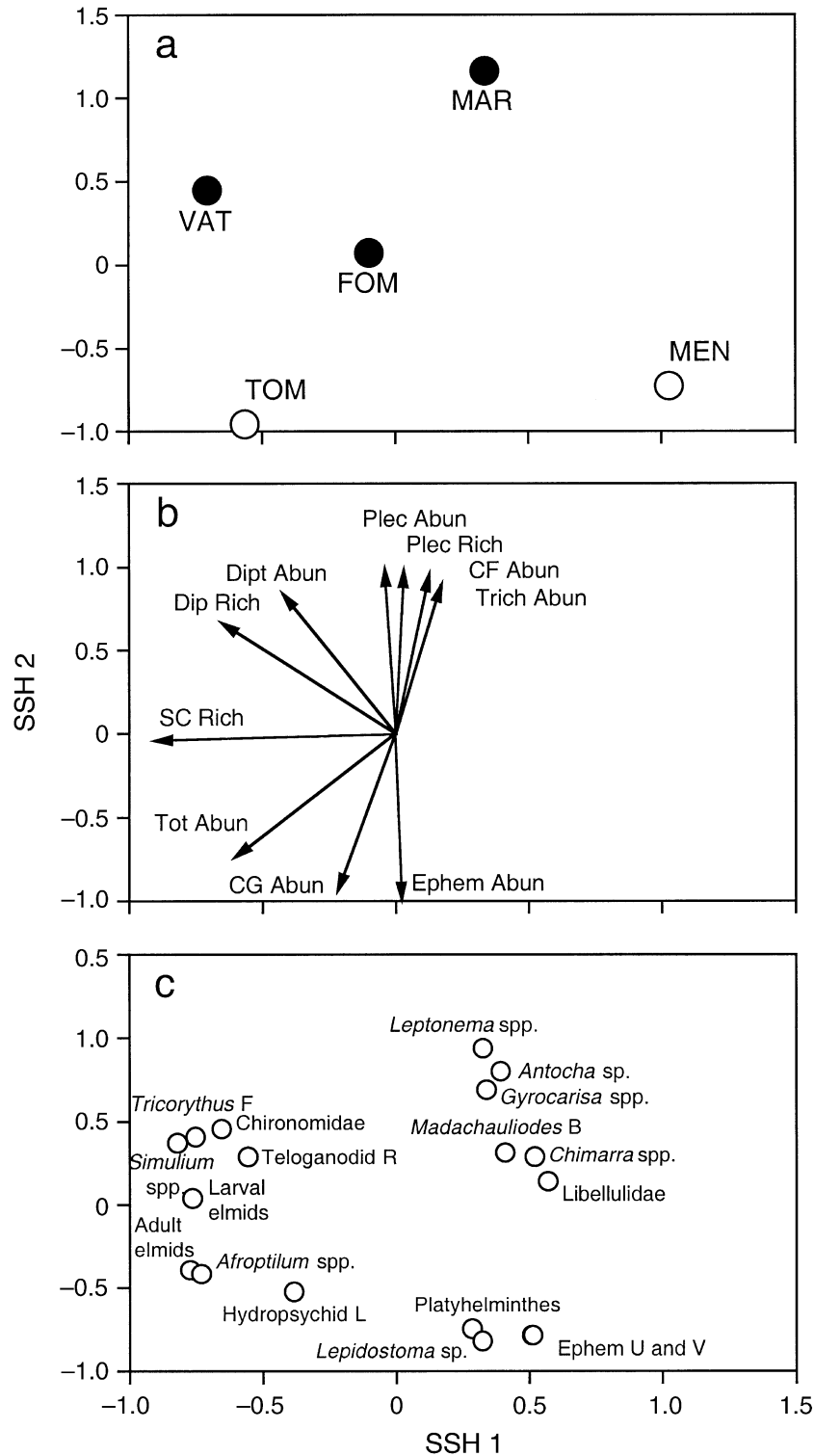
FIG. 3. Semi-strong hybrid multidimensional scaling (SSH) ordination of macroinvertebrate communities from forest and agriculture streams sampled in 1996. (a) SSH ordination plot of macroinvertebrate communities based on Bray-Curtis dissimilarities using untransformed abundance data, stress = 0.01. Solid symbols are forest streams, open symbols are agriculture streams. (b) Principle axis correlation (PCC) vectors for highly correlated ($r > 0.9$) insect orders and functional feeding groups. Abbreviations are as follows: Rich, richness; Abun, abundance; Tot, total; Dipt, Diptera; Plec, Plecoptera; Trich, Trichoptera; Ephem, Ephemeroptera; SC, scraper; CF, collector–filterer; CG, collector–gatherer. (c) PCC vectors for taxa accounting for 90% of overall dissimilarity between stream types.
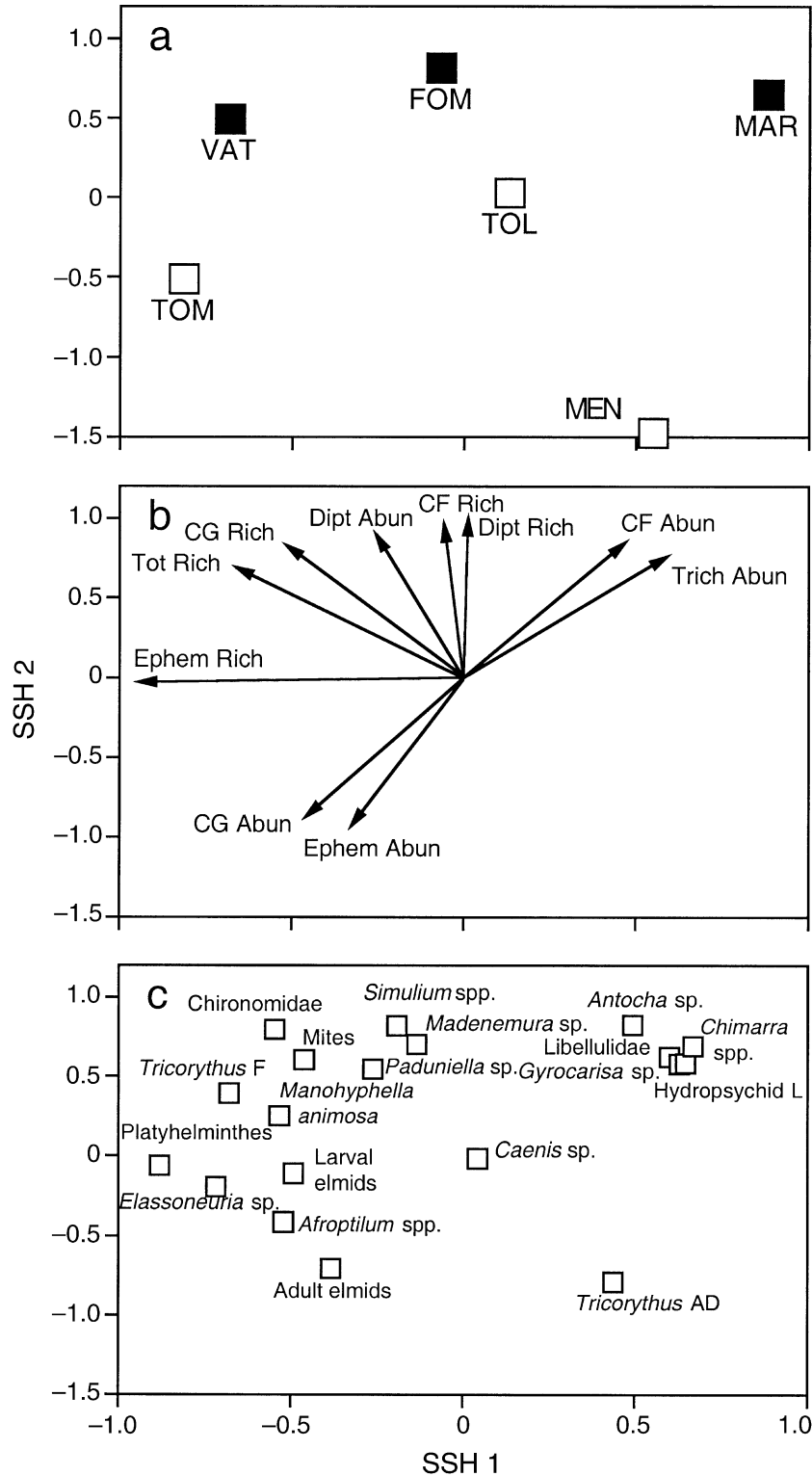
FIG. 4. Semi-strong hybrid multidimensional scaling (SSH) ordination of macroinvertebrate communities from forest and agriculture streams sampled in 1998. (a) SSH ordination plot of macroinvertebrate communities based on Bray-Curtis dissimilarities using untransformed abundance data, stress = 0.01. Solid symbols are forest streams, open symbols are agriculture streams. (b) Principle axis correlation (PCC) vectors for highly correlated ($r > 0.9$) insect orders and functional feeding groups. Abbreviations are as in Fig. 3. (c) PCC vectors for taxa accounting for 90% of overall dissimilarity between stream types.

TABLE 3. Mean densities (individuals/m^2 ± 1 SE) of taxa that accounted for differences between stream types and years and measures of dissimilarity.

| | 1996 | | 1998 | | F96 v. A96 | |
Taxon	Forest	Agriculture	Forest	Agriculture	$\bar{D}i$	$\bar{D}i/$SD$(\bar{D}i)$
Non-Insecta						
Platyhelminthes	0.7 ± 0.5	1.2 ± 0.4	2.6 ± 1.2	2.5 ± 1.1	1.0	1.4
Mites	0.9 ± 0.4	0.3 ± 0.2	3.6 ± 0.8	0.8 ± 0.4	N	N
Ephemeroptera						
Afroptilum spp.	13.7 ± 2.1	49.4 ± 24.6	42.9 ± 3.5	54.5 ± 13.0	37.1	**1.5**
Elassoneuria sp.	1.2 ± 0.3	1.6 ± 0.3	0.7 ± 0.3	2.3 ± 2.2	N	N
Tricorythus F	10.3 ± 4.0	5.8 ± 5.8	18.0 ± 5.4	17.5 ± 9.0	9.0	1.2
Tricorythus AD	0	0	0	6.5 ± 6.5	N	N
Tricorythus AE	0	0	0	1	N	N
Caenis sp.	0	0.5 ± 0.5	0.1 ± 0.1	2.9 ± 2.4	N	N
Manohyphella animosa	0	0	5.3 ± 4.3	0	N	N
Ephem R	0.8 ± 0.8	0.0	0.0	0	0.9	0.7
Ephem U	0.1 ± 0.1	8.4 ± 8.4	0.0	0	11.0	0.9
Ephem V	0.1 ± 0.1	2.4 ± 2.4	0.1 ± 0.1	0	3.2	0.9
Odonata						
Libellulidae	1.3 ± 0.5	1.3 ± 0.1	6.4 ± 2.1	2.5 ± 1.3	0.8	**1.8**
Plecoptera						
Madenemura sp.	0.5 ± 0.1	0.0	1.3 ± 0.5	0	N	N
Megaloptera						
Madachauliodes B	0.9 ± 0.5	0.2 ± 0.2	0.6 ± 0.3	0.1 ± 0.1	1.0	1.1
Trichoptera						
Chimarra spp.	1.2 ± 0.5	0.2 ± 0.1	4.4 ± 1.6	0.6 ± 0.6	1.1	1.3
Hydropsychid L	3.2 ± 2.3	3.5	36.1 ± 16.2	11.3 ± 5.9	3.6	**2.5**
Leptonema sp.	8.1 ± 3.8	0.9 ± 0.8	0.7 ± 0.2	1.8 ± 0.9	9.0	1.1
Paduniella sp.	0.0	0.0	1.1 ± 0.7	0	N	N
Lepidostoma sp.	0.2 ± 0.1	0.9 ± 0.8	0.9 ± 0.7	0.8 ± 0.3	1.1	1.0
Gyrocarisa spp.	3.5 ± 1.1	0.9 ± 0.9	12.6 ± 5.5	7.3 ± 5.5	3.4	1.4
Coleoptera						
Adult elmids	0.7 ± 0.5	1.7 ± 0.1	0.7 ± 0.2	2.8 ± 0.2	1.2	1.3
Larval elmids	0.3 ± 0.1	1.1 ± 1.1	0.7 ± 0.2	3.5 ± 1.8	1.1	1.3
Diptera						
Antocha sp.	1.6	0.0	5.3 ± 0.9	0.6 ± 0.6	2.0	1.2
Simulium spp.	1.6 ± 1.0	1.1 ± 0.6	8.0 ± 1.5	1.8 ± 1.1	1.5	1.0
Chironomidae	3.6 ± 0.9	1.9 ± 1.1	14.0 ± 1.2	8.5 ± 3.3	2.5	**1.5**
Total overall dissimilarity					90	

Notes: $\bar{D}i$, contribution of each taxon to the overall dissimilarity between two groups. $\bar{D}i/$SD$(\bar{D}i)$, the ratio of $\bar{D}i$ for all sample pairs between groups to the standard deviation of $\bar{D}i$, which is a measure of the importance of each taxon in discriminating communities between groups. Good discriminating taxa for each comparison are shown in bold type. ''N'' denotes that the taxon did not contribute to 90% of the overall dissimilarity between groups.

(TOL). Mean canopy cover in study reaches of forest streams was significantly higher (Table 4). Temperature regimes differed between forest and agriculture streams (Fig. 5 and Table 4). Both mean daily mean temperature and mean daily maximum temperature were significantly higher in agriculture streams (Table 4). Mean daily minimum temperature was higher in agriculture streams than in forest streams but not significantly so ($P = 0.22$; Table 4). Soluble reactive phosphorus (SRP) concentrations were consistently below detection limits (<6.8 μg/L) in all streams in 1997 and 1998 (Table 5). There were no significant differences between forest and agriculture streams in concentrations of $NO_3 + NO_2$ or NH_4, although there was evidence for slightly higher concentrations of NH_4 in agriculture streams (Table 5).

Cumulative percentage curves of particle sizes in riffle substrata of the six streams revealed no distinct differences in particle size class distributions (Fig. 6). Five of the streams had extremely similar riffle substrata; one agriculture stream (MEN) had proportionately more particles in the 32–180 mm (intermediate axis) size classes (Fig. 6).

Percentage sediment cover on particles in riffle substrata was low in all streams (Table 6). Embeddedness was generally below 25%, indicating a low level of particle burial in riffles of all streams (Table 6). There was no significant difference between forest and agriculture streams in either percentage sediment cover or percentage embeddedness (Table 6).

Mean storage of coarse benthic organic matter (CBOM) was significantly (threefold) higher in forest

TABLE 3. Extended.

F98 v. A98		F96 v. F98		A96 v. A98	
$\bar{D}i$	$\bar{D}i/\text{SD}(\bar{D}i)$	$\bar{D}i$	$\bar{D}i/\text{SD}(\bar{D}i)$	$\bar{D}i$	$\bar{D}i/\text{SD}(\bar{D}i)$
1.2	1.0	1.5	1.1	1.1	0.9
2.1	**1.8**	2.0	**1.8**	N	N
14.9	1.1	20.5	**5.1**	27.2	**1.7**
1.7	0.9	N	N	2.3	1.6
9.1	1.1	7.9	**1.5**	12.7	**1.5**
5.7	0.7	N	N	7.7	0.6
N	N	N	N	1.0	0.6
1.9	0.8	N	N	2.2	0.8
3.8	0.8	3.9	0.8	N	N
N	N	N	N	N	N
N	N	N	N	8.4	0.9
N	N	N	N	2.4	0.9
3.1	1.4	3.4	**1.9**	1.1	0.8
0.9	**1.5**	N	N	N	N
N	N	N	N	N	N
2.8	**1.6**	2.3	**1.6**	N	N
18.6	1.1	22.1	**1.5**	7.5	**1.5**
N	N	5.4	1.2	1.2	1.4
0.8	1.0	N	N	N	N
N	N	N	N	N	N
7.3	1.3	6.9	**1.6**	5.4	0.9
1.5	**9.8**	N	N	1.0	**4.3**
2.2	**1.9**	N	N	2.6	**1.5**
3.4	**2.7**	2.5	**2.4**	N	N
4.7	**1.8**	4.4	**2.1**	1.2	1.3
4.5	0.9	7.4	**3.5**	5.6	**1.6**
90		90		90	

TABLE 4. Mean values of habitat variables measured in forest and agriculture streams ($n = 3$ of each stream type), Ranomafana National Park, Madagascar, 1996–1999.

Variable	Units	Year	Mean ± 1 SE		P
			Forest	Agriculture	
Canopy cover	%	1996–1998	76 ± 4	5 ± 5	**<0.001**
Daily mean water temperature	°C	1999	17.0	17.5	**0.012**
Daily maximum water temperature	°C	1999	17.5	18.4	**0.0003**
Daily minimum water temperature	°C	1999	16.6	16.9	0.19
NO_3-N + NO_2-N concentration	μg/L	1997–1999	65 ± 3	59 ± 4	0.21
NH_4-N concentration	μg/L	1997–1999	15 ± 7	27 ± 5	0.24
Sediment cover	%	1999	2.71 ± 1.62	0.9 ± 0.21	0.35
Embeddedness	%	1999	18.47 ± 5.5	15.75 ± 4.23	0.72
Leaf litter standing crop	g AFDM/m²	1997	7.21 ± 2.35	0.92 ± 0.27	0.06
Total coarse organic matter	g AFDM/m²	1997	22.84 ± 2.68	7.79 ± 1.48	**0.008**
Epilithon standing crop	g AFDM/m²	1998	4.18 ± 0.36	3.04 ± 0.36	0.09
Epilithon standing crop	g AFDM/m²	1999	2.43 ± 0.44	2.31 ± 0.57	0.88

Notes: Significant differences ($P < 0.05$) between stream types in ANOVAs are shown in bold. AFDM = ash-free dry mass.
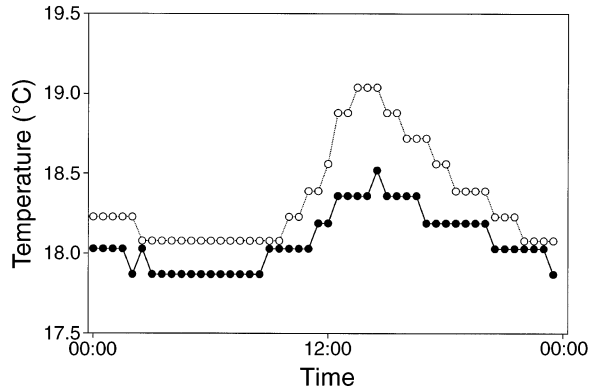
FIG. 5. Diel changes in water temperature in a forest stream (MAR; closed circles) and agriculture stream (TOM; open circles), 5 May 1999, Ranomafana National Park, Madagascar.

streams than in agriculture streams (Table 4), although high spatial variability within streams led to a lack of statistical difference between individual streams (Fig. 7). Mean storage of leaf litter was eightfold higher in forest streams, although the difference was not significant ($P = 0.06$) because of relatively low storage of leaf litter in one forest stream (MAR; Fig. 7).

Mean epilithon standing crop in forest streams was either higher than or similar to that of agriculture streams in 1998 and 1999 (Table 4). In neither year were standing crops significantly different. In 1998, epilithon standing crop was relatively consistent within stream type (forest and agriculture; Fig. 8a). In 1999, standing crop of epilithon on cobbles was lower than that measured in 1998 in both forest and agriculture streams and was highly variable, showing no consistent pattern with stream type (Fig. 8b).

DISCUSSION

Deforestation in the Ranomafana region of eastern Madagascar is associated with distinct changes in the structure of stream insect communities, including community simplification, shifts in the relative importance of functional feeding groups, and associated declines

in species richness. Although we could not study agriculture streams prior to impact, the proximity of our study streams and location within the same river network suggest that agriculture streams were similar to forest streams before deforestation of their catchments began. In addition, our results corroborate light-trapping studies that have inferred declines and loss of stream taxa caused by catchment deforestation. We discuss these community differences with respect to differences between forest and agriculture streams in physicochemical factors, habitat, and relative availability of basal food resources.

Differences in macroinvertebrate community structure

Forest streams were characterized by species-rich, diverse communities composed primarily of collector–gatherers and collector–filterers belonging to the orders Trichoptera, Ephemeroptera, Plecoptera, and Diptera. In contrast, simplified agriculture stream communities were dominated by generalist collector-gatherer taxa mostly belonging to the order Ephemeroptera. Increases in collector–gatherers were responsible for the largest difference in taxonomic structure of streams affected by deforestation: mayflies (Ephemeroptera) were present at much higher abundance and biomass in these streams. In addition, a few taxa were largely responsible for this difference (i.e., Baetidae, *Afroptilum* spp. and Leptohyphidae, *Tricorythus* spp.). This pattern is consistent with other studies that have shown large increases in generalist mayfly taxa in streams affected by canopy removal (Hawkins et al. 1982, Gurtz and Wallace 1984, Behmer and Hawkins 1986, Wallace and Gurtz 1986).

Differences in the relative importance of functional feeding groups were associated with large differences between stream types in the relative importance of insect orders, as well as significant net declines in species richness and diversity of insect communities in streams affected by deforestation. Trichoptera and Diptera showed large net declines in agriculture streams. These orders were largely represented by the shredder and

TABLE 5. Means and ranges of concentrations of PO$_4$-P, NH$_4$-N, and NO$_3$ + NO$_2$-N in the six study streams, Ranomafana National Park and peripheral zone, 1997–1999.

Site		PO$_4$-P			NH$_4$-N			NO$_3$ + NO$_2$-N	
	n	Mean (μg/L)	Range (μg/L)	n	Mean (μg/L)	Range (μg/L)	n	Mean (μg/L)	Range (μg/L)
Forest streams									
Mariavaratra	4	<6.8	†	8	6	<3–12	8	69	61–77
Fomopohonona	8	<6.8	†	12	10	<3–29	12	60	46–71
Vatoharanana	8	<6.8	†	12	28	<3–63	12	68	49–81
Agriculture streams									
Tomaro	8	<6.8	†	12	27	<3–79	12	52	30–64
Tolongoino	4	<6.8	†	8	18	10–25	8	62	41–80
Menarano	4	<6.8	†	8	36	23–50	8	63	54–72

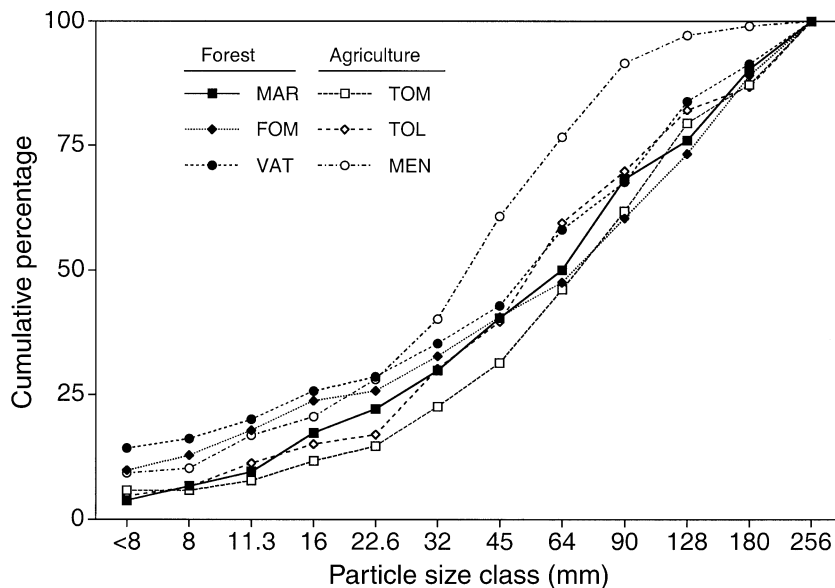† All PO$_4$-P concentrations were below detection limits.

FIG. 6. Cumulative percentage distributions of sediment particle sizes in riffle substrata of the six study streams, April–May 1999, Ranomafana National Park, Madagascar.

small filter–collector taxa that were present at lower densities in streams draining deforested areas. One insect order (Plecoptera) has almost disappeared from agriculture streams; we found one individual in the Tolongoina (TOL) agriculture stream in 1998. Plecoptera were relatively rare in forest streams. Trichoptera and Plecoptera are also two of the stream insect groups that exhibit a high degree of micro-endemism and which appear to be particularly sensitive to catchment disturbance (Gibon et al. 1996).

Our community inventories are likely to be very incomplete for several reasons. First, we sampled riffle habitats only; taxa that specialize in other micro-habitats were unlikely to be sampled. Second, sorting macroinvertebrates to morphospecies doubtless led to the lumping of many true species. Lumping of species would lead to underestimates of diversity both within and among streams. For example, emergence trap samples from the Mariavaratra (MAR) forest stream (Rabeson 2001) have indicated the presence of at least six species of *Afroptilum* (Ephemeroptera; M. D. Hubbard, *personal communication*). In addition, the naucorid genus *Aphelocheirus* may be represented by a different species in each of the streams (R. Sites, *personal communication*). Identification of insects collected in this study is ongoing. Results to date clearly illustrate both the high diversity of forest stream communities in eastern Madagascar and our generally low level of knowledge. For example, the Odonata are perhaps the best understood of the major aquatic insect orders in Madagascar (Gibon et al. 1996). However, the emergence trapping mentioned above has already yielded at least two new species and one new genus in this order (T. W. Donnelly, *personal communication*). Our lack of species-level identification probably led to underestimates of actual differences in community structure between forest and agriculture streams. Nonetheless, use of morphospecies data in multivariate analyses proved to be a robust technique in studying the effects of perturbation on these poorly understood communities.

TABLE 6. Percentage of sediment cover and embeddedness of >100 substrate particles randomly selected for the pebble counts conducted in each stream during May 1999.

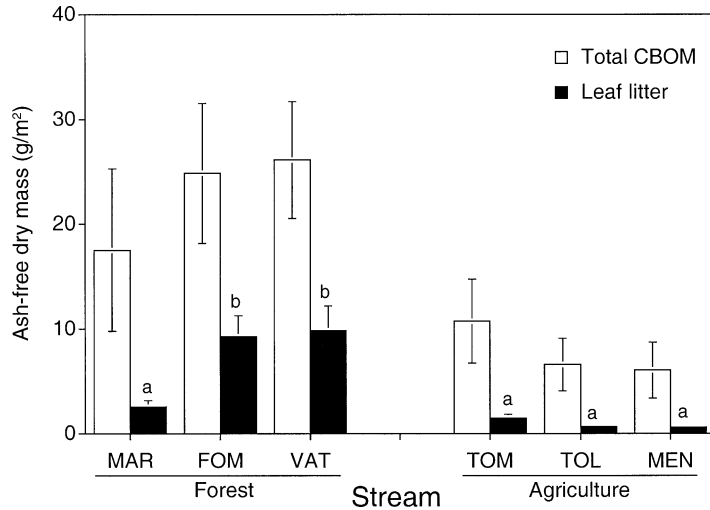| Site	n	Sediment cover (%)		Embeddedness (%)	
		Mean (±1 SE)	Range	Mean (±1 SE)	Range
Forest streams					
Mariavaratra	104	2.45 ± 0.73	0–40	21.54 ± 2.64	0–90
Fomopohonona	101	0.05 ± 0.05	0–5	26.09 ± 2.65	0–90
Vatoharanana	105	5.63 ± 1.15	0–80	7.79 ± 1.74	0–60
Agriculture streams					
Tomaro	102	0.54 ± 0.31	0–30	22.35 ± 2.63	0–80
Tolongoina	106	0.91 ± 0.45	0–40	17.12 ± 2.42	0–70
Menarano	107	1.25 ± 0.48	0–30	7.79 ± 1.72	0–60

FIG. 7. Total coarse benthic organic matter and leaf litter storage in the six study streams, December 1997–January 1998, Ranomafana National Park, Madagascar. Different letters above bars indicate significant differences ($P < 0.05$); $n = 10$ transects. No significant differences in total coarse benthic organic matter were found between individual streams.

Mechanisms driving community differences

Differences in the relative availability of basal food resources are likely of paramount importance in explaining differences in insect community structure fol-

FIG. 8. Standing crops of epilithon on cobbles in the six study streams in (a) 1998 ($n = 5$) and (b) 1999 ($n = 8$). Different letters above bars indicate significant differences ($P < 0.05$). No significant differences were found between streams in 1998.

lowing deforestation. Mean storage of organic matter was significantly higher in forest streams relative to agriculture streams. While standing crops of epilithic biofilm were not different between stream types, measurements of epilithic metabolism have showed that mean gross primary production of biofilms in agriculture streams, although low, is three times higher than in forest streams (20.6 vs. 7.3 mg $O_2 \cdot m^{-2} \cdot h^{-1}$; Benstead 2001). In addition, stable isotope analysis has confirmed that carbon sources (i.e., terrestrial detritus vs. in situ primary production) explain much of the variability in the relative biomass of 11 major insect taxa in forest and agriculture streams (J. P. Benstead and C. M. Pringle, *unpublished manuscript*).

We believe that these data, in combination, provide strong evidence that differences in stream community structure are driven in large part by differences in basal resource availability. Specifically, taxa that depend largely on food resources of terrestrial origin (e.g., leaf litter and seston) decline in agriculture streams. Examples include the detritivorous shredders, such as *Madenemura* (Plecoptera), and small collector–filterers, such as *Simulium* (Diptera) and *Chimarra* (Trichoptera). Conversely, agriculture stream communities are dominated by taxa that do not depend on terrestrial carbon and that can take advantage of increased in situ primary production. Examples in this group include the baetid and tricorythid mayflies (Ephemeroptera) and large, omnivorous collector–filterer *Leptonema* (Trichoptera). Densities and biomass of collector–gatherers were consistently higher in agriculture streams relative to those in forest. Gut analysis has indicated that these taxa are feeding predominantly on amorphous detritus derived from the matrix of epilithic biofilms (J. P. Benstead and C. M. Pringle, *unpublished manuscript*). Higher production and turnover of carbon by epilithic biofilms in agriculture streams appears to be supporting the relatively high abundance and biomass of these
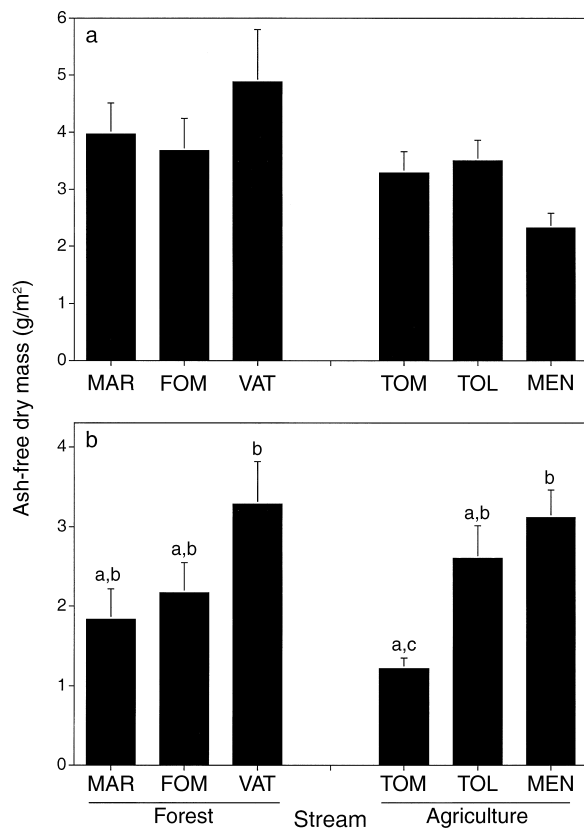
generalist taxa, as indicated by stable isotope analyses of representative collector-gatherer taxa (J. P. Benstead and C. M. Pringle, *unpublished manuscript*).

We found no evidence for elevated sedimentation rates in riffle habitats of agriculture streams. This was an unexpected result given that forest clearance, particularly that of riparian zones, often gives rise to increased soil erosion and subsequent inputs of sediment into streams (Waters 1995, Harding et al. 1998). In addition, the central highlands of Madagascar experience some of the highest erosion rates in the world (>250 Mg·ha^{-1}·yr^{-1} [1 Mg = 1 metric ton]; Randrianarijaona 1983, Wells and Andriamihaja 1997), largely as a result of clearance of original vegetation cover. We did not measure suspended sediment loads in this study. Higher sediment loads may occur in agriculture streams during storms, particularly during the wettest part of the year (December–March). However, differences in turbidity and sediment cover between forest and agriculture streams were not apparent during any non-cyclone-season months (i.e., April–January; J. P. Benstead, *personal observations*).

Several potential explanations exist for the observed lack of sedimentation in agriculture streams. First, the soils of the region are characterized by very high infiltration capacity (Balko 1998). High infiltration rates may prevent overland flow and associated soil erosion. In addition, the surface geology of the region differs from the lateritic clays that predominate on the central highlands of Madagascar. Soils on much of the eastern escarpment are derived from metamorphic rocks (i.e., granites and schists) outcropping from the Precambrian basement layer that comprises the island's main geologic feature (Du Puy and Moat 1996). Second, much of the evidence for the effects of deforestation on increased sediment inputs is derived from studies of logging activities (e.g., Douglas et al. 1992) or from whole-catchment deforestation experiments (e.g., Likens et al. 1970, Gurtz et al. 1980). In contrast, much of the deforestation currently occurring in the tropics is not whole-catchment in scale but patchy, resulting in fragmented forest embedded in a matrix of modified vegetation (Schelhas and Greenberg 1996). Deforestation in eastern Madagascar conforms to this patchy pattern. Typically, areas <1 ha in area are cleared at a time. In addition, trees are cut by hand and crops are established and provide ground cover before the onset of the wet season. Third, rice paddies are a common feature of riparian areas in eastern Madagascar. All three agriculture streams had paddies adjacent to at least one bank within the vicinity of each study reach. Rice paddies may act as ''mini-wetlands,'' providing a sink for sediment originating from erosion upslope. Lastly, the headwaters of all the agriculture streams lie within the protected forest of Ranomafana National Park (Fig. 1). Protection of headwater reaches may be crucial in preventing excessive sediment inputs into agriculture streams.

Our results indicate that increased sedimentation is not a dominant response to deforestation in the agriculture streams we studied. It therefore appears unlikely that this frequently important form of abiotic disturbance (Waters 1995, Harding et al. 1998) is responsible for differences in macroinvertebrate communities between forest and agriculture streams. Temperature regimes in agriculture streams were different from those of forest streams, exhibiting significantly higher daily means and maxima, presumably as a result of canopy loss. Thermal tolerances are known to be important in explaining distributions of certain stream insect taxa, particularly the Plecoptera (Quinn and Hickey 1990, Quinn et al. 1994, Collier and Smith 2000). However, while temperature is a potentially important factor in explaining our results, it remains uncertain whether the differences in temperature regimes that we observed between stream types were large enough to affect taxa that are sensitive to increased temperatures.

Finally, we found no difference between streams with respect to concentrations of major nutrients. Increases in nutrient export (especially of NO_3) have been reported from whole-catchment deforestation experiments (e.g., Likens et al. 1970). Again, the small-scale, patchy nature of deforestation in the Ranomafana area may explain any lack of effect in this study. In addition, sinks for nutrients have been modified in addition to sources. For example, uptake by epilithic biofilm communities may be more rapid in agriculture streams due to higher primary production caused by increased light levels.

Implications for stream conservation in eastern Madagascar

Forest cover in the eastern biome of Madagascar has declined by at least 63% (7.4×10^4 km^2) since the island was colonized 2000 yr BP (Green and Sussman 1990). In this time, perhaps 3×10^5 km of stream and river channel have been affected by deforestation in the region. Our data support those of light-trapping surveys (e.g., Gibon and Elouard 1996, Sartori et al. 2000) in showing that relatively undisturbed stream communities in eastern Madagascar are species rich and highly diverse. Removal of forest cover results in loss or declines of specialist forest stream species and replacement by simplified communities that are dominated by generalist taxa (Gibon and Elouard 1996; Elouard and Gibon 2003). A combination of significant deforestation, micro-endemism, and habitat specialization has likely led to historic extinction of stream insect species in eastern Madagascar's rain forest biome. This pattern is set to continue if predictions of future deforestation rates are proved correct (Green and Sussman 1990). Indeed, estimates of future extinctions of stream insects approach 70% of species in some groups (e.g., the forest-specialist mayflies in the su-

perfamily Ephemeroidea) over the next 40 yr (Elouard and Gibon 2003).

Madagascar's recently improved framework for habitat conservation provides much hope for the future preservation of the country's extraordinary biological heritage (Benstead et al. 2000). However, decisions relating to the protected areas network are rarely taken from a catchment perspective and lack of biodiversity information often means freshwater habitats are not given the attention they deserve (but see Ganzhorn et al. 1997). What does the future hold for Madagascar's stream ecosystems, particularly those draining the remaining eastern rain forest biome? Although future inclusion of a minority of streams in the expanding network of protected areas is likely, deforestation has already affected many streams and continues to do so in the "unreserved matrix." Given Madagascar's current and projected fuel wood crisis (Jolly 1989, Richard and O'Connor 1997), we believe that an opportunity may exist for riparian reforestation in eastern Madagascar. Our data suggest that shifts in invertebrate communities of low-order streams affected by deforestation are being driven principally by the biotic variables and processes controlled by riparian vegetation (Cummins et al. 1989, Gregory et al. 1991, Sweeney 1993). Reestablishment of riparian vegetated zones would limit primary production, increase inputs of terrestrial carbon, and buffer thermal regimes (e.g., Scarsbrook and Halliday 1999). We therefore advocate the creation and maintenance of multiuse, community, riparian forests that would serve both economic and ecological functions in eastern Madagascar, particularly in areas adjacent to the low-order streams most affected by clearance of riparian vegetation. Similar multiuse forests have been proposed and implemented in rain forest corridor creation projects within the Masoala National Park in northeastern Madagascar (Holloway 2000). Although the establishment of such forests might be problematic for many reasons (e.g., riparian areas are often used for paddy rice production), it may represent the only avenue open for the future preservation of Madagascar's unique stream insect assemblages. Finally, we estimate that more than half a million km of stream and river channel are affected by deforestation in the tropics each year. Our results suggest that the effects of deforestation on tropical stream biodiversity may be underestimated and, consequently, not given sufficient weight in conservation policy and management.

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