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Land use and the ecology of benthic macroinvertebrate assemblages of high-altitude rainforest streams in Uganda

AVENTINO KASANGAKI*, LAUREN J. CHAPMAN† AND JOHN BALIRWA‡
*Institute of Tropical Forest Conservation, Mbarara University of Science & Technology, Kabale, Uganda
†Department of Biology, McGill University, Montreal, PQ, Canada
‡National Fisheries Resources Research Institute, Jinja, Uganda

SUMMARY

1. In sub-Saharan Africa, tropical forests are increasingly threatened by accelerating rates of forest conversion and degradation. In East Africa, the larger tracts of intact rainforest lie largely in protected areas surrounded by converted landscape. Thus, there is critical need to understand the functional links between large-scale land use and changes in river conditions, and the implications of park boundaries on catchment integrity.
2. The objective of this study was to use the mosaic of heavily converted land and pristine forest created by the protection of the high-altitude rainforest in Bwindi Impenetrable National Park, Uganda to explore effects of deforestation on aquatic systems and the value of forest in buffering effects of adjacent land conversion. A set of 16 sites was selected over four drainages to include four categories of deforestation: agricultural land, deforested upstream (of the park boundary), forest edge (park boundary) and forest. We predicted that forest buffer (downstream or on the edge) would moderate effects of deforestation. To address this prediction, we quantified relationships between disturbance level and both physicochemical characters and traits of the macroinvertebrate assemblages during six sampling periods (February 2003 and June 2004).
3. Results of both principal components analysis and cluster analyses indicated differences in limnological variables among deforestation categories. PC1 described a gradient from deforested sites with poor water quality to pristine forested sites with relatively good water quality. Agricultural sites and deforested upstream sites generally had the highest turbidity, total dissolved solids (TDS), and conductivity values and low transparency values. Forest sites and boundary site groups generally exhibited low turbidity, TDS, and conductivity values and high water transparency values. Sites also clustered according to deforestation categories; forest and forested edge sites formed a cluster independent of both agricultural land and deforested-upstream.
4. Water transparency, water temperature, and pH were the most important factors predicting benthic macroinvertebrate assemblages. Sensitive invertebrate families of Trichoptera, Ephemeroptera, Plecoptera, and Odonata dominated forested sites with high water transparency, low water temperature, and low pH while the tolerant families of Ephemeroptera, Diptera, Hemiptera, and Coleoptera were abundant in agriculturally impacted sites with low water transparency, high water temperature, and high pH.
5. This study provides support for the importance of riparian buffers in moderating effects of deforestation. Forest and forested edge sites were more similar in both limnological and

Correspondence: Aventino Kasangaki, Institute of Tropical Forest Conservation, Mbarara University of Science & Technology, PO Box 44, Kabale, Uganda. E-mail: kasangaki@itfc.org

macroinvertebrate assemblage structure than sites within or downstream from agricultural lands. If the protected area cannot encompass the catchment, the use of rivers as park boundaries may help to maintain the biological integrity of the rivers by buffering one side of the watercourse.

Keywords: aquatic invertebrates, deforestation, East Africa, tropical streams, water quality

Introduction

Fresh waters, in particular freshwater streams, are among the most threatened habitat types in the world (Hering *et al.*, 2006), illustrated most poignantly in a 50% decline in the Living Planet Index for freshwater ecosystems (an indicator of trends in populations of vertebrate species) between 1970 and 2000 (Millennium Ecosystem Assessment, 2005). As anthropogenic land disturbance continues to increase worldwide, aquatic scientists are faced with the challenge of determining how human activities influence the structure and function of aquatic ecosystems and the potential for restoration of impacted waters (Sutherland, Meyer & Gardiner, 2002). Key to this is an understanding of the functional links between large-scale land use and changes in the physicochemical conditions and biotic assemblages of rivers.

In sub-Saharan Africa, tropical forests are increasingly threatened by accelerating rates of forest conversion and degradation, with recent estimates suggesting a conversion rate of 0.4–0.5% per year (Lanly, Singh & Janz, 1991; FAO, 1993; Mayaux *et al.*, 2005). The situation is particularly severe in East Africa, where many remaining forests are islands of forest surrounded largely by converted land. It is estimated that only 28% of the original rain forests that covered East Africa remain (Martin, 1991); with the majority of land clearing associated with subsistence farming and fuelwood harvest. A predictive model by Barnes (1990) estimates that by 2040, East African forests will have lost 95% of their area. Uganda has experienced an annual loss of an average of 86 400 ha of forest – or 2.1% of forest cover-per year between 2000 and 2005 (FAO, 2005). Forest clearance clearly represents an accelerating threat to freshwater systems in East Africa, and these systems, in turn provide important indicators of land use and cover change.

Deforestation has several potential impacts on the physicochemical conditions of streams and can reduce the biological integrity of water-courses (Roy *et al.*, 2003). Removal of vegetation decreases evapotranspiration, increases rates of runoff and sediment yield, and can affect hydrology and discharge regimes (Pringle & Benstead, 2001; Chapman & Chapman, 2002; Reinthal, Riseng & Sparks, 2003). In many tropical forested and savanna rivers, annual sediment yield is low; however, sedimentation increases dramatically in forested rivers following deforestation (Chapman & Chapman, 2002). Reduced evapotranspiration increases mean discharge and rates of runoff, leading to a more peaked hydrograph with high erosional power and extreme discharge response to storms (Ross, Thornes & Nortcliff, 1990; Bruijnzeel & Critchley, 1994), and an increase in total annual water yield. Removal of riparian vegetation can also lead to higher water temperature and larger diel temperature fluctuations in both temperate (Swift & Messer, 1971; Swift, 1983) and tropical (Reinthal *et al.*, 2003) streams.

The physicochemical changes induced by deforestation can affect the structure of aquatic communities (Gurtz & Wallace, 1984; Noel, Martin & Federer, 1986). Increased sedimentation and higher turbidity can reduce light penetration and lead to a decline in plankton; high sedimentation rates can also lead the disappearance of benthic rheophilic animals that are sensitive to mud on their integument and gills or lose their interstitial habitats to accumulations of silt (Chutter, 1968; Burns, 1972; Marlier, 1973; Welcomme, 1983). These include insect groups like the Ephemeroptera, Plecoptera, and Trichoptera. Severe forest modification can result in shifts to invertebrate communities dominated by small burrowing forms (e.g. larval chironomids) that may be less available to foraging fishes (Pringle & Benstead, 2001). Sporadic peaks in discharge have negative impacts on algal, insect and fish biomass (Chapman & Kramer, 1991; Pringle & Benstead, 2001). High intensity logging or clear-cut felling can also result in a dramatic decline in deadfall that creates structure for fishes and other aquatic organisms (Chapman & Chapman, 2003).

Given the small extent of rainforests in East Africa and the high intensity of conversion, studies of deforestation effects on aquatic communities are critical. Many of the larger tracts of rainforest in East Africa lie within protected areas (e.g. Kibale and Bwindi National Parks, Uganda). However, it is rare that the location of parks or other protected areas has been designed to protect aquatic systems. Even when catchments have entered into the equation, it is often only the uppermost reaches that are protected (e.g. Rwenzori Mountains National Park, Uganda, Chapman & Chapman, 2003), or rivers may run through large tracts of degraded land before entering the protected areas. In addition, rivers may serve to designate protected area boundaries and run adjacent to converted lands. Inappropriate designation of conservation areas and insufficient recognition of biophysical processes has been an impediment to freshwater conservation (Thieme *et al*., 2005). Because streams and rivers accumulate and absorb the impacts of terrestrial degradation over large spatial scales, protected forest inside park boundaries may be impacted by upstream deforestation or the deforestation of riparian zones along rivers that designate boundaries between the park and adjacent areas of heavy land use.

The objective of this study was to use the mosaic of heavily converted and pristine forest created by the protection of a high-altitude rainforest in Uganda to explore effects of deforestation on aquatic systems and the value of forest in buffering effects of adjacent land conversion. To meet this goal we quantified environmental correlates of deforestation in the rainforest in Bwindi Impenetrable National Park (Uganda) and surrounding areas and the response of benthic macroinvertebrate communities to stream degradation. A set of sites was selected over four drainages to include a range of land conversion scenarios from undisturbed rainforest to agricultural land. Specifically, we looked at four categories of deforestation: agricultural land, degraded upstream (of the park boundary), forest edge (park boundary) and forest. We predicted that forest buffer (downstream or on the edge) would moderate effects of deforestation. To address this prediction, we quantified effects of disturbance level on a suite of physicochemical variables and characteristics of the benthic macroinvertebrate assemblages, and we described the major environmental gradients of variation among sites. We focused on macroinvertebrate communities because they have proven to be particularly effective biological indicators, reflecting alterations in stream habitat and water quality associated with land use and associated influx of nutrients and pollutants into the basin (Stone & Wallace, 1998; Sponseller, Benfield & Valett, 2001; Kasangaki *et al*., 2006). In addition, Kasangaki *et al.* (2006) found that water quality characters within Bwindi National Park related to characteristics of benthic macroinvertebrate communities. We build on this earlier study to specifically explore the link between deforestation categories and both water quality and macroinvertebrate assemblage structure.

Methods

Study area

Field sampling was conducted between February 2003 and June 2004 covering three dry and three wet seasons (six sampling occasions, i.e. February, May, August, November 2003, February and May 2004) at the Bwindi Impenetrable National Park, Uganda (BINP; 0°53′ to 1°18′S and 29°35′ to 29°50′E) and in its peripheral zone (Fig. 1). Physicochemical data were averaged across the six sampling periods to produce mean values for each site. BINP is a 331-km^2 park in south-western Uganda that spans an altitudinal range of 1200–2607 m a.s.l. Vegetation consists of tropical moist high montane forest with a mixture of bamboo forest at high elevation. There are also high-altitude swamps at about 2000 m a.s.l. and papyrus swamp and grassland areas at the lower altitudes. In the north sector of the park where this study was carried out, medium- and low-elevation forest dominate. This area is dominated by stands of *Parinari excelsa* along the valleys of the rivers Ishasha and Ihihizo. Other dominant canopy trees in the North sector include *Entandrophragma excelsum* Dawe & Sprague, *Aningeria adolfi-friederici* Robyns & Gilbert, *Newtonia buchananii* Gilbert & Boutique, *Symphonia globulifera* L. and *Ocotea usambarensis* Engl. (WWF & IUCN, 1994). BINP was heavily logged in the past before it was gazetted as a national park in 1991. The park status gave Bwindi a higher protection status than it had historically. Areas of intensive logging were mainly close to the forest edge, while selective logging occurred in the forest interior for high-value timber species (Howard, 1991). Because of the high

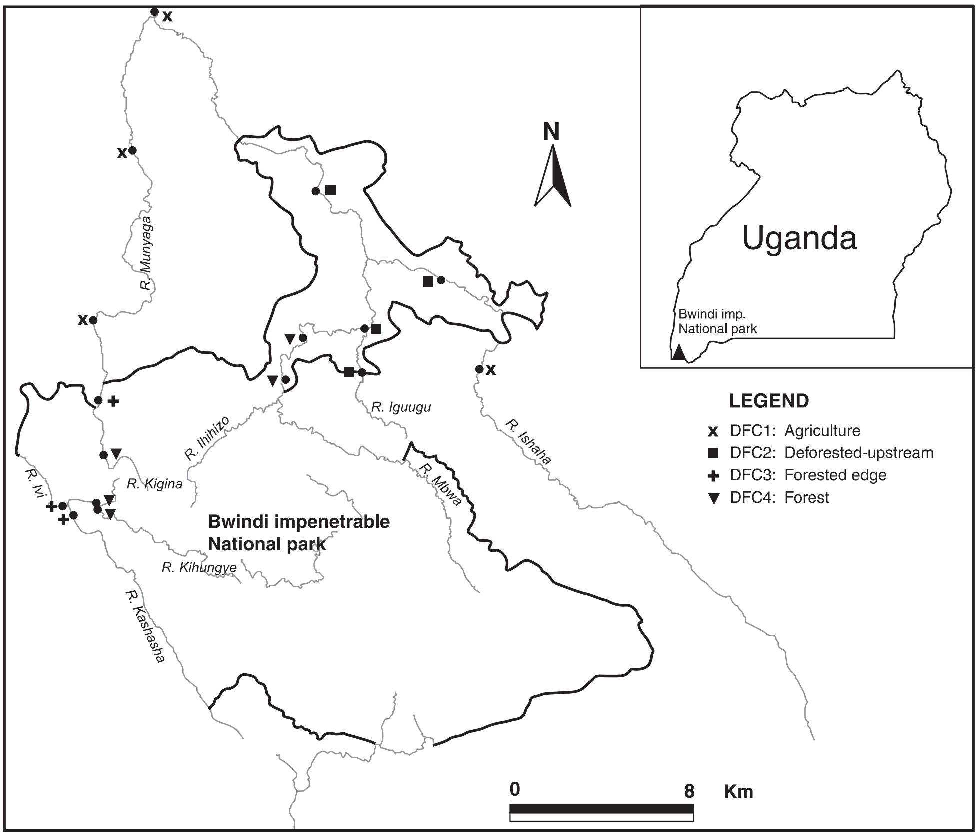

Fig. 1 Rivers of Bwindi and surrounding areas showing study sites (dark circles). Deforestation categories are indicated by the symbol next to each site.

population around the park, there is almost no forested land left outside the park, with very intensive cultivation up to the park boundary. This intensive cultivation on very steep slopes has been of great concern because of the potential for high levels of runoff and sedimentation and resultant effects on streams draining the area.

Four rivers were selected to cover an altitudinal range along a disturbance gradient from intact forested sites to degraded sites (Fig. 1, Table 1). All study rivers flow into Lake Edward to the north and include: River Ishasha (1), River Ihihizo (2), River Munyaga (3) and River Ivi (4). Sites on each of the rivers were placed into one of the four deforestation categories: agricultural land (sites IS1, IS4, MN3 and MN4), degraded upstream (IS2, IS3 and IGG), forest edge (MN2, IVI and KAS) and forest (IH1, IH2, IH3, MN1, KH1 and KH2) (Table 1), with four sites on each river system.

Stream order at the sites ranged from 2 to 5 following the Strahler (1964) classification method.

Table 1 Site name, site code, stream number, deforestation category, site elevation, and land use at study sites in rivers in and near Bwindi Impenetrable Forest, Uganda

Site name	Site code	River of origin (River no.)	Deforestation category	Altitude (m)
Ishasha 1	IS1	Ishasha (1)	1	1535
Ishasha 2	IS2	Ishasha (1)	2	1450
Ishasha 3	IS3	Ishasha (1)	2	1300
Ishasha 4	IS4	Ishasha (1)	1	1120
Iguugu	IGG	Ihihizo (2)	2	1560
Ihihizo 1	IH1	Ihihizo (2)	4	1570
Ihihizo 2	IH2	Ihihizo (2)	4	1510
Ihihizo 3	IH3	Ihihizo (2)	4	1450
Munyaga 1	MN1	Munyaga (3)	4	1560
Munyaga 2	MN2	Munyaga (3)	3	1500
Munyaga 3	MN3	Munyaga (3)	1	1420
Munyaga 4	MN4	Munyaga (3)	1	1190
Kihungye 1	KH1	Ivi (4)	4	1500
Kihungye 2	KH2	Ivi (4)	4	1480
Kashasha	KAS	Ivi (4)	3	1435
Ivi	IVI	Ivi (4)	3	1430

Deforestation category 1 = agricultural land, 2 = degraded (deforested) upstream, 3 = forested edge, and 4 = forest.

Width across the river sites ranged from 3.5 m at IGG to 23.1 m at IH2 site, and water depth ranged between 0.22 m at IGG and KAS sites to 1.33 m at IS1 and IH3 sites. Both wetted stream width and mean river depth varied seasonally, increasing in the rainy season and decreasing in the dry season. All study sites were located within an altitudinal range of 1120 m at IS4 to 1570 m a.s.l. at IH1. River gradients (slope) ranged from 2 to 5°.

Field and habitat sampling

Dissolved oxygen concentration (mg L^{-1}), conductivity (μS cm^{-1}), pH, turbidity (NTU), and water temperature (°C) were measured at sites using standard limnological equipment. At each site, we marked three cross-stream transects at the start, middle and end of 100-m stream reaches. Environmental variables were measured at three microsites on each transect and averaged to produce a site mean for each sampling period. Environmental variables were measured at a standardized time between 08:00 and 10:00 hours, because there is little diel variation in limnological characters in these fast flowing waters. Dissolved oxygen concentration (mg L^{-1}) was measured using a dissolved oxygen meter (Model 76390 YSI 95; Forestry Suppliers, Jackson, MS, USA); conductivity (μS cm^{-1}) and water temperature (°C) were measured using a YSI 30 Model 76244; and pH was measured using a digital pH testr 2 (Model 76072 Oakton; Forestry Suppliers). Water transparency was measured using a transparent tube, 1.6 m long with a miniature Secchi disc at the bottom. The water sample was poured into the tube until the Secchi disc viewed through the water sample disappeared; and depth of the water was read off from the cm-graduation on the side of the tube, providing an index of transparency, up to a maximum of 160 cm. Turbidity (NTU) and total dissolved solids (TDS) (ppm) were measured using digital meters (models MicroTPI and TDS Testr Low+, Forestry Suppliers). Discharge was estimated from the product of velocity and cross-sectional area of the river by timing the flow of buoyant sticks over a 5-m stretch (Gore, 1996). Water current was estimated using a categorical scale of 1–5 from still water to torrent (1 = low flow, 2 = medium flow, 3 = high flow, 4 = very high flow and 5 = torrential water). Mean depth, current, stream width, and substratum type were measured by cross-stream transects located at the start, mid and end of stream reaches. Riparian canopy cover was measured using a spherical densiometer in four directions at midstream at the middle transect, and an average was calculated for the site. To minimize interobserver variation in measurements, readings were taken by the same person throughout the study period. Gradient (°) was determined from an average of three replicates at start, middle, and end of stream reach using a clinometer. Variables such as type of riparian vegetation and substratum type were measured on categorical scales. Type of riparian vegetation was accorded values from 1 to 6 representing a gradient from crops as the main vegetation on riverbanks to tropical moist high forest. Substratum type was given values based on the two most dominant substratum types; these were, sand and mud = 1, silt and sand = 2, stones and sand = 3, stones and gravel = 4, stones and boulders = 5, boulders and rock = 6. Substratum type was estimated across the three transects.

Benthic macroinvertebrate sampling

A Surber sampler was used to collect aquatic insects following the method of Kasangaki *et al.* (2006). Samples were taken within a 100-m stretch of the study reach at a microsite that contained a representative substratum composition. The microsite was selected where the current was low with a mixture of substratum types at the stream edge. The same sampling site was used during each sampling period. The collected invertebrates were then sorted from debris and preserved in 5% formalin for identification. The invertebrates were later identified to family level (95.5% of taxa) where possible following Merritt & Cummins (1996) and Thirion, Mocke & Woest (1995). The numbers of invertebrates of each particular taxon were summed over the six sampling periods to represent the site.

Data analyses

To describe the variation in environmental variables across sites, means and ranges of all measured environmental variables were calculated for the 16 study sites. The major relationships among environmental variables were assessed using a Pearson's correlation matrix.

Principal components analysis (PCA) was used to describe the major environmental gradients of variation among the sites. For this analysis, the mean of each variable across the six sampling periods was used. Variables were examined for normality by visual inspection of normality on histograms fitted with normal curves; these were $\log_{10}(x + 1)$ transformed where appropriate and then relativized using the standard deviation. This transformation results in all variables having mean = 0 and variance = 1, and is considered very useful for environmental variables as it places them on equal footing (McCune, Grace & Urban, 2002). PCA was performed on 20 environmental variables representing various spatial scales from catchment characteristics to instream habitat and ecology. Only principal components (PCs) with eigenvalues >1 were retained for interpretation. Loadings were qualitatively designated as high for absolute values >0.60 (May & Brown, 2002). Factor scores in PCA were saved as variables and later used to plot sites according to deforestation category and stream of origin.

Cluster analysis using Ward's linkage and the Euclidean distance measure of dissimilarity was used to explore the relationships between sites and their environmental variables and between sites and the benthic macroinvertebrate assemblage. This analysis was also used to examine the degree to which sites clustered according to deforestation categories and stream of origin. The analysis of similarities test (ANOSIM) was used to determine whether significant differences in invertebrate assemblage composition and physicochemical variables occurred among deforestation categories (Clarke & Warwick, 1994). ANOSIM analyses were carried out using PAST Version 1.73 (Hammer, Harper & Ryan, 2007).

ANOVA was used to detect differences among deforestation categories (nested within river of origin) in three macroinvertebrate biotic indices [%Ephemeroptera, %Trichoptera and %Ephemeroptera/Trichoptera/Plecoptera (%EPT)]. Canonical correspondence analysis (CCA) was used to explore the relationships between environmental variables and benthic macroinvertebrate assemblages and was carried out in the CANOCO (ter Braak, 1987) program Version 4.5. A Monte Carlo permutation test with 499 permutations was used to test whether benthic macroinvertebrates were related to environmental variables on the first axis eigenvalue and the trace, the sum of all eigenvalues (ter Braak & Verdonschot, 1995).

Results

Effects of land-use on stream ecology

Across the 16 sites examined, conductivity was relatively low ranging from 22.7 to 145.6 μS cm^{-1}. TDS varied from extremely low concentrations (18.6 ppm) to 103.5 ppm. Turbidity exhibited a very high range from extremely clear water (1.8 NTU) to highly turbid conditions (69.4 NTU). Water transparency showed a similar pattern as turbidity ranging from 17.9 cm in a highly turbid site to 160 cm in the clearest waters with the lowest turbidity (Table 2). Water temperature ranged from 16 to 19.6 °C, while dissolved oxygen concentration was consistently high ranging from 7.4 to 8.3 mg L^{-1}. pH at all sites was acidic and ranged from 4.3 to 6.9 (Table 2).

Environmental variables including conductivity, TDS, turbidity and water transparency that are indicative of human impacts in the catchment, were correlated ($r > 0.700$, $P < 0.001$). Percentage canopy cover was negatively related to TDS, conductivity, and turbidity, and positively correlated with water transparency (TDS: $r = -0.270$, $P = 0.030$; conductivity: $r = -0.250$, $P = 0.020$; turbidity: $r = -0.260$, $P = 0.030$; transparency: $r = 0.370$, $P < 0.001$). Water temperature varied positively with most water quality variables, but was negatively correlated to water transparency and canopy cover (transparency: $r = -0.400$, $P < 0.001$; cover: $r = -0.500$, $P < 0.001$).

Principal components analysis yielded five principle components with eigenvalues >1, which explained 83% of the variance in the data. Variable loadings of the first three principle components are given in Table 3 and variables that had loadings of absolute values >0.6 were designated as high. The first three PCs accounted for 34%, 23% and 12% of the variance, respectively. The fourth and fifth components together explained 15% of the variance in the data.

Variables that loaded highly on PC1 included turbidity, conductivity, TDS, water transparency, elevation, canopy cover and riparian vegetation (Table 3). PC1 described a gradient from deforested sites with poor water quality to pristine forested sites with relatively good water quality (Fig. 2). Agricultural sites and deforested upstream sites generally

Table 2 Mean and range (in brackets) for physicochemical characteristics of 16 river sites within and near the Bwindi Impenetrable Forest of Uganda.

Sampling sites	IS1	IS2	IS3	IS4	IGG	IH1	IH2	IH3	MN1	MN2	MN3	MN4	KH1	KH2	KAS	IVI
Stream width (m)	5.3 (3.7–6.6)	8.7 (7.0–9.5)	14.4 (13.8–15.0)	16.2 (14.6–17.3)	4.3 (3.5–5.1)	9.4 (8.1–10.1)	16.1 (9.1–23.1)	12.4 (9.1–18.5)	4.9 (4.2–5.7)	8.1 (7.2–10.2)	5.0 (4.4–6.0)	7.2 (6.2–8.1)	8.8 (8.4–9.4)	7.8 (7.4–8.3)	6.3 (5.9–6.6)	10.3 (9.8–10.9)
Stream depth (m)	0.82 (0.36–1.33)	0.56 (0.35–0.73)	0.62 (0.55–0.79)	0.70 (0.59–0.85)	0.35 (0.22–0.47)	0.53 (0.32–0.77)	0.58 (0.40–0.72)	0.8 (0.64–1.33)	0.38 (0.30–0.47)	0.51 (0.28–0.72)	0.47 (0.26–0.77)	0.41 (0.35–0.48)	0.49 (0.30–0.61)	0.44 (0.24–0.60)	0.40 (0.22–0.47)	0.53 (0.46–0.60)
Stream discharge ($m^3 s^{-1}$)	2.75 (0.79–6.47)	2.26 (1.2–3.56)	5.90 (3.28–8.03)	6.70 (3.41–11.21)	0.45 (0.20–0.89)	3.10 (1.35–6.73)	2.80 (1.23–5.14)	4.30 (0.75–9.23)	0.91 (0.20–1.59)	1.60 (0.44–2.33)	1.62 (0.58–4.9)	1.97 (0.50–3.92)	1.66 (0.68–3.18)	1.29 (0.37–1.98)	1.42 (0.74–2.13)	2.68 (1.38–4.02)
% Pools	6.7 (5–10)	7.5 (5–10)	17.5 (10–25)	16.7 (10–30)	14.2 (5–30)	20.8 (10–40)	20 (10–30)	18.3 (10–20)	10 (10–10)	30.8 (5–50)	18.33 (5–40)	10 (5–20)	19.2 (10–30)	25 (10–40)	14.2 (5–20)	26.7 (10–50)
% Riffles	16.67 (5–25)	22.50 (15–30)	37.5 (20–50)	10.8 (5–20)	39.2 (20–60)	26.7 (10–50)	28.3 (10–40)	45 (30–60)	29.2 (5–60)	15.8 (5–30)	14.17 (5–25)	25 (15–40)	27.5 (20–40)	17.5 (10–35)	18.3 (5–35)	21.7 (10–50)
% Runs	76.7 (70–90)	70 (60–80)	45 (30–60)	71.7 (60–80)	46.7 (30–60)	52.5 (30–75)	51.7 (40–60)	36.7 (30–50)	60 (30–80)	53.3 (20–80)	67.5 (50–80)	65 (90–90)	53.3 (40–70)	57.5 (40–70)	67.5 (45–90)	51.7 (20–70)
Conductivity (μS cm^{-1})	145.6 (127–156.7)	128.2 (119.4–144.5)	78.6 (70–89.3)	70.2 (61.2–79.4)	51.1 (49.5–53.7)	28.3 (23.3–32.3)	28.6 (25.8–32.7)	28.9 (24.9–33.5)	22.7 (21.5–26.7)	35.8 (32.1–41.0)	38.2 (34.3–44.3)	37.8 (34.1–44.8)	39.1 (33.2–45.5)	40.9 (33.3–47.0)	45.9 (40.8–54.6)	42.9 (39.1–48.9)
TDS (ppm)	103.5 (88–115)	90.3 (84–99)	55 (49–58)	45.7 (44–48)	34.4 (33–35)	18.6 (16–22)	19 (16–22)	19.4 (16–23)	16.1 (13–18)	24.6 (24–26)	24.2 (24–25)	22 (20–23)	25.3 (21–30)	25.8 (22–30)	29.7 (28–33)	27.3 (24–30)
Turbidity (NTU)	69.4 (36.1–97.1)	85.6 (32.1–178.5)	45.7 (32.7–72.1)	45.6 (25.7–57.0)	26.7 (18.7–36.2)	11.1 (1.5–33.9)	5.0 (1.5–12.3)	5.1 (1.4–11.0)	1.8 (0.9–3.6)	2.3 (1.6–3.0)	27.5 (3.4–89.7)	17.8 (9.5–35.7)	1.5 (0.7–2.5)	1.2 (0.6–2.3)	3.0 (1.4–5.5)	1.9 (1.4–2.3)
Transparency (cm)	18.4 (10–32)	17.9 (10–28)	27.2 (15–39)	28.6 (19–37)	41.5 (29–64)	109.3 (35–160)	130 (56–160)	131.3 (77–160)	160 (160–160)	160 (160–160)	123.9 (24–160)	59.6 (25–85)	160 (160–160)	160 (160–160)	160 (160–160)	160 (160–160)
Water temperature (°C)	17.6 (17–18.5)	18.3 (17.3–19.0)	17.9 (17.4–18.8)	19.6 (18.7–20.9)	17.8 (17.0–19.0)	16.0 (14.8–17.1)	16.6 (15.9–16.9)	16.9 (16.2–17.5)	16.1 (15.3–16.6)	16.8 (16.1–17.4)	17.9 (17.6–18.4)	19.8 (19.2–20.6)	17.4 (17.1–18.0)	17.5 (17.1–17.8)	17.8 (17.3–18.0)	18.0 (17.5–18.8)
Oxygen (mg L^{-1})	7.93 (6.69–9.12)	8.20 (7.66–10.21)	8.10 (7.83–8.27)	7.80 (7.61–8.18)	7.70 (7.49–7.90)	7.90 (7.71–8.22)	8.30 (7.90–9.50)	8.30 (8.16–8.58)	7.70 (7.37–8.03)	7.80 (7.74–7.92)	7.70 (7.14–7.97)	8.28 (7.56–9.62)	7.38 (6.64–7.78)	7.47 (6.05–8.10)	7.84 (7.51–8.05)	8.01 (7.72–8.46)
pH	6.8 (6.2–7.6)	6.9 (6.1–8.0)	6.7 (6.1–7.5)	6.3 (4.9–7.2)	6.5 (5.7–7.1)	5.6 (4.6–6.8)	6.1 (4.6–7.9)	6.1 (4.6–7.9)	4.3 (3.2–5.3)	6.1 (5.1–7.0)	5.8 (4.9–6.9)	5.9 (5–7.2)	6.3 (5.1–7.4)	6.3 (5.3–7.4)	5.8 (5.0–6.9)	6.1 (5.1–6.8)

TDS, total dissolved solids.

Table 3 Principal component loadings for habitat and water quality variables from PCA of physical data from 16 river sites sampled in and around Bwindi Impenetrable Forest

Environmental variable	PC1	PC2	PC3
Elevation (m)	**−0.686**	−0.182	0.281
Stream gradient (°)	0.286	0.412	**0.657**
Canopy cover (%)	**−0.635**	0.399	0.356
Riparian vegetation	**−0.607**	0.510	0.240
Substratum type	−0.485	**0.731**	0.188
Stream width (m)	0.272	**0.753**	−0.474
Depth (m)	0.443	0.400	−0.445
Discharge ($m^3 s^{-1}$)	0.535	**0.641**	−0.499
Current	0.480	**0.644**	−0.138
Pools (%)	−0.425	0.293	−0.506
Riffles (%)	−0.300	**0.629**	0.484
Runs (%)	0.524	**−0.747**	−0.128
Specific conductance ($\mu S\ cm^{-1}$)	**0.846**	0.078	0.155
Total dissolved solids (ppm)	**0.831**	0.114	0.149
Turbidity (NTU)	**0.882**	0.138	0.345
Water transparency (cm)	**−0.827**	−0.153	−0.390
Water temperature (°C)	0.572	−0.550	0.245
Dissolved oxygen ($mg\ L^{-1}$)	0.333	0.414	0.068
pH	0.467	0.240	0.168
Proportion of variance explained	0.340	0.230	0.120

Bold values were considered high (>|0.60|).

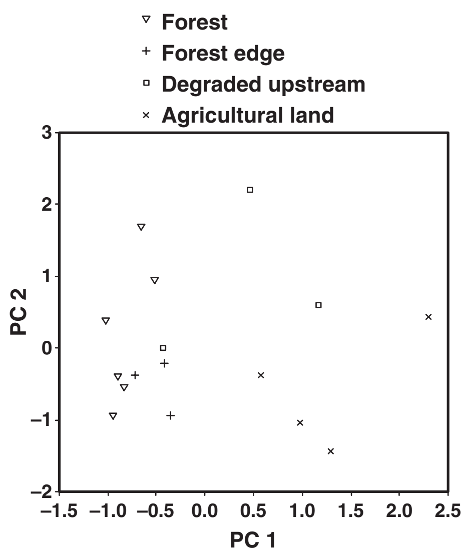

Fig. 2 Plot of ordination analysis (principal components analysis) based on environmental characters measured across 16 sites in Bwindi National Park, Uganda and surrounding areas.

had the highest turbidity, TDS, and conductivity values and low transparency values. Forest sites and boundary site groups (Fig. 2) generally exhibited low turbidity, TDS, and conductivity values and high water transparency values. PC 2 separated sites on the basis of stream width, proportion of riffles and runs, current, and substratum type.

Thirteen variables with high loadings in PCA were used in a cluster analysis to explore patterns of site association with respect to both deforestation category and river of origin. Cluster analysis was efficient at separating sites according to their deforestation categories (Fig. 3). Sites clustered less with respect to river of origin with the exception of Ishasha. The clustering associated with river of origin may reflect the fact that some rivers were dominated by a particular land use history; for example, all sites on the River Ishasha were either degraded-upstream or agricultural land. The ANOSIM test indicated a significant difference ($R = 0.355$, $P = 0.012$) in physicochemical variables among deforestation categories with pairwise tests revealing significant differences between DFC4 and DFC1, and DFC 4 and DFC2 ($P = 0.004$ and 0.012, respectively) and a marginal difference between DFC3 and DFC1 ($P = 0.085$).

Relationships between land use and benthic macroinvertebrates assemblages

Seventy benthic macroinvertebrate taxa (mostly at the family level) were identified in our study of the Bwindi rivers (Table 4). Across all sites, the invertebrate assemblage was dominated by Ephemeroptera (28.3%), followed by Trichoptera (27.4%), Diptera (17.2%), Coleoptera (13.6%), Odonata (6.1%), Plecoptera (5.8%), Hemiptera (0.7%) and the remainder, a combination of rare taxa (Decapoda, Lepidoptera, Turbellaria, Potamonautidae and Orthoptera), constituted 0.9% of the total invertebrates collected. Total family richness was highly variable across sites ranging from 17 at IS4, an agriculture site, to 39 at KH2, a pristine forest site. We tested for a difference in %Ephemeroptera, %Trichoptera and %EPT among deforestation categories, since these have been found to be useful biotic indices in other systems (Barbour *et al.*, 1999). %Ephemeroptera did differ significantly among deforestation categories (nested within river, $F_{5,7} = 4.659$, $P = 0.034$), with values averaging 21.3 ± 2.9% (SE) in forested sites, 21.1 ± 3.3% in forest edge sites, 43.3 ± 3.4% in deforested-upstream sites and 49.2 ± 10.4% in degraded agricultural land. %Trichoptera did not vary significantly among deforestation categories (nested within river, $F_{5,7} = 0.988$, $P = 0.487$), although mean values among

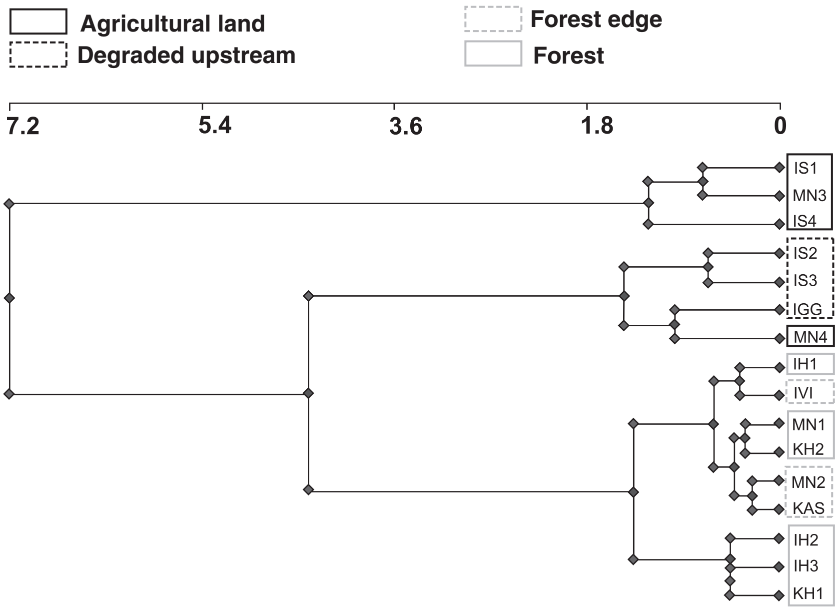

Fig. 3 Cluster analysis based on environmental characters measured across 16 river sites in Bwindi National Park and surrounding areas using Ward's linkage and the Euclidean dissimilarity measure. The shorter the distance, the more similar the sites are in terms of their physicochemical characteristics.

deforestation categories were variable ranging from 11.7 ± 4.1 in agricultural land to 37.8 ± 2.2 in forest edge sites. The cumulative index %EPT showed a marginal difference among deforestation categories (nested within river, $F_{5,7} = 3.064$, $P = 0.088$) ranging from an average of 52.3 ± 5.3% in forested sites to 64.4 ± 2.7% in forest edge sites, to 66.3 ± 4.9% in deforested-upstream sites, to 66.5 ± 6.8% in pristine forest sites.

Cluster analysis produced three major clusters of sites based on invertebrate abundances (Fig. 4). The first cluster comprised of forested sites mostly on Ihihizo stream with the exception of MN3 (deforested-upstream). IH1 and IH2, although forested, had high abundances of Chironomidae, a family that often indicates organic enrichment. The second cluster was comprised of three pristine forest sites (MN1, KH1 and KH2) and three forested edge sites (IVI, KAS and MN2). The last cluster was comprised of a mixture of deforested upstream and agricultural sites. The families Tricorythiidae and Oligoneuridae occurred almost exclusively at sites within this last cluster.

Results of the CCA show that water transparency, temperature, pH, stream width and proportion of runs were the most important predictors of benthic macroinvertebrate assemblage structure (Fig. 5). The species–environment correlation was very high (>0.842) for the first four canonical axes. This suggests that the measured environmental variables relate strongly to macroinvertebrate assemblage variation. Water transparency (an indicator of land-use effects) and pH were the most important variables accounting for variation in benthic macroinvertebrate assemblage on CCA axis I (Fig. 5). Water temperature was also an important factor on this axis. Increased water transparency was positively associated with invertebrate families such as Psephenidae, Aeshnidae, Polycentropodidae, Simuliidae, Perlidae, Gyrinidae and Lepidostomatidae (bottom left of the taxa-site biplot, Fig. 6). This corresponded to sites mostly in DFC3 (forested edge, KAS, MN2, IVI) and two sites in DFC4 (forest, IH3 and KH2). The upper left side of the biplot comprised of low water temperature, acidic and forested sites in DFC4 (forest, MN1, IH1, KH1 and IH2). The taxa dominating this cluster included the case-building Trichoptera such as Leptoceridae and Calamoceratidae; the crane flies Tipulidae; Odonata (Calopterygidae, Libellulidae and Gomphidae) and tolerant taxa such as Oligochaeta and Chironomidae. The right side of the CCA biplot corresponded to sites in DFC1 (agricultural land) and DFC2 (deforested-upstream Fig. 5). These sites were characterized by high water temperature and pH, and very turbid water. Sites in this category were dominated by tolerant Ephemeroptera families such as Trichorythidae, Caenidae and Prosopistomatidae; tolerant Diptera (Ceratopogonidae and Athericidae); Hemiptera families (Pleidae, Naucoridae and Veliidae); and

Table 4 Variation in total benthic macroinvertebrate abundance among four deforestation categories [DFC1, agricultural land; DFC2, deforested-upstream; DFC3, forested edge; DFC4, forest]

Family	Order	DFC1	DFC2	DFC3	DFC4
Hirudidae	Annelida				1
Oligochaeta	Annelida	1	1	3	7
Elmidae	Coleoptera	**143**	**109**	**102**	119
Gyrinidae	Coleoptera	10	1	18	25
Helodidae	Coleoptera	1		67	95
Hydrophilidae	Coleoptera		2	6	15
Melyridae	Coleoptera				3
Noteridae	Coleoptera		1	3	2
Psephenidae	Coleoptera	10	1	10	40
Salpingidae	Coleoptera		1		
Entomobryidae	Collembola				1
Atyidae	Decapoda	8	1		
Potamonautidae	Decapoda			1	3
Anthomyiidae	Diptera		1		
Athericidae	Diptera	0	10	13	13
Ceratopogonidae	Diptera	8	12	3	13
Chironomidae	Diptera	90	57	**148**	**362**
Dytiscidae	Diptera	3	3	2	5
Empididae	Diptera			2	
Muscidae	Diptera				1
Simuliidae	Diptera	17	6	34	43
Tabanidae	Diptera	1			
Tipulidae	Diptera	9	5	54	125
Baetidae	Ephemeroptera	**91**	**68**	**138**	**245**
Baetiscidae	Ephemeroptera				1
Caenidae	Ephemeroptera	**170**	**89**	27	65
Ephemerellidae	Ephemeroptera	10	5	9	19
Heptageniidae	Ephemeroptera	**96**	**135**	**133**	65
Leptophlebiidae	Ephemeroptera	58	12	36	56
Neoephemeridae	Ephemeroptera	2	3		
Oligoneuridae	Ephemeroptera	18	1		
Prosopistomatidae	Ephemeroptera	6	16	5	9
Tricorythiidae	Ephemeroptera	46	34	9	13
Hydrometridae	Hemiptera	1			
Naucoridae	Hemiptera	8	3	1	2
Nepidae	Hemiptera				3
Pleidae	Hemiptera	4	7	1	7
Veliidae	Hemiptera	1	3		3
Cossidae	Lepidoptera				1
Noctuidae	Lepidoptera		1		
Pyralidae	Lepidoptera		1	1	3
Nematoda	Nematoda			1	3
Aeshnidae	Odonata	3		33	23
Agrionidae	Odonata			3	2
Calopterygidae	Odonata	3	3	1	7
Gomphidae	Odonata	18	9	30	75
Lestidae	Odonata			1	1
Libellulidae	Odonata	40	6	33	74
Petaluridae	Odonata				2
Protoneuridae	Odonata	1		2	
Acrididae	Orthoptera			1	1
Tettigonidae	Orthoptera			1	5
Hydracarina	Ostracoda	6	13	2	3
Perlidae	Plecoptera	75	26	83	**162**
Brachycentridae	Trichoptera				6
Calamoceratidae	Trichoptera	2		15	39
Hydropsychidae	Trichoptera	**94**	**155**	**429**	**270**

Table 4 *(Continued)*

Family	Order	DFC1	DFC2	DFC3	DFC4
Hydroptilidae	Trichoptera				1
Lepidostomatidae	Trichoptera	25	1	15	35
Leptoceridae	Trichoptera	20	13	81	**314**
Limnephilidae	Trichoptera			1	3
Odontoceridae	Trichoptera			3	
Philopotamidae	Trichoptera	3		51	34
Polycentropodidae	Trichoptera	1	2	5	9
Psychomiidae	Trichoptera	3	1		3
Ptilodactylidae	Trichoptera	1			
Xiphocentromidae	Trichoptera				2

The five dominant taxa for each deforestation category are indicated in bold.

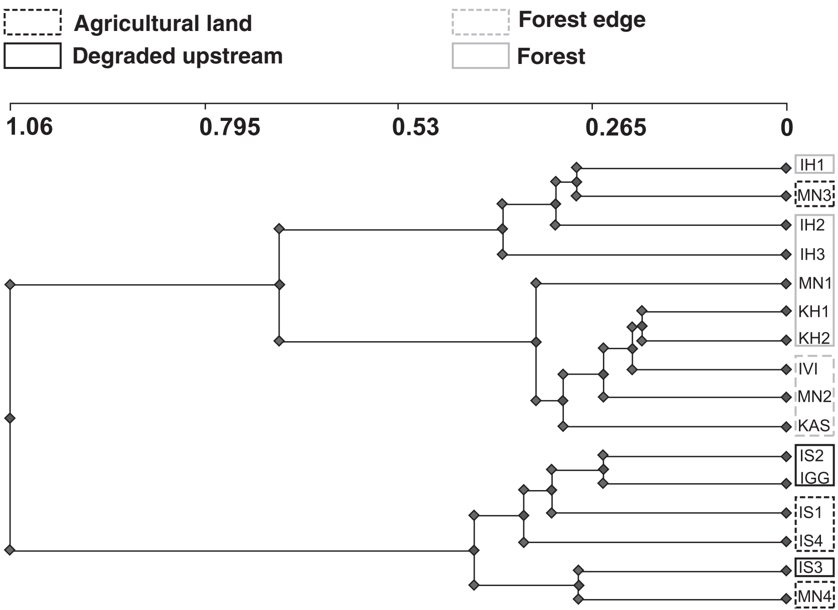

Fig. 4 Cluster analysis based on abundance of benthic macroinvertebrates measured across 16 river sites in Bwindi National Park and surrounding areas using Ward's linkage and the Euclidean dissimilarity measure. The shorter the distance, the more similar the sites are in terms of their macroinvertebrate assemblage structure.

Elmidae and Dytiscidae (beetles, Fig. 6). The water mites (Hydracarina) were also associated with sites in the agricultural and upstream degraded sites.

The cumulative variation explained by the first two axes of the taxa–environment relationship in the CCA was 69%. This implies that the measured environmental variables were sufficient in explaining much of the variance in the benthic macroinvertebrate assemblage. The Monte Carlo permutation test on the first CCA axis was highly significant ($F = 3.24$, $P = 0.002$) and for all axes ($F = 2.2$, $P = 0.004$) indicating a strong relation between the invertebrate assemblage and the measured environmental variables.

ANOSIM indicated a marginally significant difference ($R = 0.209$, $P = 0.058$) in assemblage composition among the four deforestation categories, while pairwise comparisons indicated a significant differences in benthic macroinvertebrates between DFC2 and DFC4 ($P = 0.032$) and marginal differences between DFC1 and DFC3, and DFC1 and DFC4 ($P = 0.084$ and 0.073, respectively).

Discussion

Ecology of Bwindi rivers – general patterns

In general, the limnological characteristics of the rivers of Bwindi Impenetrable National Park and surrounding areas are similar to that of other forested streams and rivers in tropical regions (Harrison, 2006). The forested sites were characterized by low conductivity, low temperature, acidic water, low turbidity and low TDS, high water transparency and high dissolved oxygen concentration. Forested river waters

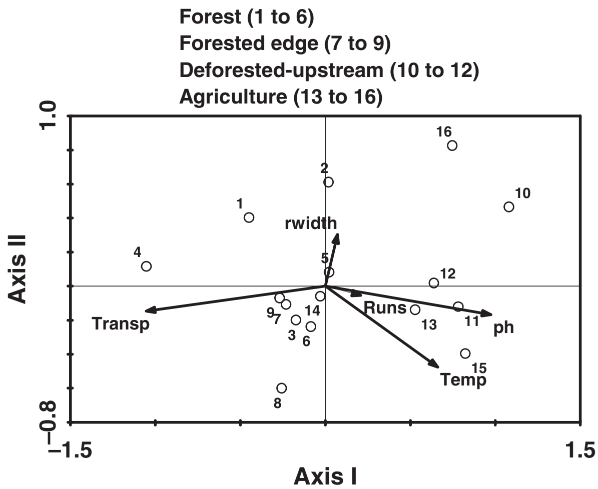

Fig. 5 Ordination diagram (canonical correspondence analysis, CCA) of sample sites (open circles) and environmental variables (arrows). The length of an arrow and its closeness to CCA axes is a measure of its strength. The sites from 1 to 16 are as follows: IH1, IH2, IH3, MN1, KH1, KH2, MN2, IVI, KAS, IS2, IS3, IGG, MN3, MN4, IS1, IS4, respectively. Deforestation categories are: forest (1–6); forested edge (7–9); deforested-upstream (10–12) and agriculture (13–16).

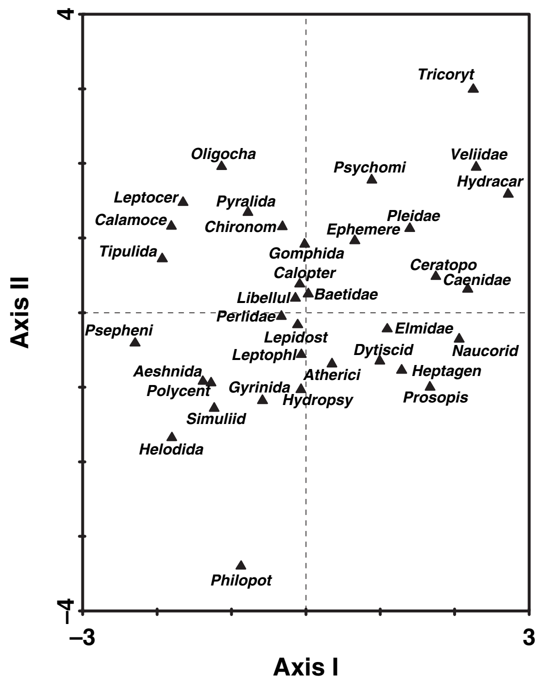

Fig. 6 Ordination diagram (canonical correspondence analysis) of benthic macroinvertebrate assemblages. Full names of family codes are given in Table 4.

in the tropics are frequently impoverished, with low conductivity, low turbidity, a low silt load and low pH (associated with accumulation of humic acids, Beadle, 1974). In combination with heavy shading, this leads to relatively low water temperatures and low primary production (Marlier, 1973; Welcomme, 1979, Welcomme, 1985; Welcomme & de Merona, 1988). In streams of the Ruwenzori Mountains in Uganda, Busulwa & Bailey (2004) reported low conductivity values overall (12–220 μS cm^{-1}) within an altitudinal range 900–4200 m. Values for Bwindi river sites fall within this range, although on average they never exceeded 145 μS cm^{-1}. The probable factor influencing the low conductivity at Bwindi relative to the Ruwenzori streams may be the nature of the underlying geology. In Bwindi, water conductivity was generally low at high altitudes and increased with a drop in elevation. However, this general trend was confounded by human impacts at high altitudes where deforested sites were characterized by higher conductivity. Turbidity and TDS mirrored conductivity patterns. This may be explained by the fact that turbid waters carry with them a high load of dissolved and suspended materials, and a high concentration of ions leading to high water conductivity. Water temperature was generally low in forested parts of the rivers. The findings are consistent with those of Reinthal *et al.* (2003) and Busulwa & Bailey (2004) who reported low temperatures in the forested streams of Madagascar and the Ruwenzori Mountains of Uganda, respectively. The reduced temperature in forested streams is a result of shading by riparian vegetation that reduces insolation resulting in low water temperature (Swift, 1983; Riseng, 1997; Pringle & Benstead, 2001; Chapman & Chapman, 2003). Despite the overall similarity of Bwindi rivers to other forested rivers in the tropics, variation in physicochemical conditions among sites was reflective of the degree of human impact.

Effects of land use on physicochemical parameters

Deforestation category was a major predictor of physicochemical conditions at a given site. Agricultural sites and deforested upstream sites generally had the highest turbidity, TDS and conductivity values, and had low transparency values. Forest sites and boundary sites generally exhibited low turbidity, TDS and conductivity values, and high water transparency values. Mean conductivity at an agricultural site (IS1) was six times higher than the lowest mean value at a forested site (MN1) despite comparable elevations of the two sites. This agrees in general with the earlier study of Bwindi rivers (Kasangaki *et al.*, 2006); however, the number of outforest impacted sites in this previous study was limited to one site. The high conductivity, TDS and turbidity in the degraded sites (both agricultural and deforested-upstream) are probably due to the high load of suspended materials in increased runoff from agricultural fields on the steep-sided slopes. Increased conductivity, TDS and turbidity as a result of human impacts have been reported in other studies (Trayler & Davis, 1998; Sutherland *et al.*, 2002).

Interestingly, we found evidence to support a drift or persistence of human impacts from the agricultural landscape upstream to forested sites downstream. For characters such as water transparency and turbidity, forested sites with degraded upstream areas showed higher values than forest and forested edge sites. Despite this general trend, observations of water quality variation in the River Ishasha do suggest that forest patches play a role in partial sequestering of ions and pollutants from upstream. Busulwa & Bailey (2004) reported an increase in conductivity with decreased altitude in Ruwenzori streams. This finding was found to be true for streams having their sources in forested catchments such as rivers Munyaga and Ihihizo. However, River Ishasha, which has its source in Ahakagyezi swamp and drains an agriculturally impacted catchment, showed a reverse trend in conductivity. On this river, conductivity was high upstream and tended to decrease progressively downwards as the water flows through a forested patch. Similarly, TDS and turbidity tended to decrease downstream while transparency increased. This may reflect a dilution effect of some tributaries draining into the river downstream. In addition, it is possible that as the river flows downstream ecological processes sequester some ions and contaminants downstream.

We used cluster analysis to explore the separation of sites according to both deforestation category and river of origin. The most important variables in placing sites according to deforestation category were turbidity, conductivity, TDS, water transparency, elevation, canopy cover and riparian vegetation. These environmental variables can act as good indicators of stream degradation due to deforestation and agricultural activities. Sites clustered most strongly according to deforestation category, though river of origin was also important. It is not surprising that river of origin is evident in the clustering, given that some rivers were dominated by a particular land use history, and this may also reflect geological history. However, support for the influence of deforestation on water quality was evident in that sites from more than one river were represented in each of the four clusters representing deforestation categories.

Variation in benthic macroinvertebrates with land use

Because streams and rivers accumulate and absorb the impacts of terrestrial degradation over large spatial scales (Allan, 1995), there is growing interest in exploring the predictive value of aquatic bioindicators in detecting long- and short-term impacts of land conversion. Benthic macroinvertebrates are known to be sensitive to habitat characteristics and to respond rapidly to changes in water quality (Klemm *et al.*, 1990; Rosenberg & Resh, 1993; Richards *et al.*, 1997). For these reasons, benthic macroinvertebrates have been used worldwide as biological indicators for the assessment of water quality in rivers and streams (Barbour *et al.*, 1999; Smith *et al.*, 1999). Despite knowledge of their importance, the vast majority of the work on aquatic bioindicators has focused on temperate systems. However, there is growing interest in Africa in the use of aquatic invertebrates as indicators of water quality and ecosystem change (Dallas, 1997; Thorne, Williams & Gordon, 2000; Ndaruga *et al.*, 2004; Kasangaki *et al.*, 2006). The findings of our study of the high-altitude streams of Bwindi suggest that the influence of human impacts on the physicochemical characteristics of Bwindi rivers is reflected in the benthic macroinvertebrate assemblages, especially those draining agricultural catchments; however, some of the aquatic insect biotic indices widely used in temperate systems did not effectively differentiate deforestation categories in this equatorial system or produced results contrasting to those observed in temperate systems. %Trichoptera did not effectively differentiate among deforestation categories (nested within river of origin).

Interestingly, the %Ephemeroptera did differ among deforestation categories (nested within river of origin), but showed the intriguing trend of higher abundance in agricultural areas and areas deforested upstream, a trend that does not concur with some studies of temperate waters (e.g. Harding *et al.*, 1998;

Stone & Wallace, 1998). Similarly there was a trend towards lower %EPT in the forested sites. However, a closer look at the Ephemeroptera reveals informative patterns. Sites in DFC1 and DFC2 were dominated by generalist ephemeropterans such as Trichorythidae, Caenidae and Oligoneuridae; while the highly sensitive trichopteran families such as Calamoceratidae and Leptoceridae, and other sensitive Ephemeropteran families such as Leptophlebiidae and Baetidae dominated sites in DFC3 (forested edge) and DFC4 (forest). These findings are in agreement with previous studies that have documented large increases in generalist mayfly taxa in streams affected by canopy removal (Benstead, Douglas & Pringle, 2003), but suggest use of the conventional %Ephemeroptera or %EPT may not be sensitive indicators without the integration of family-level resolution. The only Plecoptera family (Perlidae) also tended to be abundant in forested sites.

Cluster analysis indicated clustering of sites within deforestation categories, with the exception of one site, and results of the CCA revealed a clear separation of the invertebrate assemblages along a deforestation gradient. The cluster of forested sites was dominated by taxa such as Calamoceratidae, Lepidostomatidae, Perlidae and Tipulidae. Calamoceratidae and Lepidostomatidae (caddisflies) use plant material to build their cases; it is likely that deforestation deprives them of the materials to use in building their cases resulting in their absence from agricultural sites. The crane flies (Tipulidae) are shredders and are known to be important in organic matter breakdown in streams. Their absence or occurrence in low numbers at deforested sites may be attributed to lack of plant material (a result of deforestation) on which to feed. Similar findings were reported by Benstead *et al.* (2003) in their study of effects of deforestation on Madagascar's freshwater biodiversity. Benstead *et al.* (2003) argued that insect community structure changed following deforestation due to differences in the relative availability of basal food resources, with agricultural stream communities dependent on *in situ* primary production and forest stream communities dependent largely on food resources of terrestrial origin. In the rivers of Bwindi and surrounding areas, we observed a decline in taxa that depend largely on food resources of terrestrial origin (mostly leaf litter), including the shredders Diptera, Perlidae, Tipulidae and the collector filterer Simuliidae. The increase of caenid mayflies in agriculturally impacted streams has been explained by their adaptability to fine substrata and slow currents (Hynes, 1970; Dudgeon, 1999; Iwata, Nakano & Inoue, 2003), removal of riparian vegetation may have benefited this taxon.

The results of this study suggest that removal of riparian vegetation in a high-altitude equatorial rainforest negatively affects benthic macroinvertebrate assemblages through reduction in the number of sensitive taxa and dominance by the intolerant taxa, patterns consistent with studies in Madagascan forests that have observed that removal of forest cover results in loss or declines of specialist forest taxa and replacement by simplified communities that are dominated by generalist taxa (Gibon, Elouard & Sartori, 1996; Elouard & Gibon, 2003).

With respect to useful bioindicator taxa for these high-altitude rainforest streams, our results suggest that generalist Ephemeroptera (Caenidae, Trichorythiidae and Oligoneuridae) were the best bioindicators of agriculturally impacted sites (both DFC1 and DFC2). Case building caddisflies (Leptoceridae, Lepidostomatidae, Hydropsychidae and Calamoceratidae), stoneflies (Perlidae) and craneflies (Tipulidae) were good bioindicators of pristine forest conditions. Surprisingly, Chironomidae emerged as an abundant species in both DFC3 and DFC4; however, this may have represented some sites on catchments close to human settlements where there is discharge of non-treated human waste such as at IH1, IH2 (forest) and MN2 (forest edge).

Forested riparian buffers have proven effective in moderating the impacts of deforestation on water quality in some aquatic systems, and there are increasing efforts to explore the value of riparian zone retention and/or restoration as a means of safeguarding the quality of running waters. Several studies in temperate zones have demonstrated that buffer strips are effective in removing soluble nitrogen and phosphorus and sediment (Comerford, Neary & Mansel, 1992) and trapping sediment, nutrients and other contaminants (Carothers, 1977). The streamside vegetation afforded by forested buffer zones can provide shade necessary for natural temperature regimes and improve stream ecosystem health (Bunn, Davies & Mosisch, 1999). Our study of equatorial high-altitude rainforest streams also provides support for the importance of riparian buffers in moderating effects of deforestation. Forest and forested edge sites were more similar in both limnological and macroinvertebrate assemblage structure than sites within or downstream from agricultural lands. If the protected area cannot encompass the catchment, the use of rivers as park boundaries may help to maintain the biological integrity of the rivers by buffering one side of the watercourse. In an earlier study of Bwindi rivers Kasangaki *et al.* (2006) found evidence of ecological recovery through regeneration of forest in formerly encroached areas that had experienced some degree of logging. These findings support the role of rainforest buffers and forest regeneration in maintenance and restoration of river systems.

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