

## APPLIED ISSUES

# Deforestation alters the resource base and biomass of endemic stream insects in eastern Madagascar

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## SUMMARY

1. Rainforest streams in eastern Madagascar have species-rich and diverse endemic insect communities, while streams in deforested areas have relatively depauperate assemblages dominated by collector-gatherer taxa. We sampled a suite of benthic insects and their food resources in three primary rainforest streams within Ranomafana National Park in eastern Madagascar and three agriculture streams in the park's deforested peripheral zone. We analysed gut contents and combined biomass and stable isotope data to examine stream community responses to deforestation in the region, which is a threatened and globally important hotspot for freshwater biodiversity.
2. Gut analyses showed that most taxa depended largely on amorphous detritus, obtained either from biofilms (collector-gatherers) or from seston (microfilterers). Despite different resource availability in forest versus agriculture streams, diets of each taxon did not differ between stream types, suggesting inflexible feeding modes. Carbon sources for forest stream insects were difficult to discern using  $\delta^{13}\text{C}$ . However, in agriculture streams dependence on terrestrial carbon sources was low relative to algal sources. Most insect taxa with  $\delta^{13}\text{C}$  similar to terrestrial carbon sources (e.g. the stonefly *Madenemura*, the caddisfly *Chimarra* sp. and *Simulium* blackflies) were absent or present at lower biomass in agriculture streams relative to forest streams. Conversely, collector-gatherers (*Afroptilum* mayflies) relied on algal carbon sources and had much higher biomass in agriculture streams.
3. Our analyses indicate that a few collector-gatherer species (mostly Ephemeroptera) can take advantage of increased primary production in biofilms and consequently dominate biomass in streams affected by deforestation. In contrast, many forest stream insects (especially those in the orders Plecoptera, Trichoptera and Diptera) depend on terrestrial carbon sources (i.e. seston and leaf litter), are unable to track resource availability and consequently decline in streams draining deforested landscapes. These forest-specialists are often micro-endemic and particularly vulnerable to deforestation.
4. The use of consumer biomass data in stable isotope research can help detect population-level responses to shifts in basal resources caused by anthropogenic change. We also suggest that restoration of vegetated riparian zones in eastern Madagascar and elsewhere

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could mitigate the deleterious effects of deforestation on sensitive, endemic stream taxa that are dependent on terrestrial carbon sources.

**Keywords:** algae, freshwater biodiversity, riparian vegetation, terrestrial detritus, tropical streams

## Introduction

Madagascar is currently identified as a hotspot for freshwater biodiversity based on its endemic fishes, crustaceans and molluscs and the threat to their continued survival [World Conservation Monitoring Centre (WCMC), 1998]. The island's stream insect fauna was very poorly understood until recently but available evidence now indicates that it is extremely diverse and exhibits high levels of endemism (>95%; Gibon, 2000). For example, the numbers of recently discovered, mostly undescribed species of Trichoptera and Ephemeroptera in Madagascar exceed 500 and 200, respectively. Madagascar is now thought to harbour 30–50% of Africa's species in major stream insect orders – in an area 50 times smaller than the mainland (Elouard & Gibon, 2003).

Stream insect biodiversity is greatest in eastern Madagascar, where the principal threat to stream communities is deforestation caused by swidden (slash-and-burn) agriculture (Benstead *et al.*, 2000, 2003a). Deforestation rates in the eastern rainforest belt were estimated at  $1110 \text{ km}^2 \text{ year}^{-1}$  between 1950 and 1985 (Green & Sussman, 1990), affecting approximately 4500 km of stream channel annually (Benstead, Douglas & Pringle, 2003b). This transition has clearly affected Madagascar's endemic stream invertebrate fauna. Based on light trapping of adults and larval collections, many of the stream insects found on the island's eastern slope have limited distributions and appear to be restricted to forested areas (Gibon, Elouard & Sartori, 1996; Gibon, 2000). Larval collections in Ranomafana National Park in eastern Madagascar have also revealed distinct differences between forest stream communities and those of its deforested peripheral zone. Forest streams are characterised by species-rich, diverse communities composed primarily of collector-gatherers and collector-filterers represented by the orders Trichoptera, Ephemeroptera, Plecoptera and Diptera. In contrast, simplified 'agriculture' stream communities are dominated by collector-gatherer taxa mostly belonging to the order Ephemeroptera (Benstead *et al.*, 2003b).

Although the relationships among deforestation, community simplification and loss of endemic stream taxa in these streams are clear, the mechanisms driving such shifts are not. Removal of terrestrial vegetation 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 basal food resources (Likens *et al.*, 1970; Webster *et al.*, 1992). Neither sedimentation of stream substrata or drastically elevated water temperatures are dominant responses to deforestation in the Ranomafana region (Benstead *et al.*, 2003b). However, mean leaf litter storage in agriculture streams is 13% of that in forest streams, while mean gross primary production by epilithic biofilms is 280% higher (Benstead, 2001; Benstead *et al.*, 2003b). Assuming that pronounced community shifts between stream types are not being driven by abiotic disturbance caused by sedimentation or modified temperature regimes, we hypothesised that endemic macroinvertebrate populations were responding principally to changes in the relative availability of food sources (i.e. leaf litter and wood versus algae and associated biofilm communities).

Stable isotope analysis is a useful technique for testing such hypotheses (Peterson & Fry, 1987) and has two advantages over more traditional diet analysis through the quantification of gut contents. First, it provides a measure of what carbon sources are actually assimilated by a consumer, rather than merely what is consumed. Secondly, it provides a longer record of feeding history (i.e. much greater than gut passage time). However, stable isotopes cannot distinguish between some resource classes (e.g. coarse versus fine particulate organic matter). This level of information, obtained through gut content analysis, can greatly facilitate interpretation of stable isotope results. For this reason, using these techniques in combination provides the most powerful method of examining food web interactions (Winterbourn, Cowie & Rounick, 1984; Hart & Lovvorn, 2002, 2003). One shortcoming of stable isotope food web studies is that they rarely include

abundance, biomass or secondary production data. Such data can be useful in situations where (i) the relative importance of basal resources differs between sampling sites (e.g. because of anthropogenic disturbance) and (ii) communities include species with relatively rigid feeding modes. Such species are unlikely to respond to shifts in basal resources by changing their feeding behaviour but will instead respond by declining in abundance, biomass or growth rate.

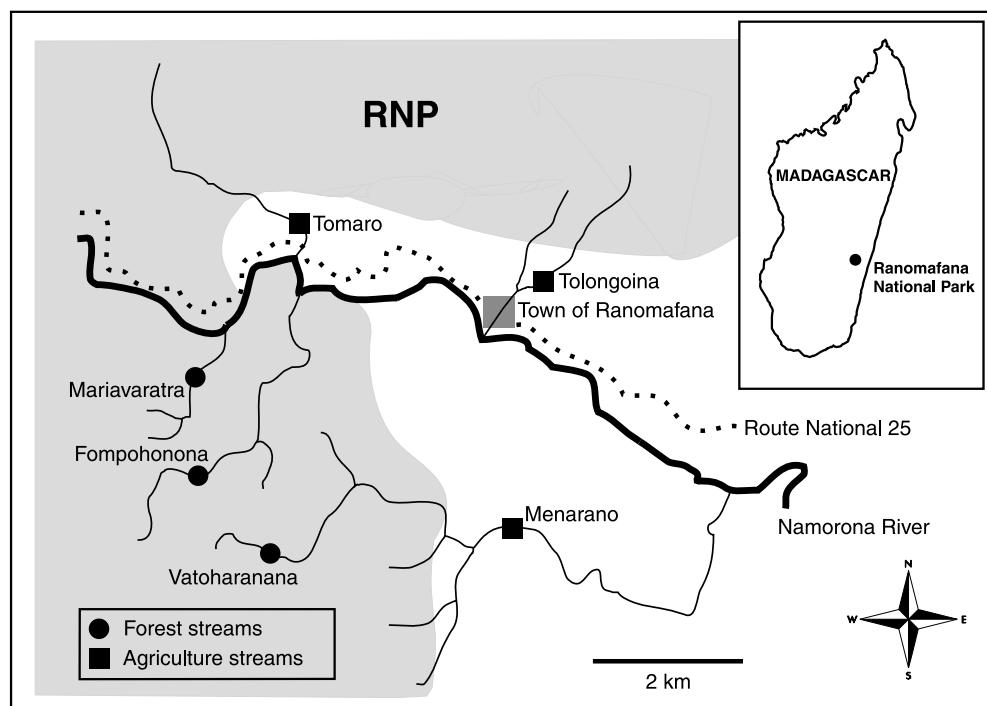
In this study, we used stable isotopes, gut analyses and biomass data to ask the following questions about macroinvertebrate communities in streams draining forested and deforested areas in eastern Madagascar: (i) how much does the relative importance of algal carbon and terrestrial carbon for food webs differ between forest streams and streams draining deforested areas? (ii) do endemic insects switch diets in response to shifts in the relative importance of basal food resources caused by deforestation? and (iii) what can species-level biomass and stable isotope data tell us about mechanisms driving the observed differences in insect community structure between the two stream types?

## Methods

### Study site

This study was conducted at 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 in eastern Madagascar. The park spans altitudes of 400–1500 m a.s.l. Vegetation consists of primary and secondary lowland and premontane tropical rainforest. The peripheral zone is a buffer area, extending 3 km from the park boundary, in which land use consists of slash-and-burn agriculture, secondary (fallow) vegetation, riparian rice paddies and remnant forest patches. Mean monthly precipitation in the region varies seasonally and can be extremely high (14–1171 mm per month, September 1992 to June 1994; Balko, 1998).

Six streams were used in the study (Fig. 1 and Table 1); three were within forest protected by RNP while three were in deforested areas within or near the peripheral zone. All were small (5.3–13.7 m mean width), fast-flowing streams with gravel, cobble and boulder substrata, at 700–1100 m a.s.l. All study streams flow into the Namorona River (approximately



**Fig. 1** Map showing location of Ranomafana National Park (RNP) in Madagascar (inset) and the six study streams. Only part of the park is shown (shaded region); the peripheral zone extends 3 km from the park boundary.

**Table 1** Description of stream reaches sampled in Ranomafana National Park and peripheral zone, eastern Madagascar, April to May 1999

Stream	Mean width* (m)	Mean maximum depth* (m)	Mean temperature (°C)	Mean conductivity ( $\mu\text{S cm}^{-1}$ )	Substratum	Mean canopy cover (%)	Land use
<i>Forest</i>							
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
<i>Agriculture</i>							
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

\*Measured at 10 transects along a 300-m study reach.

fifth order), which has seasonal flows that peak in February and March (Chaperon, Danloux & Ferry, 1993). Canopy cover ranged from 71–83% in the three forest streams and was 0–14% in the agriculture streams (Table 1). No fertilisers or pesticides are used by the region's subsistence farmers. For more information on these streams, see the paper by Benstead *et al.* (2003b)).

#### Sample collection and analysis

From each stream we qualitatively collected coarse particulate organic matter (CPOM), epilithic biofilms, fine benthic organic matter (FBOM) and seston. CPOM was collected from natural accumulations in each stream. Biofilms were scrubbed from cobbles with a stiff toothbrush and filtered onto glass fibre (GF) filters (0.7 µm nominal pore size). FBOM was washed from cobbles collected from depositional areas, passed through a 1-mm sieve and filtered onto GF filters. Seston was collected by filtering 3–4.5 L of stream water through GF filters. All samples were immediately dried at 50 °C for 72 h.

A suite of stream insects, representing all major functional feeding groups, was selected for collection from each stream (Table 2). Most of these taxa were present in both forest and agriculture streams, although they varied in biomass between stream types (Benstead *et al.*, 2003b). Depending on the size of each taxon, three to 30 individuals were collected from riffles using a Surber sampler. Guts were

removed from large taxa (*Libellula* spp., *Madachauliodes* sp. and *Leptonema* sp.). All other taxa were kept in stream water for 6–8 h to clear their guts. Samples were then dried at 50 °C for 72 h. Stable isotope samples were collected in April to May 1999, with the exception of *Chimarra* sp. from one stream and seston from two streams (collected in July 1999).

Primary consumers were collected concurrently for gut analysis. The mayfly *Elassoneuria* sp. was excluded because the final instars collected had re-absorbed their guts. With few exceptions, at least five individuals of each taxon were collected from each stream and preserved immediately in Kahle's fluid (Wiggins, 1996). We collected invertebrates for gut content and stable isotope analysis on one occasion only, potentially limiting the generality of our results (especially of gut analyses) to the season of relatively stable flow (April to November) outside the wet season. The streams we studied do not receive an annual pulse of terrestrial carbon inputs because <5% of tree species in the Ranomafana region are deciduous (D. Turk, personal communication).

Guts of large taxa (*Leptonema* and *Lepidostoma*) were removed under a stereomicroscope. Gut contents were separated from gut tissue, suspended in water, sonicated for 1 min and filtered onto 25-mm membrane filters (Gelman Sciences Metricel® (Ann Arbor, MI, U.S.A.) GN-6 gridded; 0.45-µm pore size). Filters were dried for 20 min at 40 °C, placed on slides and cleared with immersion oil. Cover slips were placed onto the filter and sealed with clear nail varnish

**Table 2** Consumers sampled for C and N stable isotopes in this study. Codes to each consumer are listed in alphabetical order and refer to Figs. 2 & 3

Code	Taxon	FFG	Mean ( $\pm 1$ SE) biomass (mg AFDM m $^{-2}$ )		Number of streams where found	
			Forest	Agriculture	Forest	Agriculture
AFR	<i>Afroptilum</i> spp. (Ephemeroptera: Baetidae)	CG	35 $\pm$ 4	409 $\pm$ 284	3	3
APH	<i>Aphelocheirus</i> spp. (Hemiptera: Naucoridae)	PP	9 $\pm$ 4	8 $\pm$ 4	3	3
CHI	<i>Chimarra</i> spp. (Trichoptera: Philopotamidae)	CF	33 $\pm$ 9	14	3	1
ELA	<i>Elassoneuria</i> spp. (Ephemeroptera: Oligoneuriidae)	CG	30 $\pm$ 13	21 $\pm$ 19	3	3
GYR	<i>Gyrocarisa</i> spp. (Trichoptera: Petrothrincidae)	Sc	10 $\pm$ 3	6 $\pm$ 4	3	3
LEP	<i>Lepidostoma</i> spp. (Trichoptera: Lepidostomatidae)	Sh	5 $\pm$ 3	6 $\pm$ 3	2	3
LEN	<i>Leptonema</i> spp. (Trichoptera: Hydropsychidae)	CF	442 $\pm$ 29	905 $\pm$ 444	3	3
LIB	<i>Libellula</i> spp. (Odonata: Libellulidae)	Pr	149 $\pm$ 70	128 $\pm$ 105	3	3
MAC	<i>Madachauliodes</i> sp. (Megaloptera: Corydalidae)	Pr	39 $\pm$ 38	95	3	1
MAD	<i>Madenemura</i> sp. (Plecoptera: Notonemouridae)	Sh	2 $\pm$ 1	0	3	0
SIM	<i>Simulium</i> spp. (Diptera: Simuliidae)	CF	17 $\pm$ 6	6 $\pm$ 3	3	2
TRI	<i>Tricorythus</i> spp. (Ephemeroptera: Leptohyphidae)	CG	51 $\pm$ 21	173 $\pm$ 48	3	3

FFG indicates presumed functional feeding group based on Merritt & Cummins (1996) and mouthpart morphology: CF, collector-filterer; CG, collector-gatherer; PP, piercing predator; Pr, predator; Sc, scraper; Sh, shredder.

(Cummins, 1973). Preparation of slides for all other taxa was similar except that gut contents were teased out directly into glycerol under a stereomicroscope.

Gut contents were separated into five diet categories: amorphous detritus (i.e. non-cellular aggregations of organic particles; Hall, Wallace & Meyer, 2000; Hart & Lovvorn, 2003), leaf and wood detritus, diatoms, filamentous algae and animal material. Gut contents were quantified using standard techniques by measuring the relative area of each diet category using a phase contrast compound microscope (100 $\times$  or 400 $\times$  magnification) equipped with a video camera and personal computer running Image-Pro<sup>®</sup> Plus image analysis software (Version 3.0.1 for Windows, Media Cybernetics, Silver Spring, MD, U.S.A.). We identified and measured at least 50 gut particles from randomly selected fields in each of four guts (two to three guts for some taxa in some streams) of each taxon in each stream (Cummins, 1973; Hall *et al.*, 2000). For each stream and insect taxon we calculated the mean percentage area of gut particles ( $n = 4$  guts for most taxa) in each of the five diet categories. In order to test for differences in diets of taxa between forest streams and agriculture streams, we compared means ( $n = 3$  for forest and agriculture streams) for each diet category in each taxon using Wilcoxon ranked-sum tests (SAS Institute Inc., 1994).

We calculated mean biomass (mg ash-free dry mass per square metre) of our focal insect taxa from

samples collected from each stream within 12 months of our isotope sampling (May to July 1998; Benstead *et al.*, 2003b). Briefly, we took 10 Surber samples (0.093 m $^2$ ; mesh 600  $\mu$ m) from the same shallow riffles sampled for the current study. Lengths of insects 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. We used mouthpart morphology and Merritt & Cummins (1996) to assign taxa to functional feeding groups. Biomass of each insect taxon was compared between forest and agriculture streams using nested analysis of variance.

Coarse particulate organic matter and FBOM samples were ground in a ball mill prior to analysis; all other samples were ground by hand using a spatula. Dried biofilm, seston and FBOM samples were first separated from GF filters using a clean razor blade. Individuals or subsamples of each taxon were combined to form a single composite sample for each stream site. Samples were weighed using a microbalance and combusted in a Carlo Erba (Milan, Italy) NA 1500 CHN analyser coupled to a Finnigan Delta C mass spectrometer (Thermo Electron Corp., Waltham, MA, U.S.A.) as a continuous flow system. A laboratory working standard (bovine liver) was placed every 12 samples. Isotope ratios are expressed as  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  (with units of permil) according to the following equation:

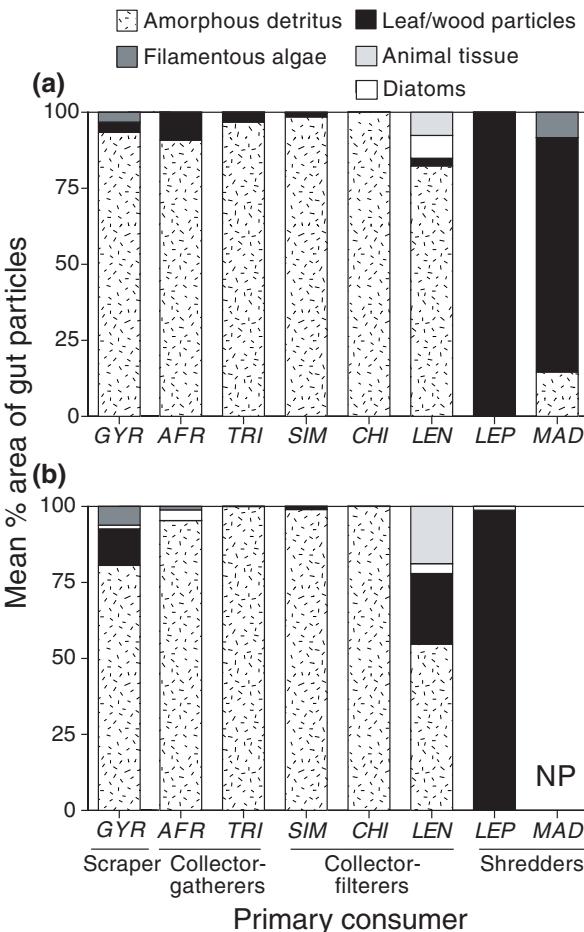
$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where  $R_{\text{sample}}$  is the  $^{13}\text{C} : ^{12}\text{C}$  or  $^{15}\text{N} : ^{14}\text{N}$  ratio of the sample and  $R_{\text{standard}}$  is the  $^{13}\text{C} : ^{12}\text{C}$  or  $^{15}\text{N} : ^{14}\text{N}$  ratio of the standard (PeeDee belemnite carbonate for  $\delta^{13}\text{C}$  and atmospheric N for  $\delta^{15}\text{N}$ ). We combined isotope and biomass data in bubble biplots ( $\delta^{13}\text{C}$  versus  $\delta^{15}\text{N}$ , with size of symbol representing relative biomass) to examine relationships between differences in biomass of insect taxa between forest and agriculture streams and their carbon and nitrogen sources.

## Results

Analysis of gut content data revealed no significant differences between forest and agriculture streams in any diet category for any of the insect taxa (Wilcoxon ranked-sum tests,  $P > 0.05$ ). With the exception of shredder taxa (*Lepidostoma* sp. and *Madenemura* sp.), all insects showed a heavy reliance on amorphous detritus (77–100% in forest streams, 47–100% in agriculture streams; Fig. 2). Guts of *Lepidostoma* sp. contained almost 100% leaf and wood particles. The other shredder, *Madenemura* sp., was absent in agriculture streams. Its diet in forest streams included leaf and wood particles with some amorphous detritus and filamentous red algae (*Audouinella* sp.). The scraper (*Gyrocarisa* sp.) consumed mostly amorphous detritus but also leaf and wood particles and filamentous green algae. The filter-feeding hydropsychid caddisfly *Leptonema* sp. was the only omnivorous consumer; its diet in both stream types included amorphous detritus, leaf and wood particles, diatoms and animal tissue. The other two collector-filterers (*Simulium* spp. and *Chimarra* spp.) had almost 100% amorphous detritus in their guts (Fig. 2).

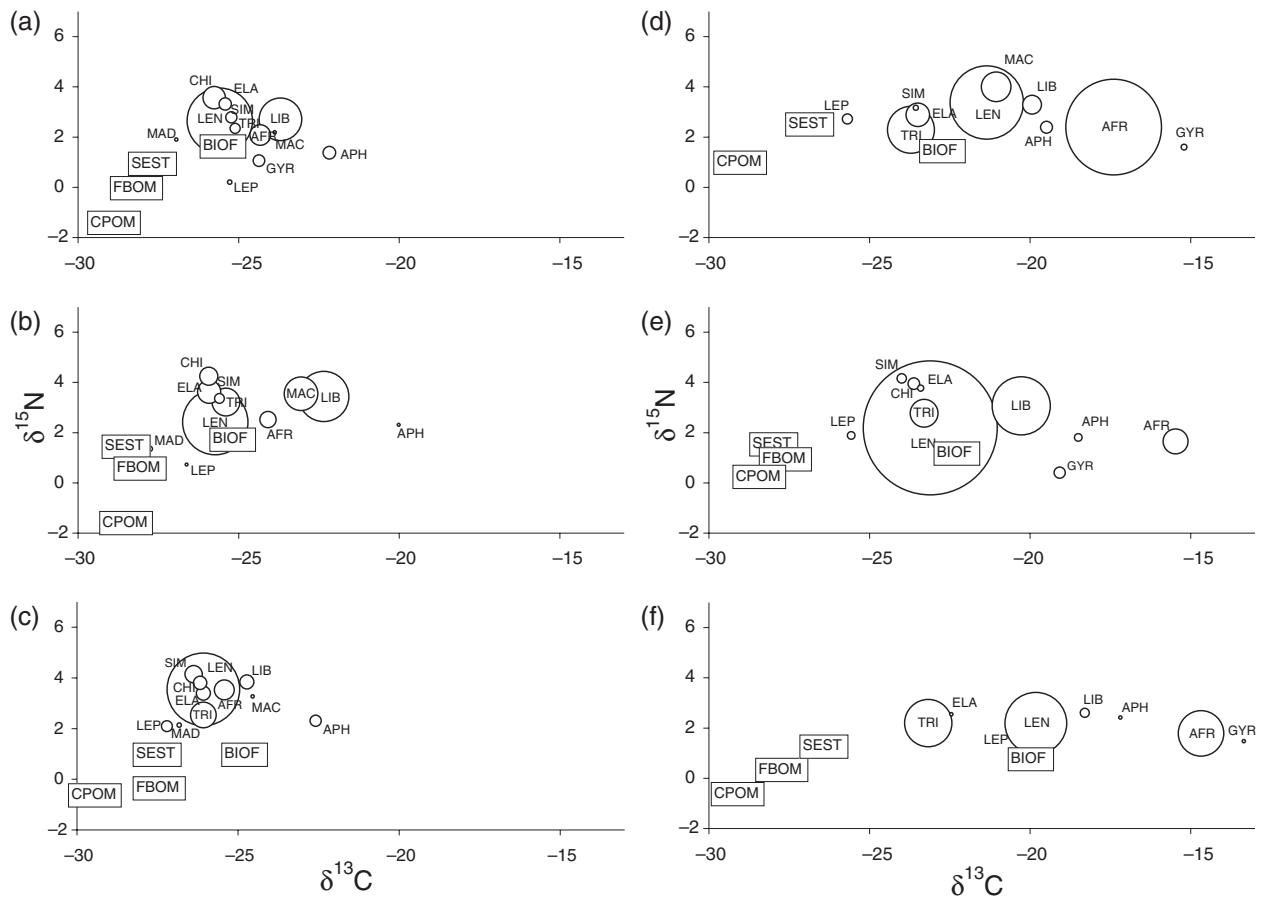
In forest streams,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of CPOM were within the range expected for terrestrial detritus (Boon & Bunn, 1994). FBOM and seston were apparently derived primarily from terrestrial CPOM (Fig. 3a–c). Biofilm in forest streams was enriched in  $^{13}\text{C}$  and  $^{15}\text{N}$  relative to other basal food resources and was within the range reported in other studies (Boon & Bunn, 1994). In agriculture streams,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of CPOM were similar to those in forest streams (Fig. 3d–f). As in forest streams, the signatures of FBOM and seston indicated that these two sources were derived from terrestrial CPOM (possibly



**Fig. 2** Mean relative proportions of food categories in guts of nine primary consumer insects in (a) forest streams and (b) agriculture streams, Ranomafana National Park, Madagascar, April to May 1999;  $n = 4$  guts for most taxa in each stream ( $n = 3$  streams of each type). GYR, *Gyrocarisa* sp.; AFR, *Afroptilum* spp.; TRI, *Tricorythus* spp.; SIM, *Simulium* spp.; CHI, *Chimarra* spp.; LEN, *Leptonema* sp.; LEP, *Lepidostoma* sp.; and MAD, *Madenemura* sp.; NP, not present.

from forested headwaters). Agriculture stream biofilm was greatly enriched in  $^{13}\text{C}$  relative to that of forest streams (Fig. 3).

Forest and agriculture streams differed in the  $\delta^{13}\text{C}$  value of their insect communities (Fig. 3). Among forest stream insects, the shredder taxa *Madenemura* sp. and *Lepidostoma* sp. were clearly obtaining energy primarily from consumption of CPOM (Figs. 2 & 3). However, isotope data indicated that both taxa, and particularly *Lepidostoma*, assimilated some algal C. Interpretation of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of other taxa was complicated by the proximity of biofilm  $\delta^{13}\text{C}$  to the  $\delta^{13}\text{C}$  of terrestrial carbon sources and by the



**Fig. 3** Stable isotope ratios ( $\delta^{15}\text{N}$  versus  $\delta^{13}\text{C}$ ) of basal resources and endemic insects from (a) Mariavaratra forest stream, (b) Fompononona forest stream, (c) Vatoharanana forest stream, (d) Tomaro agriculture stream, (e) Tolongoina agriculture stream and (f) Menarano agriculture stream, Ranomafana National Park, Madagascar, April to May 1999. Boxes are basal resources (size of boxes is arbitrary): CPOM, coarse particulate organic matter; FBOM, fine benthic organic matter; SEST, seston; and BIOF, biofilm. Circles are consumer taxa: AFR, *Afroptilum* spp.; APH, *Aphelocheirus* spp.; CHI, *Chimarra* spp.; ELA, *Elassoneuria* sp.; GYR, *Gyrocarisa* sp.; LEP, *Lepidostoma* sp.; LEN, *Leptonema* sp.; LIB, *Libellula* spp.; MAD, *Madenemura* sp.; MAC, *Madachauliodes* sp.; SIM, *Simulium* spp.; and TRI, *Tricorythus* spp. Size of circles is relative to biomass of taxa in riffles in 1998.

ambiguous sources of carbon contained within biofilms. These non-shredder taxa were assimilating either CPOM-derived sources such as seston or biofilm (which could include terrestrial carbon) or a mixture of food resources.

Trophic support of insects in agriculture streams was evidently not dominated by terrestrial sources of carbon (Fig. 3d–f). Most taxa appeared to be deriving energy from biofilm or from a mixture of biofilm and terrestrially derived carbon sources. The baetid mayfly *Afroptilum* sp. and grazing caddisfly *Gyrocarisa* sp. were greatly enriched in  $^{13}\text{C}$  compared with any food resource, suggesting reliance on a relatively enriched, unsampled component of the food web or selective assimilation of a biofilm component.

Biomass data indicated that most taxa that had relatively depleted (i.e. more terrestrial)  $\delta^{13}\text{C}$  signatures were present in agriculture streams at significantly lower biomass than in forest streams (Fig. 3; Table 2). These taxa included the shredder *Madenemura* ( $P = 0.01$ ) and the microfilterers *Chimarra* ( $P = 0.06$ ) and *Simulium* spp. ( $P = 0.0002$ ). Conversely, the baetid mayfly taxon *Afroptilum* was greatly enriched in agriculture streams and was present at significantly higher biomass ( $P < 0.0001$ ; Table 2; Fig. 3). However, the relationship between  $\delta^{13}\text{C}$  and relative biomass was not clear-cut, particularly for taxa present at relatively low biomass. For example, biomass of the shredding caddisfly *Lepidostoma* differed little between forest and agriculture

streams (Fig. 3), as did that of the scraper *Gyrocarisa*, despite its relative  $^{13}\text{C}$  enrichment in agriculture streams.

Trophic structure of the food webs was difficult to discern using isotope data and standard trophic enrichment values (Peterson & Fry, 1987). Predators were more enriched in  $^{13}\text{C}$  relative to most of their potential prey, but  $\delta^{15}\text{N}$  values in both forest and agriculture stream insects showed a high degree of overlap between primary consumers and predators (Fig. 3).

## Discussion

Our previous research showed that streams draining deforested areas outside Ranomafana National Park had insect communities very different from forest streams within the park (Benstead *et al.*, 2003b). Forest streams had taxonomically diverse communities composed mainly of collector-gatherers and collector-filterers. In contrast, deforested peripheral zone streams were dominated by mayfly collector-gatherers. Stable isotope analysis revealed that carbon sources for insects differed between forest and agriculture streams. Insects from agriculture streams appeared to be more dependent on biofilm C. The  $\delta^{13}\text{C}$  signature of forest stream biofilm was not distinct from that of CPOM, making discrimination of ultimate carbon sources (autochthonous versus allochthonous) difficult in forest streams. Epilithic biofilms are complex communities of algae, bacteria, fungi, protozoa and micrometazoa embedded in a polysaccharide matrix (Lock *et al.*, 1984). It seems probable that the  $\delta^{13}\text{C}$  signatures of biofilms in forest streams were similar to that of CPOM because of uptake and incorporation of terrestrially derived dissolved and particulate organic matter by heterotrophic components (i.e. fungi and bacteria) of biofilms in these shaded streams (Rounick & Winterbourn, 1983; Hall & Meyer, 1998). Alternatively, the  $\delta^{13}\text{C}$  of biofilm in forest streams may have reflected the true signature of the autotrophic component (i.e. epilithic algae) of the biofilm. Recent research has shown that the  $\delta^{13}\text{C}$  signatures of epilithic algal communities are positively related to gross primary productivity (GPP) because carbon ( $\text{CO}_2$ ) limitation in more productive communities results in greater incorporation of  $^{13}\text{C}$  (Finlay, Power & Cabana, 1999; Finlay, 2001). However, given the

generally low GPP rates of these biofilms ( $<20 \text{ mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ; Benstead, 2001), the relative importance of terrestrial versus algal contributions to biofilm C is a more likely explanation for differences between  $\delta^{13}\text{C}$  signatures of biofilm in forest and agriculture streams.

Although the source and trophic role of biofilm C in the forest streams was unclear because of its ambiguous  $\delta^{13}\text{C}$  signature, several lines of evidence point toward relatively greater use of biofilm as a food resource in agriculture streams. First, CPOM was clearly not a dominant resource for agriculture stream food webs. All agriculture stream taxa were dependent on biofilm, a mixture of biofilm and terrestrially derived C or unsampled (selectively grazed or assimilated) food resources that were even more enriched in  $^{13}\text{C}$  than the bulk biofilm signature. Secondly, differences in C source may partly explain differences in biomass of many insect taxa between forest and agriculture streams. Several taxa that were more dependent on relatively depleted (i.e. more negative) C sources such as CPOM (and showed small shifts in  $\delta^{13}\text{C}$  values between forest and agriculture streams) had lower biomass in agriculture streams relative to forest streams. Conversely, taxa that were more dependent on biofilm C (and showed large shifts in  $\delta^{13}\text{C}$  values between stream types) had higher biomass in agriculture streams relative to forest streams. Shifts in  $\delta^{13}\text{C}$  values indicate that insect taxa able to take advantage of increased primary productivity (in the form of algal C contained in biofilms) have greater total biomass in agriculture streams relative to forest streams. Taxa that were more dependent on forms of C that are terrestrially derived (e.g. CPOM and seston), and that cannot effectively exploit increases in primary productivity because of obligate feeding modes (i.e. shredding and microfiltering), have lower biomass in agriculture streams.

Large shifts in  $\delta^{13}\text{C}$  values in some taxa did not appear to be due to shifts in feeding mode. We found no evidence that insect feeding modes differed between forest and agriculture streams. Collector-gatherers fed on a food resource common to both stream types (i.e. amorphous detritus derived from biofilms). Stable isotope data indicated that the relative importance of algal C in biofilms was higher in agriculture streams than in forest streams. Stable isotope values of invertebrates that fed on biofilms (seen as amorphous detritus in guts) reflected this shift toward algal C. Consequently, the success of

collector-gatherer species in agriculture streams appears to be a result of their ability to capitalise on higher primary production by biofilms in streams draining deforested landscapes.

Microfiltering taxa (i.e. *Chimarra* and *Simulium* spp.) also consumed amorphous detritus (>98%) in forest and agriculture streams. However, these two collector-filterer taxa had lower biomass in agriculture streams, while collector-gatherers (i.e. *Afroptilum* spp. and *Tricorythus* spp.) consuming amorphous detritus were present at higher biomass. The origin of the amorphous detritus consumed by micro-filtering taxa was likely very different from that consumed by collector-gatherers.  $\delta^{13}\text{C}$  values showed that the presumed source of amorphous detritus for collector-filterers (seston) was apparently derived from terrestrial sources in both forest and agriculture streams. In addition,  $\delta^{13}\text{C}$  values of these two taxa were more depleted (i.e. closer to CPOM) than any other non-shredder taxa in agriculture streams. Sestonic (i.e. entrained) amorphous detritus (consumed by micro-filterers such as *Simulium* and *Chimarra* spp.) is composed of inorganic particles, organic debris and microorganisms in a mucopolysaccharide matrix and is formed by abiotic flocculation and bacterial aggregation (Carlough, 1994). In contrast, the amorphous detritus consumed by collector-gatherers is likely derived from the polysaccharide matrix and associated microbes within biofilms (Couch & Meyer, 1992; Hall & Meyer, 1998; Hart & Lovvorn, 2003). Differences in appearance of amorphous detritus between guts of collector-filterers and collector-gatherers supported this distinction (J. P. Benstead, personal observations). Collector-filterer guts contained amorphous detritus that was flocculent in appearance, with a markedly three-dimensional structure. In contrast, amorphous detritus from collector-gatherer guts had a more uniform, plate-like appearance that was indicative of its biofilm origin (Ledger & Hildrew, 2000). Comparison of these two feeding strategies illustrates the role of feeding mode in controlling relative responses of stream insect taxa to deforestation. Low abundance of insects that are dependent on seston in agriculture streams suggests that this terrestrially derived food resource may be present at lower concentrations in these streams.

The case of the stonefly shredder *Madenemura* sp. (MAD) illustrates the fate of many other forest-specialist insect taxa that we could not include in

our isotope sampling because they were not found in any agriculture stream (Benstead *et al.*, 2003b). Differences between forest and agriculture streams in the availability of CPOM may be of prime importance in explaining the absence of *Madenemura* in agriculture streams. The other shredder we included, *Lepidostoma* sp. (LEP), did not show relatively low abundance in agriculture streams. However, isotope data suggested that this taxon may assimilate more algal C than *Madenemura*. *Lepidostoma* may therefore be less vulnerable to reductions in CPOM in agriculture streams.

The  $\delta^{13}\text{C}$  signatures of *Afroptilum* and *Gyrocaris* suggested that these taxa were selectively feeding on (or assimilating) a relatively enriched component of biofilm in agriculture streams (i.e. more enriched than the bulk biofilm sample). Gut analysis showed overwhelming consumption of non-cellular, amorphous detritus by these two taxa. This detritus was likely bacteria, fungi and associated polysaccharide layers that were dependent largely on dissolved organic matter from autotrophic components of the biofilm (Haack & McFeters, 1982; Haack, Burton & Ulrich, 1988). Our results are similar to those of early stable isotope research in New Zealand streams, which are dominated by collector-gatherers. Winterbourn *et al.* (1984) found that the resource base for these taxa shifted along a stream continuum, from terrestrial C at forested headwater sites to autochthonous C at more open sites downstream. Some taxa were clearly dependent on algal C, although their guts contained mostly amorphous detritus and very few algal cells. Winterbourn *et al.* (1984) suggested that these insect taxa were feeding on epilithic organic layers (i.e. biofilms) composed of heterotrophic organisms (dependent on algal exudates for energy) and their extracellular products (i.e. polysaccharide slimes). An analogous situation is likely in our agriculture streams.

In summary, our study illustrates the utility of relating consumer biomass data to natural abundance isotope signatures. Several workers have proposed the use of abundance or biomass data in conjunction with stable isotope analysis (Rounick, Winterbourn & Lyon, 1982; Doucett *et al.*, 1996; Finlay, 2001). However, we are aware of only two previous studies that have related the biomass or secondary production of consumers to their respective natural abundance  $\delta^{13}\text{C}$  signatures (Junger & Planas, 1994; McCutchan & Lewis, 2002; but also see Lewis *et al.*, 2001). Such data

are important when comparing disturbed habitats with reference sites and where consumers have relatively inflexible feeding modes. These taxa will likely respond to decreases in food resources through declines in abundance, biomass or secondary production, not changes in  $\delta^{13}\text{C}$  signature.

The results of our study, and of related research (Benstead *et al.*, 2003b), also indicate that simplification of stream macroinvertebrate communities in eastern Madagascar, including loss of specialist (often micro-endemic) forest taxa, can be driven largely by biotic processes rather than by abiotic disturbance (e.g. sedimentation). Specifically, deforestation causes shifts in the relative importance of basal food resources that many forest-specialist species are unable to track. Overall, our results suggest that some of the negative impacts of deforestation on sensitive invertebrate taxa could be reduced by maintenance of vegetated riparian zones. Riparian vegetation would serve two important functions (Gregory *et al.*, 1991). First, vegetation would be a source of CPOM. Secondly, shading of the streambed would lower insolation and primary productivity rates. The creation and maintenance of vegetated riparian zones would likely be challenging (e.g. in eastern Madagascar, riparian areas are often used for paddy rice agriculture). However, such a measure could perhaps be integrated into development initiatives through the design of riparian zones that are economically productive while serving an ecological function. Similar forest corridor creation projects have been initiated in north-eastern Madagascar to link forest patches (Holloway, 2000). Without such steps, stream communities in Madagascar will continue to lose unique assemblages of endemic species. Our findings are also applicable to other regions. Estimates of stream transformation by tropical deforestation currently exceed  $5 \times 10^5 \text{ km year}^{-1}$  (Benstead *et al.*, 2003b). Consequently, disruption of linkages between terrestrial and stream habitats, and associated declines in freshwater biodiversity, may be widespread in the tropics.

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