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Primary Research Paper

Links between anthropogenic perturbations and benthic macroinvertebrate assemblages in Afromontane forest streams in Uganda

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Abstract

Relationships between environmental variables and benthic macroinvertebrate assemblages were investigated among several sites that varied in disturbance history in Bwindi Impenetrable National Park, an Afromontane site in East Africa. Environmental variables were correlated with the level of past catchment disturbance – logging, agricultural encroachment, and present tourism activity. For example, sites in medium and high disturbance categories had higher values of specific conductance and lower water transparency than low disturbance category sites, these environmental variables may therefore act indicators of ecological quality of rivers. Environmental variables such as conductivity and water transparency were found to be good predictors of benthic macroinvertebrate assemblages, with anthropogenically stressed sites having lower diversity than the reference sites. Impacted sites were dominated by tolerant taxa such as chironomid and leeches, while 'clean water' taxa such as Ephemeroptera, Plecoptera and Trichoptera dominated at minimally impacted sites. Comparison of sites with different disturbance histories provided evidence for differences in benthic macroinvertebrate communities that reflect the state of forest restoration and recovery. We recommend quarterly monitoring of water quality to act as an early warning system of deterioration and tracking ecological recovery of previously impacted sites.

Introduction

The relationships between anthropogenic disturbance and benthic macroinvertebrates (BMI) assemblages in assessing human impacts on aquatic ecosystems have received little attention in tropical Africa. Elsewhere, benthic macroinvertebrates have received considerable attention in the study of running water ecosystems (Cummins, 1992), and have been the subject of numerous studies on links between assemblage characters and environmental variables (Tate & Heiny, 1995). Invertebrate communities are good indicators of water quality conditions (Resh, 1995; De shon, 1995). They are ubiquitous; therefore, they can be affected by environmental perturbations in many different types of aquatic systems and in microhabitats within those waters. The large number of species involved offers a spectrum of responses to environmental stress (Abel, 1989). Their sedentary nature allows effective spatial analyses of pollutant or disturbance effects (Abel, 1989). In addition, they have long life cycles compared to other groups, which allows elucidation of temporal changes caused by perturbations (Abel, 1989). As a result, benthic macroinvertebrates can act as continuous monitors of the water they inhabit, enabling long-term analysis of both regular and intermittent discharges, variable concentrations of pollutants, single or multiple pollutants, and changes in catchment properties.

Studies of temporal variation in the community structure of streams (Scrimgeour & Winterbourn, 1989) have indicated that physical disturbances can be important determinants of their community structure (Resh et al., 1988). Bender et al. (1984) recognized two general types of disturbance: pulse and press, based on the nature and duration of their effects. Pulse disturbances are generally characterized as catastrophic events of relatively short duration, while press disturbances tend to be longer in duration. Logging is a large-scale, press disturbance of the terrestrial ecosystem, which can have a significant impact on streams by altering temperature regimes (Reinthal et al., 2003), flow regimes (Borman & Likens, 1979), primary production (Noel et al., 1986), organic matter dynamics (Webster et al., 1983), and macroinvertebrate community structure (Gurtz & Wallace, 1984). Land use subsequent to forest removal also affects aquatic communities in several ways. For example, Lenat & Crawford (1994) found that non point-source run off not only eliminated intolerant taxa found at the forested site in North Carolina, but also promoted development of different tolerant communities at the agricultural and urban sites. In tropical rivers, Pringle & Benstead (2002) reported a reduced habitable area for Ephemeroptera, Plecoptera and Trichoptera following deforestation in addition to altered river discharge and an increased light and water temperature.

The value of aquatic macroinvertebrates as indicators of aquatic and terrestrial change has long been recognized with the vast majority of the work on aquatic bioindicators focusing mainly 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 et al., 2000; Ndaruga et al., 2004). In this study, we examined variation in abundance, richness, and other biotic indices of benthic macroinvertebrate communities in relation to environmental variables and condition of the surrounding landscape in Bwindi Impenetrable National Park, Uganda. Despite its global significance as a World Heritage Site, the freshwater biodiversity of Bwindi remains undocumented to date. Bwindi experienced severe anthropogenic disturbance in the past including selective logging, mining, and encroachment for agriculture; and these may have impacted the water quality and biota of the numerous streams that drain the park. Although park protection is now enforced, the high human population density and associated agricultural activities outside the park may still impact streams that do not lie entirely within the park. We hypothesized that environmental variables would predict benthic macroinvertebrate (BMI) assemblages and that BMI biotic indices would reflect past and present anthropogenic disturbances on the forest. The four principle objectives of the study were:

1. to characterize benthic macroinvertebrate communities in terms of taxonomic richness and diversity;
2. to assess impacts of current and past perturbations on stream water quality and BMI communities and to compare benthic community in previously disturbed and relatively undisturbed sites;
3. to investigate relationships between invertebrate communities and selected environmental factors; and
4. to identify macroinvertebrate taxa and physico-chemical variables that can act as indicators of water quality and catchment properties.

Study sites

Bwindi Impenetrable National Park is an Afromontane rainforest ranging between 1160 and 2607 m altitude in South Western Uganda (0° 53′–1° 8′ S; 29° 35′–29° 50′ E). The forest was initially gazetted a forest reserve in 1932 and became a National Park in 1991 to protect its population of the critically endangered mountain gorilla (*Gorilla gorilla beringei*) and the rich plant and animal diversity (McNeilage et al., 2001). The park is approximately 331 km^2 of extremely rugged terrain characterized by numerous steep-sided hills and narrow valleys. The park is a forest island in an agricultural landscape that supports one of the highest densities and fast growing human population in rural Africa, 220 persons per km^2 with a growth rate of 2.7% as per 1991 population census (Gubelman et al., 1995). Human use of the forest was extensive in the past with logging and agricultural encroachment causing the greatest damage. When Bwindi was gazetted a national park, logging was banned; and areas of the park under human habitation and cultivation were reclaimed.

Bwindi is an important water catchment area. It gives rise to several major rivers that flow to the drier country to the north and west of the park and to the densely populated agricultural areas to the south. About 80% of the drainage is to Lake Edward to the north of the forest via the Ivi, Munyaga, Ntengyere, Ihihizo, and Ishasha rivers.

Twelve sampling sites were established across four streams in the National Park (see Fig. 1). Stream and site selection was based on past and present human use of the forest. Kajembajembe Stream is located in an area that was intensively logged for timber. Three sites (KJ1, KJ2 and KJ3) were located along its elevational gradient (see Fig. 1, Table 1). River Mbwa drains an area that was previously encroached for agriculture; it flows close to the park boundary that is a dirt road. Three sites (MB1, MB2 and MB3) were located from upstream to downstream. MB1 and MB2 sites were selectively logged on forest patches close to the sites and there was agricultural

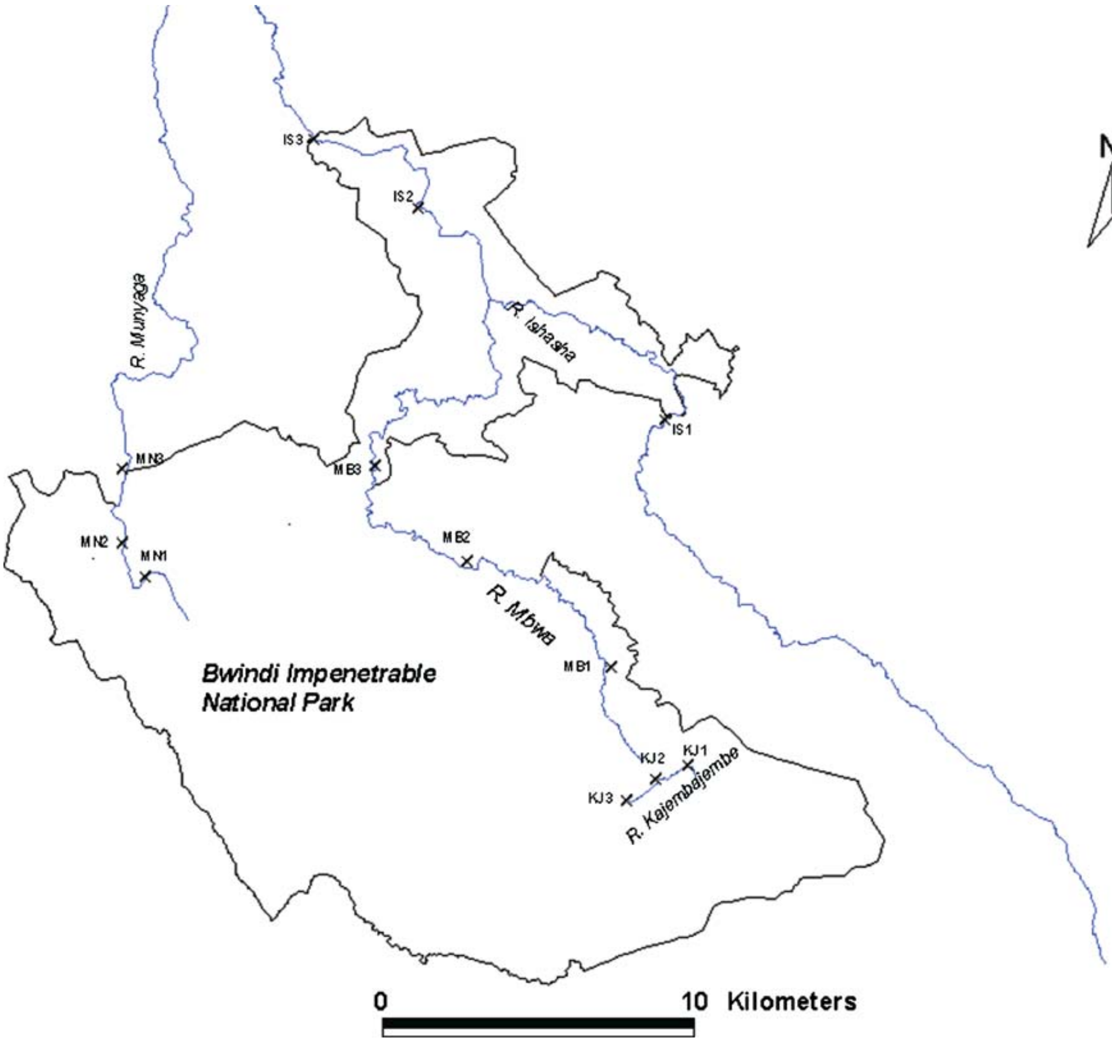

Figure 1. Map of Bwindi Impenetrable National Park, Southwestern Uganda showing location of the 12 sample sites. Three sites were located on each of the of the four study streams.

Table 1. Site description, mean stream depth, width, and altitude for 12 sampling sites in Bwindi Impenetrable National Park, Uganda

Site	Site description	Elevation (m)	Mean width (m)	Mean depth (m)
MB1	Medium disturbance, selectively logged and formerly under agriculture	1970	2.1	0.2
MB2	Medium disturbance, selectively logged and formerly under agriculture	1680	3.4	0.3
MB3	Low disturbance, in-forest, but near a dirt road	1570	9.6	0.6
IS1	High disturbance, agricultural watershed	1530	5.2	0.8
IS2	Medium disturbance, selectively logged forest, upstream agriculture	1300	20.4	0.5
IS3	Medium disturbance, selectively logged forest, upstream agriculture	1250	11.2	0.7
MN1	Low disturbance, forested	1680	4.7	0.4
MN2	Low disturbance, forested	1580	4.1	0.3
MN3	High disturbance, ecotourism activities and human settlements	1490	4.3	0.4
KJ1	High disturbance, intensively logged	2220	1.2	0.1
KJ2	High disturbance, intensively logged	2120	1.4	0.1
KJ3	High disturbance, intensively logged	2090	1.2	0.2

encroachment 1 km on average from the sites. MB3 site is within the forest close to a dirt road. River Ishasha flows from intensively cultivated steep sided hills, and as a result carries a high runoff load from the fields. Site one (IS1) on River Ishasha was located at a point where the river is about to enter the forest from an agricultural landscape, and the other two sites (IS2 and IS3) were located downstream where the river flows within the forest that was selectively logged (see Fig. 1). River Munyaga originates from within the forest that was selectively logged, and it flows downstream through a gorilla eco-tourism area consisting of park headquarters as well as tourism campsites. Sites MN1 and MN2 were located within the forest, and MN3 was located at a point where the river departs an eco-tourism area (park headquarters and tourist camps), but the other bank is forested (see Fig. 1). All sites on the four streams were within an altitudinal range of 1250 to 2220 m above sea level. All sites were categorized into three levels of disturbance i.e. low, medium and high at the inception of the study, based on our knowledge of the sites and aerial photographs of 1990 and 2003 (see Table 1). Sites in the low disturbance category (MB3, MN1 and MN2) were located within the forest where very little logging took place. Sites placed in the medium disturbance category were located in areas where selective logging for high value timber took place and upstream is agriculturally impacted (IS2 and IS3) and where selective logging and encroachment for agriculture took place in the past some 1 km from the stream banks MB1 and MB2). The high disturbance category included sites located where intensive logging took place (KJ1, KJ2 and KJ3), or is in an agricultural catchment area (IS1) or dense human settlements and activities are adjacent (MN3).

Materials and methods

Riparian vegetation measurement

The riparian vegetation condition was assessed using a transect method. Belt transects of 5 m width and 10 m length (50 m^2), set perpendicular to stream flow, were established on both banks at the beginning and end of 100 m stream reach (four belt transects, 200 m^2 area in total per reach). The diameter at breast height (dbh) of every tree > 5 cm dbh was measured to the nearest 1 cm. The stand density (trees/square meter), mean dbh (centimeter), and basal area (square centimeter/square meter) were calculated from the data for the four transects in each study site.

Physicochemical parameters

Stations were sampled monthly from August 2000 to July 2001 to quantify seasonal changes in physico-chemical parameters. Surface water levels were measured from fixed objects such as trees and rocks by the stream banks and water transparency was indexed using a plastic tube (1.6 m long) with a miniature Secchi disc at the bottom. pH was measured with a pH testr 2 (Model 76072 Oakton). Conductivity and water temperature were measured with an YSI 30 meter; dissolved oxygen was measured with an YSI 95 meter. 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 and discharge calculated using the formula:

$$Q = Wdla/t$$

where Q – Discharge (m^3/s); W – bank-full-width of the river (m); d – mean depth (m); l – distance (m) over which the float travels in time t (seconds); a – coefficient, which varies with the nature of the sediment (0.8 for rough, and 0.9 for smooth sediments respectively).

Invertebrate sampling

The 12 sites were sampled for macroinvertebrates every two months over the study period. Samples were taken from riffles and pools at the edge of the streams using a Surber sampler. The water was disturbed about 1 m upstream from the sampler for 1 min so that the current could carry the dislodged macroinvertebrates into the sampler. The net (mesh 363 μm) was 1.34 m long. All invertebrates were preserved in 70% ethanol and were later identified to family level where possible using Merrit & Cummins (1996) and Thirion et al. (1995). The number of individuals of each taxon, the total abundance of individuals, and the richness (number of taxa per sample) were recorded. We used family-level analysis for this study, because there are no comprehensive keys to the level of genera and species for this region.

Analyses

Data were analyzed using Nested ANOVA (General Linear Model) to detect differences among streams, months, and sites in physicochemical parameters, taxa richness and taxa abundance. The mean and coefficient of variation of physicochemical variables were calculated to provide an index of their seasonal variation.

Classification and ordination of macroinvertebrate data

Ordination of sites by taxa was performed using detrended correspondence analyses (DCA) on natural log-transformed abundance data using DECORANA. Ordination by DCA arranges sites with similar taxonomic composition to cluster more closely together and produces site scores that can be related to environmental variables. Stepwise multiple regression analysis was carried out between DCA axis 1 and 2 scores with environmental variables to identify the best predictors of DCA axes. McGarigal et al. (2000) recommended that canonical correspondence analysis (CCA) be used whenever DCA is performed because comparison of the results will provide information beyond what either analysis alone can provide. CCA was used to evaluate the relationships between taxa abundance and the environmental variables, and was performed using the program CANOCO (ter Braak, 1987). CCA compares variation in community composition by constraining ordination axes to be linear combinations of environmental variables. The resulting taxa-environmental biplot is an ordination diagram in which taxa and sites are represented by points, and arrows represent environmental variables. A Monte Carlo permutation test with 199 permutations was used to test whether taxa abundance was related to environmental variables on the first axis eigenvalue and the trace, the sum of all the eigenvalues (ter Braak & Verdonshot, 1995). Finally, stepwise multiple regression analysis was used to explore the environmental predictors of BMI assemblages.

Biotic indices

Several indices and scores were used to examine variation in invertebrate diversity with disturbance history. Diversity indices are mathematical expressions that use three components of community structure: richness (number of categories present), evenness (uniformity in the distribution of individuals among categories), and abundance (total number of organisms present). The most widely used diversity index is the Shannon because it is stable in any spatial distribution and is insensitive to rare species. A Shannon diversity (H') index was calculated for the pooled data for each site (Shannon & Weaver, 1948). The higher the value of H', the greater the diversity. Ephemeroptera, Plecoptera and Trichoptera (EPT) abundance, taxa richness, and Chironomidae abundance were used as indices of ecological quality as they are globally used in water quality assessments.

Results

Riparian trees and herbaceous undergrowth differed according to the location of the sites in relation to altitude. Riparian trees at Kajembajembe sites were dominated by *Neoboutonia macrocalyx*, *Dombeya goetzenii*, *Prunus africana*, *Allophylus* sp., *Alangium chinense* and *Galiniera coffeoides*, while the herbaceous undergrowth consisted of *Mimulopsis arborenscens*, *Impatiens sodenii*, *Mimulopsis solmsii*, and *Sericostachyus scandens*. At River Mbwa sites *Cyathea manniana*, *N. macrocalyx*, *Myrianthus holstii*, *Carapa grandiflora*, *Cassine aethiopica* and *Cassipourea gummiflua* dominated the riparian trees. The herbaceous vegetation composed of *Justicia justrata*, *S. scandens*, *Pillea holstii*, and *Palisota manii*. Riparian vegetation on river Munyaga sites was dominated by *C. manniana*, *C. aethiopica*, *N. macrocalyx*, and *Leplea mayombensis* (trees) while *Cyathea cameroniana*, *J. justrata*, *Todalia asiatica*, and *I. sodenii* were the dominant herbs. The forested sites on river Ishasha had *C. manniana*, *Trichilia volkensii*, *Allanblackia kimbiliensis*, *Musanga cecropioides*, and *A. chinense* as the dominant riparian trees; the dominant herbs were *Marantachloa* sp., *Leptaspsis* sp., *Asplainum* sp. and *Oprismenus* sp. The agricultural site had no riparian trees; the herbs were mainly *Galisonga* sp., *Penicetum* sp., *Paspalum* sp. and spear grass most of which are characteristic of bush fallow. Basal area per square meter ranged between 0 cm^2/m^2 at IS1 and 174.4 at IS3 and did not differ significantly among disturbance categories ($p = 0.214$). Tree density differed significantly among disturbance categories ($p = 0.014$) and the Bonferroni post hoc test revealed significant differences between the low and high impact category ($p = 0.020$), and between the medium and the high disturbance category ($p = 0.032$).

Variation in physicochemical variables

With the exception of water level (among streams) and water transparency (among sites) all the measured physicochemical parameters showed significant variation among streams, months, and sites on a given stream (see Tables 2 and 3). Transparency was lowest at the Ishasha sites; particularly IS1 (20 cm, Table 2) a site draining agriculturally impacted areas. Transparency was highest at the three Munyaga sites where it was always greater than 160 cm. Conductivity varied across sites from 23.1 to 155.3 $\mu S\ cm^{-1}$ and was highest on Ishasha sites that drain an agricultural catchment (see Table 2). Lowest conductivity values were recorded at sites draining in-forest areas (MB3, MN1 and MN2). Conductivity decreased from upstream to downstream for all rivers except on the Munyaga stream. Across sites, mean pH varied from 4.2 to 7.2, and was lowest at the two upstream Munyaga sites (MN1 and MN2) (see Table 2). The low acidity of MN3 compared to its upstream sites MN1 and MN2 may be due to the dilution effects of a tributary that joins Munyaga before site MN3. Dissolved oxygen varied between 6.7 and 8.7 mg l^{-1} and was lowest at the higher elevation sites of Kajembajembe. Mean water temperature varied between 13.8 and 18.7 °C and was lowest at the Kajembajembe sites and highest at the Ishasha sites (see Table 2). Generally, shaded sites tended to have low water temperature compared to open sites (*t*-test, $p < 0.001$). Mean discharge varied from 0.2 to 6.9 m^3/s and was highest at IS3 and lowest at MB1. There was seasonal variation in discharge at all sites (coefficient of variation >30%). Stream

Table 2. Mean values for a suite of physical and chemical characteristics of the stream sites in Bwindi Impenetrable National Park, Uganda

River	Site	Parameter	pH	CO (μs/cm)	DO (mg/l)	Temp (°C)	TR (m)	*L* (m)		*Q* (m^3/s)
Mbwa	MB1	Mean	6.2	49.7	8.1	14.5	1.2	1.1	0.8	0.2
		CV	6	15	8	5	26	3	13	46
	MB2	Mean	6.4	35.6	8.3	15.7	1.0	0.8	0.6	0.8
		CV	3	13	8	4	48	10	18	34
	MB3	Mean	6.5	27.8	8.4	17.0	1.1	1.6	3.2	3.3
		CV	5	15	1	4	41	7	19	47
Ishasha	IS1	Mean	7.1	155.3	7.9	18.4	0.2	1.8	2.5	2.4
		CV	4	5	6	3	57	8	17	74
	IS2	Mean	7.0	82.2	8.7	17.9	0.3	1.5	2.8	6.4
		CV	5	11	10	3	62	5	9	42
	IS3	Mean	7.2	78.6	8.3	18.7	0.2	1.4	3.7	6.9
		CV	6	10	2	3	63	16	14	43
Munyaga	MN1	Mean	4.2	29.1	8.3	16.2	1.6	0.9	2.3	0.9
		CV	10	25	4	3	0	5	20	51
	MN2	Mean	4.8	23.1	7.9	16.4	1.6	1.5	1.8	0.3
		CV	9	23	2	3	0	3	17	34
	MN3	Mean	6.6	37.3	7.8	18.4	1.6	1.2	2.8	0.6
		CV	3	11	4	3	0	14	9	39
Kajembajembe	KJ1	Mean	6.7	57.6	6.7	14.7	0.5	1.1	0.8	
		CV	4	53	17	9	57	13	47	
	KJ2	Mean	6.5	49.2	7.4	13.9	0.7	1.1	1.0	
		CV	4	15	3	3	34	7	37	
	KJ3	Mean	6.1	47.2	7.3	13.8	0.6	1.1	0.8	
		CV	5	11	7	4	37	6	30	

The coefficient of variation (% CV) is also presented. Sample size (12) represents different months from which statistics were derived over the study period. *Discharge on Kajembajembe Stream was not measured because much of the stream is small and covered by dense herbaceous growth. CO = water conductivity; DO = dissolved oxygen; Temp = water temperature; TR = water transparency; *L* = water level; *D* = discharge; Cu = water current; *Q* = discharge; CV = coefficient of variation.

width at sampled sites varied between 1.2 m at KJ3 to 20.4 m at IS2, while mean water depth tended increase with stream size and ranged from 0.1 m at KJ1 and KJ2 to 0.8 m at IS1 (see Table 1).

Macroinvertebrate assemblages and indices

Ephemeroptera was the most abundant order comprising 47.3% of the total invertebrates followed by Diptera (16.5%), Trichoptera (15.6%), Coleoptera (9.2%); and the remaining orders comprised 11.4% (see Table 4). A total of 41 macroinvertebrate families were collected from the 12 sites over the sampling period. Family Baetidae (Ephemeroptera) occurred at all sampled sites, Caenidae (Ephemeroptera) was the most abundant (25% of total), and it occurred at all sites except at MN1 that was highly acidic (mean pH 4.2). Rare taxa (those comprising less than five individuals total across all sites) included the following families: Calopterygiidae, Chlorocyphidae, Hydrophilidae, Naucoridae, Notonectidae, and Pleidae (see Table 4). Chironomidae (Diptera) was the most abundant family at MN3 (19.5%), and the second most abundant taxa at KJ1 (22%), the most abundant being Caenidae (52.3%).

Total invertebrate abundance, taxa richness, and chironomid abundance varied among sites (p = 0.001). EPT taxon richness did not vary among rivers, among months, and among sites; however EPT abundance varied among rivers and among sites for a given river (see Table 3). Mean

Table 3. Results of nested (hierarchical) ANOVA General Linear Model of selected environmental variables and benthic macroinvertebrate metrics from 12 stream sites in Bwindi Impenetrable National Park, Uganda

Variable	Among streams	Among months	Among sites
Environmental variable			
pH	*	***	***
Dissolved oxygen	**	*	***
Conductivity	**	***	***
Temperature	***	***	***
Transparency	***	***	ns
Water level	ns	***	***
Depth	***	***	***
Current	**	***	***
Discharge[a]	*	***	***
BMI metric			
Total abundance	*	ns	***
Taxon richness	*	ns	*
Chironomidae abundance	ns	**	***
Abundance			
EPT taxon richness	ns	ns	ns
EPT	*	ns	*

*$p < 0.05$, **$p < 0.01$, ***$p = 0.001$, ns = not significant. [a]Discharge on Kajembajembe brook sites was not measured.

family richness ranged between 6 and 18 across sites. Highest taxa richness was recorded at MN3 (22), and it was lowest at IS2 (3). Family richness differed among streams and among sites on a stream, but significant seasonal trends were not detected (see Table 3). Total invertebrate abundance varied among streams and sites on a stream but did not differ among sampling times (see Table 3). The Shannon diversity index varied from 1.57 at KJ2 to 2.87 at MB2 (see Table 4). The Shannon diversity index was positively correlated with dissolved oxygen, and EPT-abundance was correlated with dissolved oxygen (see Table 5) implying that EPT tend to inhabit waters with high dissolved oxygen.

Environmental predictors of macroinvertebrate assemblages

The relative magnitude of eigenvalues for each DCA axis is an expression of the relative importance of the axis. DCA axis 1 (eigenvalue = 0.18) and axis 2 (eigenvalue = 0.11) accounted for 29% of the variance in the data set. Stepwise multiple regression model of DCA axis 1 scores with environmental variables showed that water transparency and dissolved oxygen were the best predictors on axis 1. They accounted for 94% of the variance in DCA axis 1 ($F_{(2,9)} = 36.51$, $p < 0.01$). The best predictor on DCA axis 2 was stream depth ($F_{(10,11)} = 30.99$, $p < 0.01$), which explained 76% of the variation on the axis. Five site groups/clusters were identified from plotting DCA axis 1 and 2 scores resulting in the adjustment of our sampling sites into human disturbance categories in Table 1: (i) highly impacted: silted, with no riparian vegetation, in an agricultural catchment (IS1); (ii) high disturbance: intensively logged in the past (KJ1, KJ2 and KJ3) and selectively logged and near formerly cultivated areas (MB1); (iii) medium disturbance: selectively logged forest, wide channel, fast flowing, agriculture upstream (IS2, IS3), (iv) medium disturbance: selectively logged forest, formerly cultivated (MB2), forested, near a road (MB3), and (v) low disturbance: forested (MN1 and MN2), forested, ecotourism activities and human settlements (MN3).

Results of the CCA of sites and taxa in relation to environmental variables are shown in Figure 2. In this biplot, the orientation of the environmental arrow reflects the direction of maximum change of that variable; also the longer the arrow, the greater is its influence on community composition and, for interpretation purposes, each arrow can be extended backwards through the central origin. Thus, sites or taxa with their perpendicular projections near to or beyond the tip of an arrow will be strongly positively correlated with and influenced by the environmental variable represented by that arrow. Those whose projections lie near the origin will be less strongly affected. Water transparency and dissolved oxygen were the most important variables associated with CCA axis 1 and stream depth on axis 2 (see Fig. 2); this result is in agreement with that of DCA where similar variables were the best predictors of DCA axis 1 and 2 scores. From the CCA analysis, the taxa–environment correlations were high suggesting that the eight environmental variables reasonably explained the first two ordination axes. The Eigenvalues (a measure of the strength of an axis or the amount of variation

Table 4. Cumulative number of individuals (as percentages) for macroinvertebrate taxa (families) and Shannon diversity index at 12 stream sites in Bwindi Impenetrable National Park, Uganda

Taxonomic group/site	MB1	MB2	MB3	IS1	IS2	IS3	MN1	MN2	MN3	KJ1	KJ2	KJ3
Ephemeroptera												
Baetidae	18.9	15.0	9.3	13.8	16	16	9.6	3.36	7.7	2.5	23.7	38.9
Caenidae	8.4	1.1	5.0	17.2	28	11	0	3.1	12.2	52.8	54.4	23.0
Heptageniidae	3.2	12.7	0.5	1.4	11	19	5.2	2.5	1.9	0	0.3	0
Polymitarcyidae	0	0	0	5.3	0	0	0	0	0	0	0	0
Prosopistomatidae	0	0	0	0.3	0.5	0	0	0	0.2	0	0	0
Chlorocyphidae	0	0	0	0	0	0	0.3	0	0	0	0	0
Trichorythidae	0	0	0	20.7	0	1.5	0	0	0.2	0	0	0
Ephemerellidae	2.4	2.5	7.5	11.9	0.9	0	2.7	4.5	3.5	0.8	1.7	6.1
Leptophlebiidae	13.9	3.4	0.2	1.1	0	2.3	0.3	0	2.9	0.9	0.6	1.0
Trichoptera												
Calamoceratidae	0	0.2	4.8	0	0	0.8	0.3	3.1	2.3	0	0	0.2
Hydropsychidae	9.5	10.1	8.8	8.8	25	19	17.8	2.2	15.6	0.1	1.3	1.8
Hydroptilidae	0.3	0.7	0.3	0.5	0	0	0.7	0	0.6	0	0	0
Lepidostomatidae	0.5	0.9	3.3	1.4	2.9	0	0.3	0.3	0.4	6.6	2.5	0.6
Leptoceridae	0.3	0.7	21.5	0	0	0	1.4	2.2	1.4	0	0	0.2
Limnephilidae	0.5	1.1	0.5	0.5	0.9	0	0.7	0.8	3.1	0.4	0.3	7.4
Philopotamidae	0.5	3.6	0.3	0	0	0	1.7	1.1	0	0	0.2	0
Polycentropodidae	9	3.8	0.7	0	0	0	0.7	1.4	0	0	0	0
Plecoptera												
Perlidae	0.3	2.2	15.6	0.8	3.4	3.8	28.8	12.6	8.5	0	3	1.0
Hemiptera												
Pleidae	0	0	0	0	0	0	0	0	0	0	0.2	0
Naucoridae	0	0	0	0	0	0	0.3	0	0	0.1	0	0
Notonectidae	0	0.2	0	0	0	0	0	0	0	0	0	0
Diptera												
Ceratopogonidae	1.1	0.5	1.2	0.3	0.9	1.5	1.0	1.7	3.1	1.0	0.2	0.2
Chironomidae	13.1	4.0	8.2	4.9	5.4	10	2.7	4.7	21.4	22.2	31	9.3
Culicidae	0.8	0.2	0.5	0	0.5	0.8	0	0	0.2	0.3	0.2	0.6
Dixidae	0	0	0	0	0	0	0	0	0	0.4	0	1.0
Simulidae	3.2	2.0	0.3	1.9	0	3.8	0.3	0.6	0	2.7	10	0.2
Tipulidae	9	1.6	6.0	0.3	0.5	1.5	2.7	9.8	3.5	1.2	0.2	0.6
Coleoptera												
Dytiscidae	0.8	0.2	0	3.1	0	0.8	0	0.6	0.4	0.1	0.2	0.4
Elmidae	1.1	10.7	3.5	4.2	2.5	6.2	1.7	3.9	4.1	0.2	0	0.2
Gyrinidae	0	0.5	0	0	0	0	2.7	0	0	0.1	0	0
Helodidae	3.2	4.0	0.5	0	0.9	0.8	0.7	7.0	0.8	4.8	1.3	0.6
Hydrophilidae	0	0.2	0	0	0	0	0	0	0.2	0	0	0
Psephenidae	2.6	11.8	0.8	0	0	0.8	13.4	33.3	3.8	0	0	0.2
Odonata												
Aeshnidae	0	0.7	0.2	0	0	0	1.0	0.3	0.6	0	1.0	0.4
Calopterygiidae	0	0	0	0	0	0	0	0.3	0	0	0	0
Gomphidae	0.3	0.2	0.3	0	0	0	0	0	0.6	0	0	0
Libellulidae	8.9	3.6	0.2	0	0.9	0	0.3	0	0.8	0	0	0
Protoneuridae	0	0	0	0.8	0	0	0	0.3	0	0	0	0

Continued on next page

Table 4. (Continued)

Taxonomic group/site	MB1	MB2	MB3	IS1	IS2	IS3	MN1	MN2	MN3	KJ1	KJ2	KJ3
Decapoda												
Potamidae	0	0.2	0	0	0	0	2.1	0	0	0	0	0
Hirudinea	1.8	1.3	0	0.5	0	0	0	0.3	0.2	2.4	5.6	5.6
Sphaeridae	0	0	0	0	0	0	0	0	0	0.3	0	0
H'	2.7	2.8	2.6	2.5	2.0	2.4	2.4	2.5	2.8	1.6	1.7	1.6

along an axis) were 0.490 for the first axis and 0.198 for the second axis. The cumulative variation explained by the first two axes of the taxa-environment relationship in the CCA was 57.1%. This indicates that probably other factors not measured in our study are also important in determining the invertebrate assemblage structure. According to the Monte Carlo permutation test, the first axis was highly significant ($F = 1.497$, $p = 0.005$) and for all axes, the canonical eigenvalue (1.204) was statistically significant ($F = 1.681$, $p = 0.03$), demonstrating a strong relation between the invertebrate assemblage and the measured environmental variables. Results of the stepwise multiple regression analyses show significant correlations between environmental variables (dissolved oxygen, stream width and temperature with H'; transparency and pH with mean taxa richness; and dissolved oxygen with EPT-abundance) (see Table 5). Worth noting are the best predictors of axis 1 in both DCA and CCA – water transparency and dissolved oxygen – are the best predictors of mean taxon richness (TR), and Shannon diversity, and EPT-abundance in the stepwise multiple regression analysis.

Discussion

We provide evidence that the streams flowing through human impacted sites generally differ in water quality and BMI composition from relatively undisturbed sites. Richness and total invertebrate abundance of BMI was lower at high disturbance sites than at the minimally disturbed sites. These findings are consistent with those of Marchant et al. (1994), and Stone & Wallace (1998) who reported taxonomic diversity to decrease with disturbance and increase with recovery. Although selective logging and agriculture seem to affect BMI diversity, the high richness, and diversity, data from previously impacted sites in Bwindi suggests forest recovery. This was the case at MB1 and MB2 sites that were selectively logged and agriculturally impacted in the past, but are now recovering (Mwima & McNeilage, 2003). Sites that are presently being impacted by agricultural activities (Ishasha sites) had very low water quality and invertebrate indices compared to the site previously encroached for agriculture (MB1 and MB2). Differences between the compositions of BMI communities at the impacted and non-impacted sites, as revealed by ordination

Table 5. Stepwise regression models depicting the relationships between environmental variables and biotic indices in Bwindi Impenetrable National Park, Uganda

Biotic index	r^2	p Value	Variable	r/partial correlation	p Value
H'	0.841	0.001	Dissolved oxygen	0.863	0.001
			Stream width	−0.838	0.002
			Temperature	0.741	0.014
Mean taxa richness	0.831	<0.001	Transparency	0.906	<0.001
			pH	−0.781	0.005
EPT-abundance	0.714	0.001	Dissolved oxygen	0.845	0.001

Only indices that showed significant relationships with environmental variables are presented.

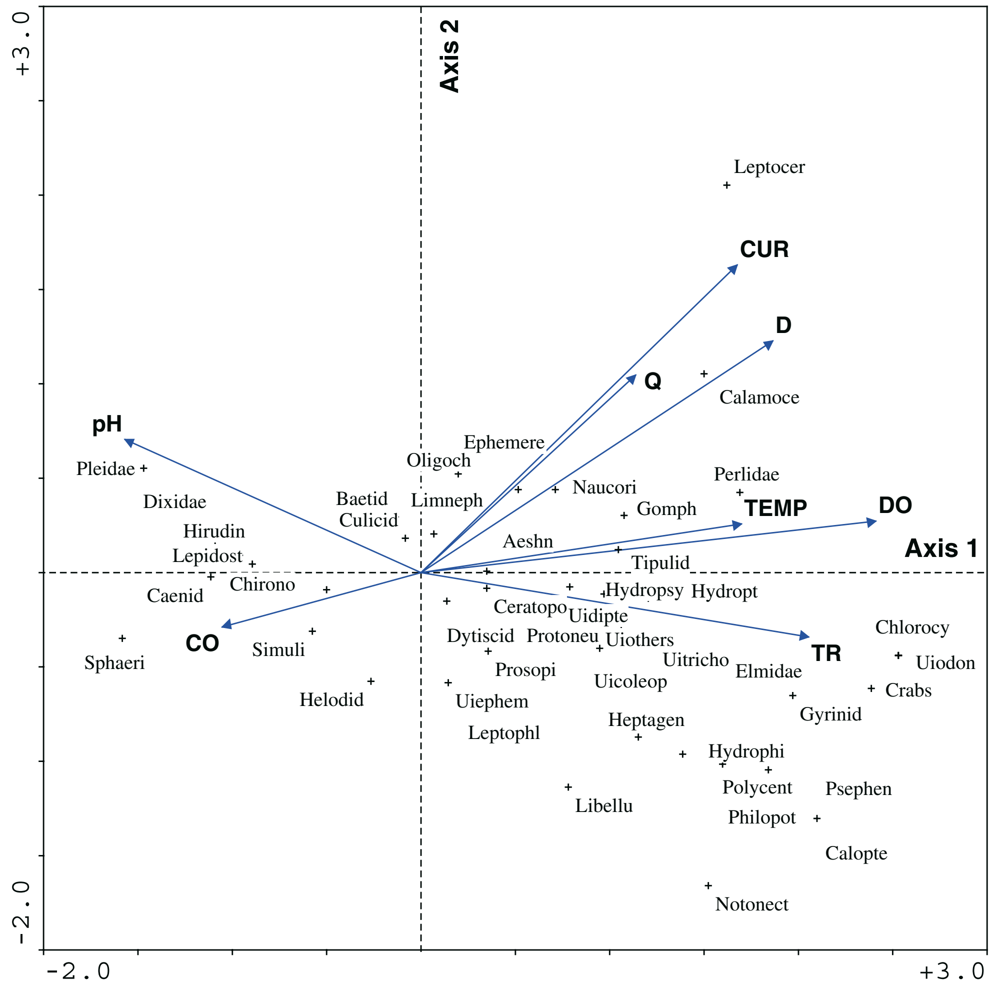

Figure 2. CCA biplot of macroinvertebrate families and environmental variables. Environmental axes extend increasingly in the direction of the arrow, they can be extrapolated in the opposite direction from the origin to depict a decreasing trend in the variables. Full names of abbreviated invertebrate taxa are given in Table 4.

and classification suggested effects of anthropogenic disturbance on water quality.

Variation in water quality with disturbance

River Ishasha had the lowest water transparencies and highest conductivity values, which likely reflects drainage of a catchment area that is intensively cultivated on steep-sided terrain. This supports earlier work by Sponseller et al. (2001) on agricultural drainage and its impact on sediment load and stream conductivity. The abundance of BMI was lower in agriculturally impacted sites than in forested streams. Such low BMI abundance suggests a decline in water quality. The families Trichorythidae and Caenidae that dominated these sites may act as indicators of high disturbance due to agricultural activities. High conductivity and low water transparency were also prevalent at Kajembajembe sites. Though located within the forest interior, past intensive logging practices on steep sided slopes created many large forest gaps, that are currently maintained by elephant browsing and excavating activities (Babaasa et al., 2004), make the Kajembajembe catchment susceptible to erosion. Thus, increased water transparency and reduced conductivity can act as indicators of recovery of previously impacted areas. Along Mbwa stream that was previously encroached for agriculture, the high water transparency is indicative of observed recovery of vegetation that is taking place. This may prevent runoff from reaching the stream. However, given the proximity of the river to a dirt road and the regenerating open forest vegetation in formerly cultivated areas, it usually gets turbid during the rainy seasons. The Mbwa river sites were also dominated by 'clean water' taxa such as Ephemeroptera, Plecoptera, and Trichoptera suggesting the importance of the recovering forest in maintaining ecosystem stability in the stream. Overall, conductivity tended to be low at in-forest minimally impacted sites and was highest at sites outside the forest. This result is in agreement with Growns & Davis (1991) who reported water conductivity to be low in forested sites. The unexpected rise in conductivity at MN3, in spite of being classified as a low disturbance site by DCA analysis, can be attributed to human activity at Buhoma camp due to gorilla tourism. Activities such as washing clothes by the streamside, and runoff from trails, roads and bare/dirt housing compounds may have contributed to increased conductivity. The progressive drop in conductivity and increase in water transparency as Rivers Ishasha and Mbwa flow through the forest highlights the importance of the forest in sequestering the sediment loads from the water. This also emphasizes the importance of existing forest remnants in improving habitat conditions and ecosystem functioning of rural streams and in providing refuges for aquatic organisms.

Relationships between benthic invertebrate assemblages and water quality characters

Biological loss of taxa is a fundamental measure of degradation because taxa represent the basic units from which higher levels of biological organization are abstracted. The diversity of benthic invertebrates was generally high in forested sites. Ishasha sites had the lowest taxa richness, which may reflect its drainage of an agriculturally impacted landscape. In eastern Madagascar, Benstead et al. (2003) in their study of BMI of forest streams versus agriculture streams found the agriculture streams to be depauperate in species and were dominated by generalist collector gatherer taxa belonging to the order Ephemeroptera. Their findings are in agreement with our results in that collector gatherers (Caenidae, Baetidae and Trichorythidae) dominated the agriculture site at IS1. Similarly, in a tropical rain forest in Borneo, Iwata et al. (2003) reported reduced abundance and diversity of benthic assemblages in slash and burn agriculturally affected streams. They concluded that slash and burn agriculture caused long-term degradation of stream communities than logging. The low diversity at these sites may also relate to the high discharge that probably dislodges and washes the invertebrates downstream. The low taxon richness in Ishasha River may also relate to its relatively large size as indicated by the negative correlation between stream width and H'. Reece & Richardson (2000) report that large river sites in British Columbia Canada have low invertebrate abundance, species richness, and diversity relative to small streams. The high taxa richness and diversity at MN3 compared to less disturbed upstream sites (MN1 and MN2) may be due to the reduced acidity at MN3 or may be explained by the intermediate disturbance hypothesis (Connell, 1978). Intermediate disturbance creates space for new taxa but prevents the domination of the community by a small number of competitive species. Maximum taxa diversity is achieved when disturbance creates gaps for new species to colonize, without destroying the larger part of the community. This indicates that anthropogenic perturbations at MN3 related to gorilla tourism are having minimal impact on the stream.

Relationship between BMI and environmental variables

Multiple regression analysis showed that water transparency, dissolved oxygen, pH, temperature and stream width were the most significant variables influencing invertebrate assemblages. The CCA biplot indicated that dissolved oxygen, water transparency, and conductivity influenced the distribution of several invertebrate taxa such as crabs (Potamidae) and psephenid beetles that preferred clear waters (high dissolved oxygen and transparency, low conductivity) such as found in Munyaga stream; whereas Chironomidae, Caenidae and Sphaeridae preferred low dissolved oxygen waters sites of KJ1, KJ2, and KJ3. The sphaerid bivalves (an enrichment tolerant taxa) (Quinn & Hickey, 1990) dominated at KJ1, which may be associated with accumulated debris due to erosion from the large forest gaps, leading to high conductivity and low water transparency. The stoneflies (Perlidae) that are particularly sensitive to deforestation (Quinn & Hickey, 1990) were most abundant in forested (MN1 and MN2) and previously impacted but recovering sites such as along Mbwa sites, with high dissolved oxygen, transparency, and low conductivity.

Agricultural land use has been negatively correlated to stream water quality (Sponseller et al., 2001; Buss et al., 2004), stream habitat quality, and benthic invertebrate community structure (Richards & Host, 1994; Richards et al., 1996). Roth et al. (1996) reported that catchment land use was the primary determinant of ecological conditions in Michigan streams, with the amount of forest having a positive relationship and the amount of agriculture having a negative relationship with index of biotic integrity (IBI) scores. Our results show that forested sites with low and medium impacts had generally high diversity of BMI and good water quality. The mechanisms by which land-use influences stream ecosystems are becoming better understood (Gordon et al., 1992). Forestland cover tends to reduce runoff of water, sediments, nutrients, to maintain more stable flows, water temperature and channel morphologies and to supply coarse organic material and debris to provide food and habitat for aquatic life. Anthropogenic disturbance of the riparian vegetation often increases runoff; destabilizes flow, temperature and channel morphology and reduces the supply of coarse organic material (Wang et al., 1997). Our results indicate that high levels of disturbance have negatively affected water quality as evidenced by depauperate BMI fauna in the high disturbance category sites.

Conclusions

Anthropogenic disturbance correlates with variation in the distribution and abundance of BMI as well as environmental variables in Bwindi streams. The BMI in a given stream reflects the nature of the water quality in that stream. Agricultural development in catchment areas has affected water quality of the streams as witnessed on Ishasha River. Twelve years after Bwindi was gazetted a National Park; our results indicate ecological recovery in formerly encroached areas such as in the Mbwa river tract as reflected in the high water transparency, and low conductivity in the stream. Although logging could have had negative effects on the water quality of affected sites; these seem not to have been long-lived, as most previously selectively logged areas do not show signs of degradation, but intensively logged areas such as the Kajembajembe catchment are still degraded. The findings also highlight the importance of forests in water purification as water quality in Ishasha River progressively improved as it flowed through the forest. Gorilla ecotourism activities around Buhoma still have low impacts on water quality at MN3 site. But as the number of people inhabiting the area increases, human activities such as paving of trails, planting grass along roads and in compounds, cleaning household items far from the river and improved sanitation will need to be encouraged. It is recommended that regular (quarterly) monitoring of water quality be carried out to act as an early warning system of deterioration and for tracking ecosystem recovery of previously impacted sites. Clean water taxa such as the crabs (Potamidae), stoneflies (Perlidae), Psephenid beetles, and the sensitive families of Trichoptera (e.g. Hydropsychidae and Leptoceridae) and Ephemeroptera (e.g. Baetidae) can act as indicators of 'good' ecological health of rivers. The dominance of taxa such as Chironomidae, Trichorythidae, and Caenidae may indicate deterioration of water quality of a given river. Water conductivity and water transparency were the most important variables in depicting the ecological health of streams.

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