INTRODUCTION

Food webs are being increasingly used by ecologists to demonstrate patterns of biodiversity and energy flow in ecosystems (Thompson et al., 2012). A significant advantage of such an approach is that food webs can generate information on community structure, competition, nutrient dynamics, and cascading effects of predation which can be difficult to detect using other methods (Winemiller et al., 2011). Furthermore, food web studies have been used to measure the effects of disturbance on aquatic systems, for example McHugh et al. (2010). showed that disturbance can have an important role in restructuring food-webs in streams. In forest stream ecosystems, food webs are typically driven by allochthonous organic inputs, (often dominated by leaf litter), as their primary energy source (Kaushik and Hynes, 1971; Vannote et al., 1980). Leaf litter is leached, colonized and decomposed by micro-organisms, and consumed by macroinvertebrate shredders (Dudgeon, 1982; Benfield, 1996; Gessner et al., 1999). As a result, leaves and wood are broken down into fine particulate organic matter (FPOM). FPOM also enter directly from the riparian zone and can be consumed by invertebrate collectors. Invertebrate shredders, grazers and collectors are the major primary consumers in forest streams, and serve as a link between basal carbon resources and the predatory invertebrates and vertebrates. The biomass of benthic algae in shaded forest streams is typically low, but may be sufficient to support populations of grazing (scraping) invertebrates (Brito et al., 2006).

Typically, food-web studies have been undertaken on small spatial scales, yet the importance of cross-ecosystem movements of materials that support local stream food-webs has been clearly demonstrated (Polis et al., 1997). Numerous studies have confirmed the importance of detrital inputs in shaping forested stream food webs (Wallace et al., 1997; Dudgeon and Wu, 1999). Food webs have also been shown to be dynamic, with taxa, links and aspects of structure changing over time and space, as demonstrated for freshwater systems by Warren (1989) and Thompson and Townsend (2012). Gut content analyses have been included in numerous studies of stream food webs to categorize the nature of materials ingested by invertebrates and fish. However, although gut content analyses provide an immediate picture of food recently ingested, they do not indicate whether the ingested materials are digested or assimilated (Rounick et al., 1982).

The aim of our study was to compare food web structure and properties in highland tropical streams flowing through catchments differing in land use. To do this we used a combination of stable isotope and gut analysis techniques. We expected that forested stream food webs would be dominated by allochthonous inputs such as coarse particulate organic matter (CPOM) and that maize streams would switch to autochthonous algae driven food webs. We also expected that maize stream food webs might be enriched with C\(_{13}\) due to maize being a C4 plant. The likely response of tea plantation streams is less...
obvious as leaching from tea plants may produce unusual effects on stream food webs.

METHODS

Study sites

The study was carried out on the Mambilla Plateau, in the south east corner of Taraba State, Nigeria (11° - 6° E and 6° - 7° N). The Plateau has a tropical montane climate. Sampling was undertaken between October 2016 and January 2017. Nine streams (second and third order) were sampled; three in forest, three in tea plantations and three in maize fields, respectively. The forested sites were within mature submontane forest in the Ngel-Nyaki Forest Reserve. Maize and tea farming are common on the Mambilla Plateau, the tea plantations being well established crops. However, cultivation of maize in the study catchments started in 2008 and since then crop planting and livestock grazing have alternated on a yearly basis (i.e., shifting cultivation). The maize crop is rarely planted right up to the stream margins and grass or shrubs form riparian buffer zones up to approximately 50 m wide between the crops (Fig. 1).

Figure 1: Location of sampling sites within the study area near Ngel-Nyaki Forest Reserve, Mambilla Plateau, Taraba State, Nigeria. Vegetation of Nigeria (White, 1983).

Trees were native Afromontane species (Deinbollia pinnata, Santiria trimera, Rafania sp., Croton macrostachyus, Anthoanta noldeae, Acacia senegalensis, Polyscios fulva, Syzygium guineense, Beilschmedia sp., Pouteria altissima and Bridelia speciosa). Bank-full stream width ranged from 4 to 12 m and substrate ranged from sand to large boulders. Basic water chemistry was similar in all nine streams; pH was 5.6–7.8, specific conductivity 30–110 µS 25 cm\(^{-1}\) and oxygen 56–80-% saturation (using digital multi-function meter, model YSI: 63-10 FT John Morris Scientific Ltd).

Basal food resources - Algae & Detritus

Basal food resources (source of carbon derived from terrestrial or in-stream producers) including fine particulate organic matter (FPOM) and algae were sampled for biomass and stable isotopes analyses. A single FPOM sample was collected from the water column at each site using plankton net (60 µm mesh), which was deployed for approximately ten minutes to collect enough material for analysis (approx. 1-2 gm DW). The FPOM sample was filtered through Advance GC50 glass fibre filters (0.5 µm pores size), oven-dried at 60°C for 48 h, and weighed. Filters were then ashed following Benfield (1996). Additional FPOM samples were collected for stable isotope
analysis following the same procedure. After filtration, the latter samples were oven-dried and ground with a pestle and mortar. For each stream, biomass of CPOM was extracted from four benthic samples taken with a hand net (30 cm x 30 cm, 500 µm mesh size). Inorganic substrates were separated from CPOM by hand-picking. Dry mass (DM) and ash-free dry mass (AFDM) of each litter sample were determined following Benfield (1996), and a single ground sample from each stream was analysed for δ15N and δ13C. Benthic algal biomass was obtained by scraping five randomly selected stones (50 mm2 each) from the stream bed using a wire brush and washing the composite slurry into pottles. These samples were later filtered using a syringe and filter paper (Whatman glass microfiber filters 0.75 µm pore size, 50 mm diameter disks) dried and weighed in the laboratory to (0.01 mg). For stable isotope analysis of filamentous algae were collected by hand, and transported in water to the laboratory. After drying, each sample (57–256 mg DM) was ground with a pestle and mortar prior to analysis of stable isotope values.

Benthic invertebrates and fish

Fish and benthic invertebrates were collected from riffles during the dry seasons (October to March) of 2016 and 2017. Benthic invertebrates were collected from 15 cobbles and boulders in riffles in each stream (n = 45 cobbles and boulders/treatment; cobbles and boulders diameters 4–35 cm) with a triangular hand net (200–400 µm mesh) placed immediately downstream. Invertebrates were placed in Eppendorf tubes, which were taken to the laboratory on ice containers. Two common species of fish, *Tilapia zilli* (Cichlidae) and *Clarias lazera* (Clariidae) were collected from pools with a hand net and used for gut content analysis and stable isotope determination. Samples collected for gut content analyses were frozen and preserved later in 70% ethanol.

In the laboratory most, benthic invertebrates were identified to family level and some to subfamily or lower. Only the most numerous taxa in each family was used in analyses. Between five to 20 individuals of common consumer taxa were gutted and examined for food contents. All predatory invertebrates and fish taxa collected were examined for gut contents, the numbers of individuals of each ranging from 10 to 15. If large numbers of individuals of a particular taxon were available (e.g., the oligoneuriid mayfly *Elassoneuria*), three to five individuals of up to three size classes were examined to assess variation in feeding with animal size. Guts of invertebrates were removed, mounted on slides in lactophenol-PVA stained with lignin pink, and examined under a Nikon SMZ 800 stereo dissecting microscope at up to 400 x magnification. Up to 10 fields were examined on each slide with a gridded reticle inserted in the eyepiece. At each grid crosshair, the four nearest food items were identified until 200 items had been identified on a slide. However, fewer than 100 items were identified on some slides from almost empty guts. Gut contents were categorised as filamentous algae, diatoms, fungi, CPOM ≥ 1 mm (usually leaf litter, wood, and gravel), FPOM < 1 mm (usually amorphous detritus) and animal parts. Most prey items were identified to family using slides and the drawings in Dudgeon (1999). The relative abundance of each category of prey type was calculated.

Stable isotope analyses

In the laboratory invertebrates were kept alive in bottles of water for ~ 15 hours to clear guts before freezing (Cummins, 1973; Parkyn et al., 2001) and were later rinsed with distilled water to remove non-animal material (e.g., detritus). Digestive tracts of the crab (*Brachyura; Potamonautidae*) were removed to avoid contamination by non-assimilated materials. Snails were decalcified with 1N HCl and rinsed in distilled water several times as in Mantel (2004). Samples of lateral muscle tissue ≥ 100 mg DM were taken from fishes, being careful to avoid bones and scales. Plant samples were rinsed and handpicked to remove biofilm, detritus and invertebrates. All samples were oven-dried at 60°C for 48 h, ground to a fine powder with a mortar and pestle, weighed and stored in Eppendorf tubes. In order to avoid contamination all grinding equipment were cleaned using 100% ethanol and Kim wipes before the grinding of a new sample. Subsamples of all animal (c. 1 mg ± 0.15 DW) and plant samples (algae, CPOM, moss) (c. 3mg DW) were used for analysis. Each individual sample was weighed to 0.1 mg. Each sample was transferred to an 8 mm x 5 mm tin capsule using a clean spatula. Tin capsules were placed in a 96-well plastic culture tray, and sent to the stable isotope facility, University of California, Davis. Results (%) are reported as δ13C and δ15N, i.e., the difference between the sample and an international standard (air for N and Peedee Belemnite for C. Analytical precision was 0.3%.

Properties of food webs

A range of food web attributes were calculated using gut content data following methods in Mantel (2004): species richness (or web size, S); number of links (or number of “ones” in the food web matrix, L); mean and maximum length of all food chains; fraction of basal species (species with no prey, i.e., basal food resources); fraction of intermediate species (species that have predators and prey); fraction of top predators not preyed upon; fraction of omnivores (animals feeding at >1 trophic level); predator-prey ratio (number of predators divided by number of prey); trophic connectance (*Ct* = L/S[S-1]; realised connectance (CR)

\[
CR = L/ S^2 - [(pp + ba)S] + (S - (pp + ba)) + (pr(pp + ba))
\]

Jaarsma et al., 1998).
The predator-prey ratio was calculated such that ‘preys’ are primary consumers and predators are ‘any species that eat prey even if they themselves are preyed upon’. The prey-predator ratio was also calculated by dividing the sum of the intermediate and basal species in the web by the sum of the top and intermediate species. Biplot of $\delta^{13}C$ and $\delta^{15}N$ values of FPOM/CPOM, algae, benthic invertebrates, and fish were used to compare patterns of isotopic variation within and between sites (forest, tea plantation and maize). Given that $\delta^{13}C$ values of dietary items are usually conserved within 1% in consumer tissues (McCutchan et al., 2003), the relative importance of alternative source of organic carbon assimilated can be assessed by the relative position of the consumer and potential food sources on the x axis of the bi-plot. In contrast to carbon isotopes, nitrogen isotope ratios of consumer tissues typically are 2.5–3.4‰ higher than tissues of their food items (McCutchan et al., 2003), enabling $\delta^{15}N$ to serve as a rough indicator of trophic position in addition to refining estimates of source contributions based on $\delta^{13}C$ values (Winemiller et al., 2011).

RESULTS

Basal food resources - algae and detritus

Significant differences in the biomass of CPOM and algae, but not FPOM were found among streams with differing land uses. CPOM was significantly higher in forest than tea plantation and maize fields’ streams, whereas, forested streams had the lowest algal biomass and maize streams the highest (Table 1).

Gut contents

Eight benthic invertebrate taxa and two fish species were used for gut analysis. They represented 75% of the total benthic invertebrates collected. Only two taxa that were found in high numbers in all three-land use system; snail Melanoides tuberculata (Thiaridae) and gynirid beetles (Table 2). The gut contents of the snail differed between forest, tea plantation and maize field streams. Individuals from the forest streams had guts filled with FPOM (65%) and diatoms (3%) and those from the tea plantation and maize sites had filamentous algae as the dominant food items (80%) with smaller amounts of diatoms (10%). The gynirid beetles had a smaller mixed diet in all three land uses dominated by FPOM, diatoms and animal parts, especially Chironominae.

The Oligoneuriid mayfly was very abundant in forested streams and also collected in tea plantation streams. Its diet was similar in both land uses and was dominated by FPOM, and diatoms, indicating it may be a filter-feeder (Table 2).

Stable isotope signatures of primary and secondary consumers

Similarly, the filter feeding hydropsychid caddisflies (of which there were at least two distinct species) were also common in forested streams. Again in both land uses they had a mixed diet of FPOM (45%) and diatoms (25%). In contrast, the gut contents of perlid stoneflies, which were found in the forested streams, were dominated by animal prey (50–90%, primarily hydropsychnids) indicating they were predators. In forested streams their gut contents were dominated by FPOM (10%) and CPOM (80%) of which 10% was wood and 70% leaves. The guts of the gomphid dragonflies were dominated by animal fragments (70%), most of which were well fragmented and difficult to identify, although Chironominae seemed an important prey (20%). Dragonfly guts also commonly contained FPOM (10%) and diatoms (10%), although these may have been accidentally ingested or in the invertebrate prey they consumed. The tipulid Leptotarsus (Tipulinae) ingested mainly CPOM (90%) 80% of which comprised leaf fragments and 10% wood in forested streams. FPOM and algae were common in maize streams. Leptotarsus seemed to be an important shredder. The two fish species Clarias lazera and Tilapia zilli consumed mainly animals (40–80% relative abundance) but also some CPOM. Dissected fish contained an average of three prey items per gut, predominantly mayfly and stonefly larvae (55–60%) (Table2).

Stable isotope values of basal food resources-algae and detritus

Biplots of $\delta^{13}C$ and $\delta^{15}N$ for basal food sources collected from riffles in forest, tea plantation and maize streams showed that FPOM was depleted in $\delta^{13}C$ enriched in $\delta^{15}N$ in forested streams compared to tea and maize streams (Fig. 2). For CPOM mean $\delta^{13}C$ and $\delta^{15}N$ values were intermediate in maize and tea streams but less enriched in forested streams (Fig. 2). Algae showed no difference in $\delta^{15}N$ between land uses, however again forested streams were depleted in $\delta^{13}C$.

Table 1: Mean biomass (± SE, n = 3 streams per land use) of basal food resources in streams across three land uses. FPOM = fine particulate organic matter, CPOM = coarse particulate organic matter, * indicates significant difference $p < 0.05$ and ** $p < 0.01$.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Forest</th>
<th>Tea</th>
<th>Maize</th>
<th>F - stat</th>
<th>P - value</th>
</tr>
</thead>
<tbody>
<tr>
<td>FPOM (g/L)</td>
<td>4.0 (1.3)</td>
<td>3.0 (0.2)</td>
<td>1.3 (0.1)</td>
<td>0.187</td>
<td>0.834</td>
</tr>
<tr>
<td>CPOM (g/m²)</td>
<td>6.0 (1.0)</td>
<td>3.2 (0.3)</td>
<td>2.0 (0.2)</td>
<td>8.727</td>
<td>0.016*</td>
</tr>
<tr>
<td>Algae (DW g/m²)</td>
<td>2.2 (0.3)</td>
<td>3.0 (1.0)</td>
<td>5.0 (0.4)</td>
<td>37.599</td>
<td>&lt; 0.001**</td>
</tr>
</tbody>
</table>
Table 2: Dominant food found in the guts of each taxon within land use (R = rare, < 5%; C = common, 5–20%; A = abundant, > 20%). – = absent. Prey – indicates invertebrate prey taxa able to be identified in guts.

<table>
<thead>
<tr>
<th>Land use</th>
<th>Consumer</th>
<th>CPOM</th>
<th>FPOM</th>
<th>Fil. algae</th>
<th>Fungi</th>
<th>Diatoms</th>
<th>Prey</th>
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<tr>
<td>Forest</td>
<td>Gomphidae</td>
<td>R</td>
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<td>R</td>
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<td>Chironomidae</td>
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<td>Hydropsychidae</td>
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<td>R</td>
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<td></td>
<td>Oligoneuriidae</td>
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<td></td>
<td>Perlidae</td>
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<td>R</td>
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<td>Chironominae</td>
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<td></td>
<td>Potamonautidae</td>
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<td>R</td>
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<td></td>
<td>Tipulidae</td>
<td>A</td>
<td>R</td>
<td>R</td>
<td>C</td>
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<td>M. tuberculatus</td>
<td>A</td>
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<td>R</td>
<td>C</td>
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<td></td>
<td>Tilapia zilli</td>
<td>–</td>
<td>C</td>
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<td>R</td>
<td>Perlidae</td>
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<td></td>
<td>Clarias lazera</td>
<td>C</td>
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<td>R</td>
<td>–</td>
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<td>Tilapia zilli</td>
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<td>C</td>
<td>C</td>
<td>R</td>
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<td></td>
<td>Clarias lazera</td>
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<td>B</td>
<td>C</td>
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<td></td>
<td>Clarias lazera</td>
<td>–</td>
<td>C</td>
<td>B</td>
<td>B</td>
<td>A</td>
<td>Chironomidae</td>
</tr>
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</table>

Figure 2: δ¹³C and δ¹⁵N biplots of algae, FPOM and CPOM collected from riffles in streams flowing through; F = continuous forest, T = tea plantation = and M = maize field on the Mambilla Plateau. Mean ± SE, n = 3.

For primary consumers (e.g., snails, mayflies and tipulids) δ¹³C and δ¹⁵N signatures were generally similar, with δ¹³C values varying little between consumers in differing land uses (Fig. 3). One notable exception was the mayflies which were highly enriched in δ¹⁵N in forested streams consistent with the high δ¹⁵N signature of FPOM and algae in these systems and with filter feeding by the mayfly Elasseoneuria. In contrast, the snails in maize streams had the lowest δ¹⁵N (Fig. 3).

For the main predators and omnivores (dragonfly larvae, crabs and fish) considerable overlap occurred between species across land uses (Fig. 4).
Fish had strongly enriched δ\(^{15}\)N signatures (10–12‰), which overlapped among land use types. In contrast, δ\(^{13}\)C values were similar although forested stream fish were slightly depleted in δ\(^{13}\)C (Fig. 4). Of the other taxa, the crabs in tea plantations had markedly lower δ\(^{15}\)N signatures indicating greater consumption of algae and FPOM in these streams. The isotope signatures of the predators and omnivores integrate dietary pathways within food webs and the results indicate they fed on a variety of prey consuming varying amount of allochthonous and autochthonous carbon.

Food web attributes differed significantly between land uses (\(F_{2,6} = 8.812, P = 0.016\)). Forested streams had significantly larger food webs (a mean of 26 taxa) compared to tea and maize which had means of 17 and 16 taxa, respectively (Table 3). Similarly, the number of links (L) were also, highest in the forest (mean 183) followed by the tea plantation (mean of 114) whereas in maize fields it was lowest (mean 79). Maximum chain length (MCL) was similar for both forest and tea plantations (mean 3) but differed with maize field (mean 2). Predator: prey ratio was highest in maize field streams (mean 4) but little difference was observed between forested streams and tea plantation streams. Trophic connectance (CT), realized connectance (CR) and linkage density (L/S) did not differ between the three (forest, tea plantation and maize fields) stream types. However, linkage complexity (SCR) differed significantly in the three streams (\(F_{2,6} = 8.812, P = 0.016\)).

**DISCUSSION**

Streams in all three land uses included a range of basal food resources including FPOM, CPOM and algae and the gut analyses indicated that bacteria and fungi were also common. Not surprisingly, CPOM biomass was significantly higher in the forested streams than in the other land uses whereas algal biomass was significantly higher in the maize streams. The food webs of forested, tea plantation and maize fields streams on the Mambilla Plateau also incorporated an assemblage of insect crustacean and mollusc primary consumers, predatory insects, carnivorous fish and omnivorous crustaceans. There were a number of limitations in our food web calculations. The values estimated for all three food webs will have been affected by limitations in the taxonomic resolution for different taxonomic groups. For example, we were not able to identify and count different diatoms, filamentous and other algal taxa within each food web. However, the results fall within the range reported by Dudgen et al. (2010). The dominance of oligoneuriid mayfly (Ellassoneuria) which is probably a filter-feeder in forested streams resulted in FPOM being an important resource. Omnipvory appeared to be uncommon in the food webs of the three types of streams in our study on the Mambilla Plateau. Crabs were collected in forested streams, and were probably omnivorous, the gut content data showed ingestion of CPOM, FPOM and algae and limited animal fragments. However, the isotope data indicated they were enriched in δ\(^{15}\)N so they may also feed on primary consumers.

Based on the gut content analyses, the relative contributions of dominant food sources in the three stream types (forest, tea plantation and maize) showed that CPOM and FPOM were dominant in forested streams, whereas in the tea plantation streams filamentous algae and fungi dominated most consumers’ guts. However, in maize field streams filamentous algae and fungi were more important as food sources for animals. Ultimately, we require a better understanding of how human disturbances such as habitat destruction affect reciprocal flows of invertebrates and other resource subsidies between linked stream and riparian habitats. Converting riparian forest to grassland can alter terrestrial invertebrate inputs to streams, thereby restructuring stream food webs (Baxter et al., 2004). However, riparian disturbance can also affect many other factors including light, temperature, and channel morphology, so research is needed to assess interactions between these and allochthonous inputs.

The present study was undertaken to determine whether a combination of stable isotope ratios and gut content analyses could provide measures of food web structure in tropical highland streams draining catchments in which land use differed. Our results tend to support generalizations made for other tropical stream ecosystems, in that they were neither simple in trophic structure nor could they be characterised as having a limited array of feeding interactions. Although macro-consumers (crabs) could be common at our sites, insect larvae and snails were the
predominant primary consumers. Additionally, our results, especially the gut analyses, suggested that autochthonous resources may have been of greater importance in supporting aquatic invertebrate populations in forested streams.

ACKNOWLEDGEMENTS
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REFERENCES


