Effects of reforestation on benthic macroinvertebrate diversity and assemblage in Costa Rican headwater streams.

Andrew E Memory.

Cloudbridge Nature Reserve, Costa Rica.

Abstract

The effects of reforestation on benthic macroinvertebrate communities were studied at twelve headwater streams located in a mixture of primary forest, rehabilitated secondary forest and pastoral land in Southern Costa Rica. The study encompassed a six month period from the end of the dry season and through the wet and dry seasons. Comparisons between forested and deforested sites showed that deforestation altered benthic macroinvertebrate assemblage composition, reduced macroinvertebrate diversity and eliminated sensitive taxa. Rehabilitated secondary forested sites displayed the highest diversity of all three catchments as well as the greatest substrate and macroinvertebrate assemblage heterogeneity. Among environmental variables canopy cover was shown to have significant effects on several environmental variables including substrate and pH ($P<0.05$). There were no significant differences in macroinvertebrate assemblage structure between seasons nor were there any significant differences in environmental variables between catchments ($P<0.05$).

Introduction

Freshwater ecosystems are regarded as one of the most endangered ecosystems on the planet (Dudgeon et al 2006; Sala et al 2000). Freshwater ecosystems represent 0.01% of all water on the planet covering a total of 0.8% of the Earth's surface (Jackson et al 2001) contained within this 0.8% are an estimated 100,000 species with a potential increase of 50,000-100,000 species residing within groundwater (Gibert & Daharveng 2002). One of the major factors impacting on freshwater biodiversity is the loss of habitat especially the loss of riparian forest (Dudgeon et al 2006). Between 1990 & 1997 5.8 ± 1.4 million hectares of tropical forest has been estimated to have been felled annually (Archard et al 2002) and since then the rate of deforestation has increased annually (Fearnside 2005). The loss of riparian vegetation has been shown to have numerous impacts on freshwater ecosystems; foremost is the loss of species diversity and major shifts in benthic community structure due to alterations in water flow regimes, increased sediment and nutrient loads, light levels, species relationships and homogenisation of biodiversity and other environmental variables (Sweeney et al 2004; Bunn & Arthington 2002; Delong & Brusven 1998; Dudgeon 2000; Ricciardi

& Rasmussen 1999). Socioeconomic trends throughout the last decade have resulted in the extensive reforestation of land previously used for agriculture (McTammany et al 2007) with the large number of studies focussing on the effects this has on streams present in temperate climates (Harding et al 1998; McTammany et al 2007). Few studies in comparison have focussed on the effects that reforestation might have in tropical ecosystems (Lorion & Kennedy 2009; Bruijnzeel 2004) with the majority of tropical studies assessing the impacts that slash and burn agriculture has had on freshwater ecosystems (Bojsen & Jacobsen 2003; Iwata et al 2003; Dudgeon 2000). Fewer studies still have focussed on the effects that reforestation may have on tropical benthic macroinvertebrate communities (Lorion & Kennedy 2009; Lorion & Kennedy 2009). Through the creation of riparian buffer zones it has been shown that impacts of deforestation can be reduced providing greater allocthonous inputs, trophic complexity and greater terrestrial- aquatic linkages (Baxter el al 2005; Tabacchi et al 1998). However reforestation of the riparian zone has been shown to have neutral to negative impacts on stream hydrology and levels of sedimentation (Bruijnzeel 2004) and in the case where exotic species have been planted resulted in the homogenisation of freshwater faunas at regional and local scales (Rahel 2002; Heino et al 2003).

In this study I investigated the extent that the reforestation of cattle pasture has moderated the effects of deforestation on benthic macroinvertebrate assemblages in head water streams in southern Costa Rica. Costa Rica has been subject to widespread deforestation historically (Sanchez-Azofeifa et al 2001). The riparian zones in all pastoral sites had been deforested before the National Forestry Law N7575 was implemented in 1996. Due to these conditions I was able to compare sites affected by deforestation, those in rehabilitation and old growth forest.

I hypothesised that as the level of canopy cover increases that species diversity will increase and the composition of benthic macroinvertebrate assemblages will be more heterogeneous. I also hypothesised that temporal dissimilarity will have reduced effects on benthic macroinvertebrate assemblages and environmental variables in forested catchments than in pastoral catchments. In order to test these hypotheses I compared benthic macroinvertebrate assemblages and environmental variables in i) primary forested reaches, ii) secondary forest under a reforestation program, iii) pastoral reaches under grazing pressure throughout a six month period covering pre-wet, wet and dry seasons.

Methods

Study Area and Sampling Sites

The study was conducted in the Upper Chuma and Chespa valleys in the Talamanca Mountain Range, Costa Rica within the Cloudbridge Nature Reserve and the Talamanca Reserve. The Cloudbridge Nature reserve and Talamanca reserve cover 4600 acres characterised by a mixture of primary and secondary forest as well as open pasture and adjoin the northern end of the Chirripo National Park. All twelve streams were located within a maximum of 15km, at a latitude of 9º28'N and longitude of 83º34'W at an elevation between 1675m and 2000m. The climate is equatorial with a mean annual temperature of 25ºC and a mean annual rainfall of approximately 5100mm, with the majority of rainfall falling between September and November. Stream temperatures typically range between 15ºC and 20ºC with little seasonal variation and stream discharge relating to rainfall events. Watersheds are steep and narrow with boulder lined pools and riffles and in forested sites, headwater streams are heavily shaded and have low nitrogen and phosphorus levels similar to other tropical headwater studies (Wright & Covich 2005).

The study included twelve sites (25m reaches) in 11 headwater streams (1-2 order). The sites were selected so that one third represented primary forested reaches, one third reforested secondary reaches and the final third farmed pastoral reaches. Resulting in a canopy cover gradient between 0% to 77% among the twelve sites. All streams were small (0.5m- 3m mean width) fast flowing streams with sand, gravel and cobble substrata. All streams flowed into the Chirripo River. No fertilisers or pesticides are used by the subsistence farmers in the pastoral sites surveyed. Secondary and pastoral sites have been subject to slash and burn deforestation during the last fifty years with secondary forest sites undergoing reforestation programs within the last decade.

Environmental Variables

Environmental variables including habitat and catchment characteristics were measured at each sampling period: pre wet season (August 2009), wet season (October/ November 2009) and the start of the dry season (December 2009) (table 1).

Canopy cover was measured at every 5m point in the centre of the streams along the transect and determined through personal observation and expressed as percentages. Each stream was categorised in relation to the degree of deforestation by the use of maps, local history and personal observations. Stream catchments were characterised into category one: primary forest with no history of deforestation, category two: secondary forest currently under a reforestation program and category three: pastoral under grazing pressure. At each five meter point along the transect cross-stream transects were placed and depth measurements (to the nearest mm) were taken at 0.25m intervals. Width measurements (to the nearest mm) were recorded at each five meter point as well as temperature and substrate type (categorised as sand, gravel and cobble) using a 0.25m²quadrat. Velocity was measured using the floatation method where a run of at least five meters along the transect at each site was selected. Temperature and pH were recorded using a HACH stream survey kit, with pH measured every 8m. To measure concentrations of nitrogen, ammonium and phosphorus, six water samples were collected at each site with concentrations determined through the use of a HACH stream survey kit. Due to issues arising from Costa Rican customs and the availability of sampling chemicals, the number of water samples was reduced to two samples for the final sampling period. Furthermore due to a faulty conductivity meter and the before mentioned customs, conductivity was unable to be assessed. Due to the remoteness of the research station periphytic algae productivity was also unable to be assessed. An environmental assessment was performed during each sampling period using the Stream reach inventory and channel stability evaluation (Pfankuch 1975).

Benthic Macroinvertebrate Sampling

Benthic macroinvertebrates were measured at each sampling period. At each site four surber samples (area 0.25m², mesh size 250µm) were taken at random intervals along the length of the transect. Litter substrates were absent in all sites. Samples were preserved in 70% ethanol and transported back to the lab for identification. All macroinvertebrates were fully examined using a stereoscopic microscope to family level with the majority being identified to sub family level and genus using the available taxonomic key (Merritt & Cummins 1984). All specimens were assigned to one of four major functional feeding groups, shredders, predators, collectors and

filterers according to Merritt & Cummins (1984) and Dudgeon (1994). Taxonomic richness was calculated as the total number of invertebrate taxa recorded at each site.

Data Analysis

Analysis used both continuous and categorical data. For practicality the data is presented categorically although the study enables both types of analysis.

Because diversity is comprised of two components (species diversity and species evenness) I calculated several indices covering alpha and beta diversity. Each index measured a different aspect of diversity. Each has received support in reviews and other studies on the topic (Death 2002; Bojsen & Jacobsen 2003). For the indices such as the Fisher Alpha Diversity, which have encountered criticism (Jost 2007) I have included further tests of diversity. The indices used for analysis are:

1) Species density (S) as defined as the number of species collected along a specified area of habitat.

2) Margalef's Index (Clifford & Stephenson 1975) which is a measure of species richness represented by the formula:

$Dmg=(S-1)/lnN$

(N represents the total number of individuals collected within the specified sample area or sample)

3) The Berger- Parker dominance index (Berger & Parker 1970), which is a measure of evenness/ dominance represented as

$D=N_{max}/N$

N_{max} represents the number of individuals of the dominant species.

4) Simpson's Index (1949) which is another measure of evenness and calculates the probability of two species drawn from a population being of the same species. Simpson's index is represented by the formula.

$D_{Simpson} = \Sigma\ n_i(n_i\text{-}1)\ /\ N(N\text{-}1)$

Where *ni* equals the number of species towards the *ith* individual. The Simpson Index is weighted towards the most dominant species present however it is supported by numerous authors (Death 2002) because it better represents the entire species-abundance distribution than other indices such as the Shannon-Wiener Index.

Increases in the Berger-Parker dominance index and Simpson Diversity Index represent a decrease in species evenness.

5) Fisher's Alpha Diversity Index (Fisher et al 1943), which measures species richness independent of the sample size/ number of individuals.

$S=a*ln(1+n/a)$

6) Whittaker's Beta Index (Wilson & Schmida 1984): Describes the relationship between the total number of species and the mean species richness found at each sampling site.

$\beta=S/\square\text{-}1$

7) Routledge's Beta (Wilson & Schmida 1984) describes the total number of species and the number of species pairs that have overlapping distributions.

$$\beta_R = \frac{S^2}{2r+S} - 1$$

$$\beta_I = \log(T) - \left[\left(\frac{1}{T}\right)\sum e_i \log(e_i)\right] - \left[\left(\frac{1}{T}\right)\sum \alpha_i \log(\alpha_i)\right]$$

$$\beta_E = \exp(\beta_I) - 1$$

The analysis of Fisher's Alpha Diversity Index, Simpson's Diversity Index and Margalef's Index between the environmental variables in all three sample treatments was analysed through the use of Spearman rank correlation. Alpha diversity describes the local diversity or point diversity of a site whereas beta diversity represents the change in diversity from site to site. All calculations of diversity were made to species level.

The relationship for each taxa and environmental variables (Table 2) were tested using single factor ANOVA after testing for normality and homogeneity of variances and subsequent appropriate log transformations had been made. All analysis was conducted through R:1.5.1 statistical software.

Results

Habitat Characteristics

All Primary forest sites had high levels of canopy cover between 65 and 71% (mean 68%) while canopy cover in secondary sites ranged from 31-59% (mean 47%; Table 1). Pastoral sites had no cover. Stream substrate was comprised of sand, gravel and cobbles with each being represented within each environment; primary sites were dominated by sandy substrates (mean 72%) whereas pastoral sites were dominated by mainly cobble substrates (mean 67%) and secondary sites equally comprised of each substrate class (Table 1). Streams were small to moderate in size; mean depth ranged from 4cm to 20cm, current velocity from 0.02 to 0.13m/s and mean stream width from 95cm to 2m in all twelve sample sites. Water temperature was consistent throughout all environments (16.3-17.8) as to pH (6.98-7.4). The most pronounced difference in environmental variables between sites was found between the secondary forest and pasture and the level of pH and nitrogen (P<0.05). The level of canopy cover was shown to have significant effects on the level of pH, depth and amount of cobble substrate between sites (P<0.05).

(Table 1. Environmental characteristics (means and ranges) between primary forest stream sites (n=4), secondary forest stream sites (n=4) and pastoral stream sites (n=4) in the Chespa and Chuma valley's, Costa Rica)

	Primary Sites	Secondary Sites	Pasture Sites
Canopy Cover%	68.1 (64.9-71.1)	47 (31.2-59.4)	0.00
Catchment Category	1-2	1-2	1-2
Mean Depth (m)	0.06 (0.04-0.09)	0.07 (0.06-0.08)	0.17 (0.14-0.2)
Mean Width (m)	1.10 (0.95-1.3)	1.07 (0.8-1.4)	1.4 (0.78-2.1)
Mean Current Velocity (ms^{-1})	0.03 (0.02-0.05)	0.041 (0.02-0.05)	0.18 (0.04-0.32)
Water Temperature	17.7 (17.6-17.8)	16.7 (16.3-17.2)	16.8 (15.4-17.8)
pH	7.08 (6.98-7.1)	7.225 (7.1-7.4)	7.2 (7.1-7.4)
PO4-P (μm1^{-1})	0.32 (0.3-0.34)	0.34 (0.27-0.4)	0.28 (0.27-0.3)
NH3-N (μm1^{-1})	0.00	0.0003 (0-0.001)	0.03 (0.01-0.06)
NO3-N (μm1^{-1})	0.42 (0.4-0.5)	0.81 (0.54-1.1)	0.78 (0.4-1.3)
Pfankuch Diversity Index	43.58 (41.3-46.6)	64 (55.8-72.4)	87.75 (69-100.9)
Substrate Types			
Sand %	72.25 (60.8-88.9)	36.67 (24.1-47.1)	9.6 (1.7-17.42)
Gravel %	14.2 (3.6-21.4)	32.4 (23-45)	22.4 (15.4-30.7)
Cobble %	13.6 (7.5-18.3)	28.2 (21.4-35.3)	67.17 (56.5-75.7)
Habitat Types			
Pool %	8.4 (2.5-13.7)	11.25 (6.8-14.1)	17.25 (11.1-28.2)
Riffle %	25.5 (3.7-53.3)	21.9 (4.4-51.4)	38.5 (25.6-56)
Run %	65.25 (39.2-83.6)	68.58 (42.2-87.3)	44.25 (25.6-55.8)

Species Diversity and Abundance

A combined total of 53 macroinvertebrate families were collected with a total of 334 taxa covering all 12 sample sites (Table 2). Macroinvertebrate density and the number of individuals at a site ranged from 30 to 131 individuals m^{-2} and 11 to 27 taxa per site m^{-1}. In primary forested sites the number of taxa ranged from 17 to 23 taxa per site^{-1}, in secondary forested sites the number ranged from 20 to 27 taxa per site^{-1} and the pastoral sites ranged from 11 to 21 taxa per site^{-1}. Pastoral sites were the most depauperate in the number of taxa between the three treatments with 78 taxa despite having the greatest density of individuals (84 per m^{-2}; Table 2). Secondary forested sites displayed the greatest species richness between the three treatments but also displayed the lowest density of individuals (total number of taxa 138; density of individuals 63 (per m^{-2})), (Table 2).

(Table 2. Densities of individuals (per m⁻²) of macroinvertebrate families found in the primary forested, secondary forested and pastoral stream sites in the Chuma & Chespa valley's, Costa Rica. Means and ranges (bracketed) of the total number of macroinvertebrate taxa and density of individuals (per m⁻²) are displayed at the bottom of the table. Families and orders are presented in bold. The functional feeding groups displayed are Shr=Shredders, Pre=Predators, Col=Collectors and Fil=Filter Feeders.)

Taxonomic Groups		Secondary Sites	Primary Sites	Pastural Sites	Functional Feeding Group
Diptera	**Tipulidae**	3.33	5.58	0.25	Shr
	Limoniinae	2.75	5.08	-	Shr
	Tipulinae	-	0.08	-	Shr
	Chironomidae	2.17	0.33	6.50	
	Tanypodinae	4.08	5.58	1.42	Pre
	Chironominae	0.75	3.83	0.08	Col
	Diamessinae	0.42	-	-	col
	Podominae	0.50	-	-	col
	Simulidae				
	Simulium	0.58	1.25	0.33	Fil
	Prosimulium	1.50	1.83	0.67	Fil
	Blephariceridae	0.08	-	-	Fil
	Ceratopogonidae	0.33	0.33	-	Pre
	Thaumaleidae	0.25	-	-	Pre
	Brachycera	0.25	-	-	Pre
	Orthorrhapha	0.17	-	-	Col
	Cyclorrhapha	0.25	-	-	Col
	Psychodidae	-	0.25	-	Col
	Chaoboridae	-	0.08	-	Pre
Coleoptera					
	Haliplidae	0.50	0.08	2.33	shr
	Hygrobiidae	0.08	-	-	Pre
	Elmidae	4.67	3.25	2.75	Col
	Cylloepus	0.25	0.08	-	Col
	Neocylloepus	0.58	0.17	-	Col
	Lara	0.08	0.08		Col
	Rhizelmis	-	0.25	-	
	Ancryonyx	0.25	-	0.08	Col
	Chrysomelidae	-	0.08	-	shr
	Gyrinidae	-	-	0.08	pre
	Amphizoidae	-	-	0.08	pre
	Staphylinidae	0.42	-	-	pre
Trichoptera	**Hydropsychidae**				
	Macronematinae	2.42	2.50	0.50	Fil
	Arctopsychinae	2.25	0.92	1.42	Fil
	Hydropsychinae	2.58	0.83	0.92	Fil

	Diplectroninae	0.25	0.08	0.08	Fil
	Helicopsychidae				
	Helicopsychinae	0.33	0.08	-	Fil
	Hydroptilidae				
	Hydroptilinae	0.08	0.17	0.67	Col
	Neotrichiini	0.17	0.92	0.75	Col
	Leucotrichiini	1.67	0.25	18.75	Col
	Ptilocolepinae	0.25	0.67	0.83	Col
	Orthotrichiini	0.50	0.25	0.17	Shr
	Polycentropodidae	0.67	-	-	Col
	Molannidae	0.08	-	-	Col
Plecoptera	**Pteronarcyidae**	2.67	1.67	4.00	Shr
	Taeniopterygidae	0.08	-	-	Shr
	Peltoperlidae	0.25	-	0.08	Shr
	Chloroperlidae	-	-	1.25	Shr
Hemiptera	**Corixidae**	0.75	0.92	1.58	Pre
	Belostomatidae	0.08		0.08	Pre
	Gelastocoridae	-	0.08	1.67	Pre
	Ochteridae	-	-	0.08	Pre
Ephemeroptera	**Potamanthidae**	0.25	0.08	0.08	Col
	Ephemerellidae	0.33	0.58	-	Col
	Tricorythidae	2.67	0.17	2.75	Col
	Behningiidae	5.67	3.50	21.50	Pre
	Oligoneuridae	0.17	-	2.17	Fil
	Palingeniidae	0.25	0.25	-	Col
	Heptageniidae	2.92	1.00	1.67	Col
	Baetiscidae	0.33	-	1.17	Col
	Ametropodidae	0.08	-	-	Col
	Polymitarcyidae	0.08	-	-	Col
Odonata	**Zygoptera**	0.08	-	0.42	Pre
Lepdioptera	**Tortricidae**	0.08	-	-	Shr
Arthropod		0.42	0.17	0.17	pre
Collembola	**Isotomidae**	0.17	0.17	-	Col
	Poduridae	0.08	-	-	Col
	sminthuridae	-	-	-	Col
	Entomobryidae	-	-	0.75	Col
Annelida		0.58	1.00	0.08	Shr
Oligochaeta		4.25	2.50	2.75	Shr
Gammerus		0.17	10.67	-	Col
Mollusca					
	Gastropoda	-	1.08	0.25	Col
Crustacea		-	0.17	0.08	Col
Total number of taxa		138 (20-27)	118 (17-23)	78 (11-21)	
Mean number of individuals m-²		62.83 (30-92)	64.75 (39.3-72)	83.75 (34-131)	

Fisher's alpha diversity index was only significantly correlated with stream depth (P<0.05) out of the environmental variables and was greatest within secondary forest sites (Fisher's alpha=28.32) followed by primary forest (Fisher's alpha=15) and finally pastoral sites (Fisher's alpha=8.1). Margalef's diversity index however was strongly correlated with the level of canopy cover, NH3, Stream stability (Pfankuch index), velocity, sand, cobble and depth (P<0.05) and followed the same pattern as Fisher's alpha with secondary forest sites having the highest scores and pastoral sites the lowest. The total number of taxa was significantly related to stream depth and the number of individuals (per m^{-1}) (P<0.05).

Whittaker's beta index indicates that within habitats that beta diversity is greatest within pastoral sites (0.083) compared to primary forested sites (0.001) and secondary forested sites (0.001). Routledge's Beta index however shows that in terms of over lapping species pairs that beta diversity is greatest in secondary forested sites (0.21) followed by pastoral sites (0.19) and then by primary forested sites (0.052).

This indicates lower heterogeneity among macroinvertebrate taxa in primary forested sites than in the other two treatments. The Berger- Parker Dominance Index was greatest in primary forested sites (0.7) followed by pastoral (0.37) and secondary forested sites displaying the lowest score (0.23). The Simpson index also displayed primary forested sites as having the greatest score (0.83) followed by secondary forested sites (0.64) and finally by pastoral sites (0.35).
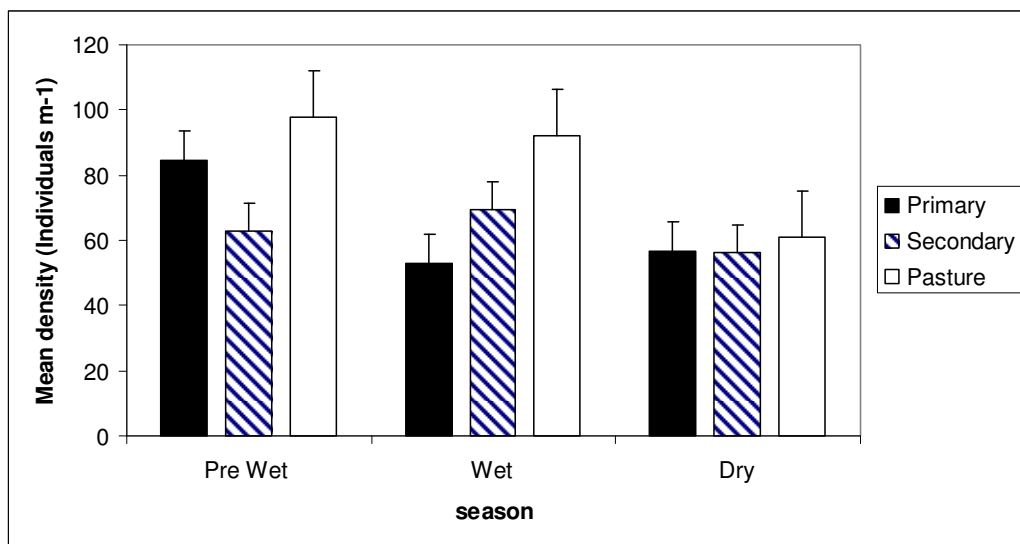
(Figure 1. Mean macroinvertebrate density in primary, secondary and pastoral streams sites during the pre wet, wet and dry seasons.)

Macroinvertebrate Assemblage Structure

Coleoptera, diptera, ephemeroptera and trichoptera were the dominate orders in the macroinvertebrate densities in all three environments (Figure 2). The families Behningiidae and Hydroptilidae comprised 54% of the total number individuals (per m^{-2}) in pastoral sites. In primary forest sites, the families tipulidae, chironomidae and order gammerus comprised 48% of the total number of individuals (per m^{-2}) and in secondary sites the families hydropsychidae, tipulidae and chironomidae comprised 34% of individuals (per m^{-2}) (Figure 2). The ten dominant macroinvertebrate family densities were shown to have significant correlations between one or more of the environmental variables ($P<0.05$). These families are tipulidae, chironomidae, haliplidae, hydropsychidae, hydroptilidae, pteronarcyidae, tricorythiidae, behningiidae, heptageniidae and the order gammerus. The families' heptageniidae, tipulidae, haliplidae, tricorythiidae, behningiidae and order gammerus displayed significant correlations with several environmental variables: canopy cover, temperature, velocity, depth, sand, cobble, gravel, pH, N, NH3 and P ($P<0.001$).
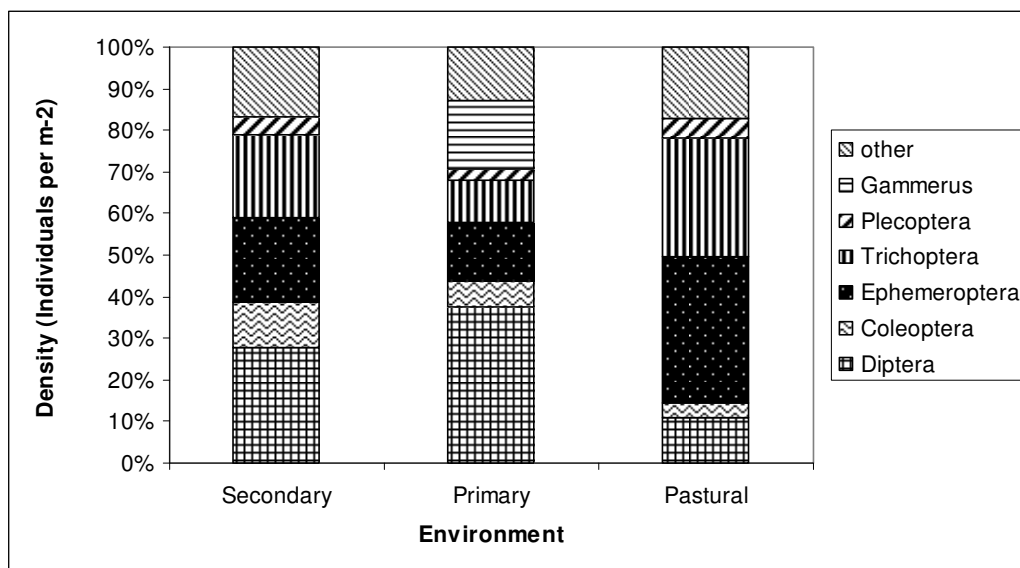
(Figure 2. Density of individuals (per m^{-2}) of the major macroinvertebrate groups found within the three catchment types.)
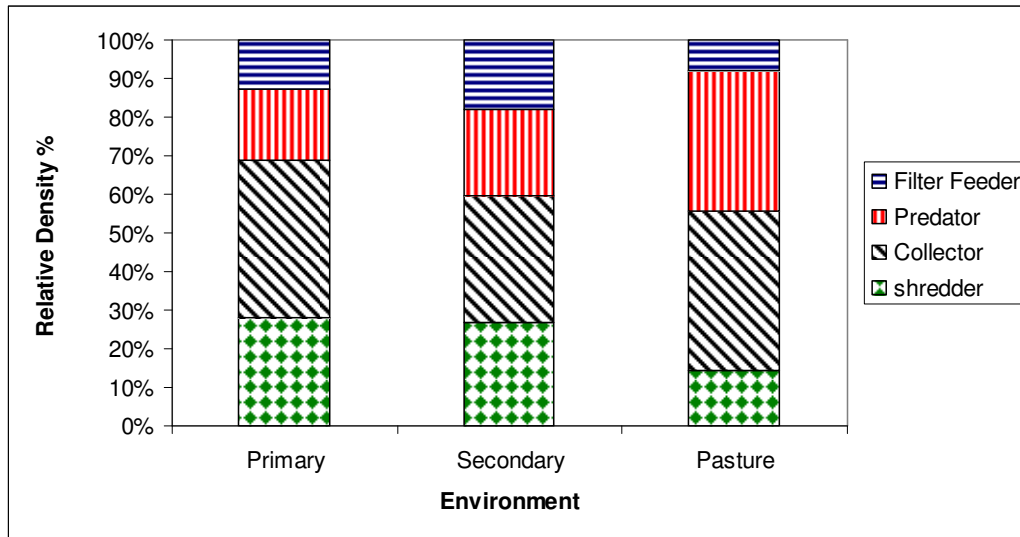
(Figure 3. Relative density of the four major functional feeding groups and changes between catchment type).

Functional Feeding Groups

The total absolute densities of individuals (per m^{-2}) as well as per treatment densities individuals (per m^{-2}) of functional feeding groups were significantly correlated with one or more environmental variables ($P<0.05$), except for shredders ($P>0.05$). The total number of collectors were shown to be significantly correlated with phosphorus, gravel and sand ($P<0.05$). Total predator densities were shown to be significantly correlated with temperature, sand and gravel ($P<0.05$). Total filter feeder densities were only significantly correlated with stream stability ($P<0.05$). Primary forested feeding group densities showed that predators, collectors and filter feeders were significantly correlated with temperature, stream stability and canopy cover ($P<0.05$). Secondary forested feeding group densities showed that collectors were significantly correlated with canopy cover ($P<0.05$) and predators displayed significant correlations with phosphorus, stream stability and canopy cover ($P<0.05$). In pastoral feeding group densities collectors were significantly correlated with pH and cobble substrate ($P<0.05$) and predators were significantly correlated with temperature, velocity and depth ($P<0.05$). The densities of shredders in all treatments as well as in absolute densities were unrelated to all environmental variables ($P>0.05$).

Temporal Dissimilarity

There was non significant differences between species richness and density of individuals (per m^{-2}) between all three sampling periods (P>0.05) (Figure 1; Table 1). There was however significant differences in the level of phosphorous and nitrogen between the wet and dry seasons in all three habitat treatments (P<0.001).

Discussion

The results show that the deforestation of primary forest to agriculture and followed by subsequent reforestation can lead to significant changes in benthic macroinvertebrate diversity and community structure in Costa Rican headwater streams. The results are of particular interest due to the extremely high taxonomic diversity of each environment and the stark differences in substrate composition as well as other environmental variables between the three environments. Although it was impossible to sample secondary forested and pastoral sites before, during and immediately after the disturbances, the geographic proximity of sampling sites and similarities in stream and geographic morphology suggest that prior to habitat modification that benthic macroinvertebrate communities were similar in diversity, abundance and composition. Hence differences observed between primary, secondary forested and pastoral sites can be attributed to changes in land use (Lorion & Kennedy 2009).

The effects of deforestation from primary forest to pasture on benthic macroinvertebrate communities resulted in significant changes in several environmental variables most notably canopy cover, substrate type, stream stability and depth (P<0.05). Canopy cover was significantly correlated with the level of pH, substrate and stream depth (P<0.05) all of which were shown to be significantly correlated to either Fisher's alpha or Margalef's indices (P<0.05). Through changes in environmental variables due to disturbance factors such as deforestation; communities have been shown to be impacted by the breakdown of species interactions, homogenisation of physico-chemical variables such as stream substrate, invasions by tolerant species and loss of keystone species (Harding et al 1998; Cardinale et al 2002; England & Rosemond 2004). The pastoral sites sampled, which were under grazing pressure displayed numerous changes in physico-chemical variables

correlated with the lack of canopy cover resulting in the macroinvertebrate assemblages having lower species diversity and alpha diversity scores as well as greater abundance than both the primary and secondary forest sites (Table 1). This result is supported by other studies and follows the trend of benthic macroinvertebrate assemblages affected by deforestation in both tropical and temperate catchments (Bojsen & Jacobsen 2003; Lorion & Kennedy 2009: Couceiro et al 2007; Harding et al 1998; Quinn 2000). The result also supports part of my hypothesis that with increasing canopy cover that benthic macroinvertebrate assemblages will have greater species diversity present and heterogeneous community composition due to an increased amount of available habitat. However the results of the beta indices show that as primary forest is converted into agriculture that beta diversity increases suggesting that primary forest sites have lower heterogeneity contrary to other tropical studies of the impact of deforestation on beta diversity (Bojsen & Jacobsen 2003). This result of lower heterogeneity of macroinvertebrate fauna in primary forest sites is further supported by the highest dominance scores in both the Berger-Parker Dominance and Simpson indices out of the three catchment types meaning that species abundance is the least even within primary forest sites (Death 2002). This lack of evenness may be due to the sand dominated substrate of primary streams (Table 1; Table 2) and in part responsible for the dominance that the family tipulidae and order gammerus (gammerus were not found in significant numbers outside primary forest sites (Table 2)), which have been found to prefer coarse substrates similar to those found in primary forest reaches (Iwata et al 2003).

In comparison to both primary and pastoral sites; secondary forest sites displayed assemblages that were similar to primary forested sites (Figure 2; Figure 3) however both substrate heterogeneity and species diversity was greater in secondary forested sites (Table 1; Table 2; Fisher's alpha=28.32). Numerous studies have investigated the reasons why species abundance is greater in habitats that display an intermediate level of disturbance (Palmer et al 1989; Townsend et al 1997; Vinson & Hawkins 1998; Lake 2000 & Petraitis et al 1989) and due to the transitionary nature of the secondary forest sites especially the successional nature of the riparian zone and stream substrate heterogeneity, which unlike primary forest and pastoral sites did not display dominance of any one form of substrate (Table 1) it is unsurprising that species richness was greater than in the other environments as there are more habitats available and hence more available resources due to the high turn over in surrounding

riparian vegetation (Graca 2001; Lorion & Kennedy 2009; McCabe & Gotelli 2000). The level of species diversity displayed by all three catchments (Table 2) is unusual in comparison to all other tropical studies which record between ninety and one hundred and fifty taxa (Velasquez & Miserendino 2003; Lorion & Kennedy 2009) in comparison to the three hundred and thirty four taxa found in this study. Due to the inability to measure primary productivity and conductivity both important factors in the amount of species diversity (Vinson & Hawkins 1998) only assumptions through other environmental variables, altitude and substrate heterogeneity can be made as to why species diversity is as high as it is (Outridge 1987; Jacobsen 2008). Secondary forest sites displayed the lowest density of individuals out of all three catchment types. This supports both the intermediately disturbed nature of the sites and the influence of substrate heterogeneity on the community as no one species dominated the benthic macroinvertebrate assemblage (Lake 2000; Outridge 1987; Table 2). Pastoral community structure was primarily dominated by *Zumatrichia* (trichoptera) and *Dolania* (ephemeroptera), (Table 2; Figure 2) with the functional feeding composition comprised predominately of collector-scrapers and predators (Merritt & Cummins 1984; Figure 3). Although primary productivity of stream sites was unable to be assessed due to the remote location of the study the community structure shares parallels with other studies on deforestation and the impacts it has on physico-chemical variables, functional feeding groups and relationships between species (Lamouroux et al 2004; Ramirez & Pringle 1998). Primary and secondary forested sites displayed more heterogeneous functional feeding groups than pastoral sites and were dominated primarily by *Tipulidae* (Diptera) and although primary forested sites displayed the greatest scores in terms of dominance and the lowest beta scores resulting in reduced species evenness and species heterogeneity amongst macroinvertebrate faunas between primary sites, the difference in relative density of functional feeding groups between primary and secondary sites is small (Figure 3). This trend in secondary and primary forest functional feeding groups and species dominance is supported in other studies (Lorion & Kennedy 2009; Benstead et al 2003).

Temporal variation between all three sampling periods was shown to have to non significant effects on the species diversity richness, density of individuals or community structure throughout all three catchment types. This is contrary to other studies on tropical headwater streams which show significant increases/decreases in

the density of individuals as seasons change from wet to dry (Bojsen & Jacobsen 2003; Dudgeon 2000). The reason for this low abundance may be due to low level of primary production, which although not measured in this study has been shown to be affected by nitrogen and phosphorus levels, which were found to have low concentration levels in all catchments (Jacobsen et al 1997; Biggs et al 2004; Table 1) and follow trends in the density of individuals found in other tropical headwater studies that display low nitrogen and phosphorus levels (Wright & Covich 2005). Nitrogen and phosphorus levels were found to significantly decrease from the wet season to the dry season (P<0.05) following the same pattern found throughout tropical studies in Asia and South America and is attributed to increased stream discharge and disturbance of periphytic algae (Dudgeon 2000; Bunn & Arthington 2002). There were no significant differences in nitrogen and phosphorus levels between sites throughout the three sampling periods (P<0.05). These results in temporal dissimilarity disprove my secondary hypothesis that the changes in temporal variations would be great have the greatest impacts on pastoral sites and minimal impacts in primary forested sites.

The planting of endemic trees species in secondary forest catchments riparian zones opposed to exotic species has been suggested as a method in maintaining species diversity at both local and regional scales (Rahel 2002). Due to the short term nature of the reforestation program at the Cloudbridge Nature Reserve it is impossible to state that homogenisation of species is being reduced despite promising early results as full rehabilitation may require several decades before returning to pre-disturbance levels (Harding et al 1998; Iwata et al 2003). The initial results do however show that since reforestation, that the heterogeneity of substrates and community composition has increased and that species diversity as a result has also increased. Should the secondary forested sites be given the time to return to pre-disturbance levels then it is likely that as canopy cover increases that species diversity and beta diversity will decrease as the substrate and other environmental variables become more homogenous and that evenness will increase as species become dominant. Should the rehabilitation of endemic riparian and forest species continue at the Cloudbridge Nature Reserve it should help promote the survival of local endemic biodiversity and ecosystem functioning until a pre disturbance state returns.

Acknowledgements

References

Achard, F; Eva, H.D; Stibig, H; Mayaux, P; Gallego, J; Richards, T. & Malingreau, J. (2002): Determination of deforestation rates of the world's humid tropical forests.- *Science* **297**:999-1002.

Baxter, C.V; Fausch, K.D. & Saunders, W.K. (2005): Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*. **50**: 201-220.

Benstead, J.P; Douglas, M.M. & Pringle, C.M. (2003): Relationships of stream invertebrate communities to deforestation in Eastern Madagascar. *Ecological Applications*. **13(5)**: 1473-1490.
Benstead, J.P; Rham, P.H; Gattolliat, J; Gibon, F; Loiselle, P.V; Satori, M. & Stiassny, M.L.J. (2003). Conserving Madagascar's Freshwater Biodiversity. *Bioscience*. **53(11)**: 1101-1111.

Berger, W. H. and Parker, F. L. 1970. Diversity of planktonic foraminifera in deep sea sediments. – *Science* **168**: 1345– 1347.

Biggs, T.W, Dunne, T. & Martinelli, L.A. (2004): Natural controls and human impacts on stream nutrient concentrations in a deforested region of the Brazilian Amazon basin. *Biogeochemistry*. **68(2)**: 227-257.

Bojsen, B.H. & Jacobsen, D. (2003): Effects of deforestation on macroinvertebrate diversity and assemblage structure in Ecuadorian Amazon Streams.- *Arch. Hydrobiol*. **158**: (3) 317-342.

Bruijnzeel, L.A. (2004): Hydrological functions of tropical forests: Not seeing the soil for the trees? *Agriculture, Ecosystems and Environment*. **104(1)**: 185-228.

Bunn, S.E. & Arthington, A.H. (2002): Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity.- *Environmental Management*. **30(4)**: 492–507.

Cardinale, B.J; Palmer, M.A. & Collins, S.L. (2002): Species diversity enhances ecosystem functioning through interspecific facilitation.- *Nature*. **415**: 426-429.

Clifford, H. T. & Stephenson, W. (1975): An introduction to numerical classification. – *Academic Press*.

Couceiro, S.R.M; Hamada, N; Luz, S.L.B; Forsberg, B.R. & Pimentel, T.P. (2007): Deforestation and sewage effects on aquatic macroinvertebrates in urban streams in Manaus, Amazonas, Brazil.- *Hydrobiologia*.**575**: 271-284.

Death, R.G. (2002): Predicting invertebrate diversity from disturbance regimes in forest streams.- *Oikos*. **97**: 18-30.

Delong, M.D. & Brusven. (1998): Macroinvertebrate community structure along the longitudinal gradient of an agriculturally impacted stream. *Environmental Management*, **22(3):** 445–457.

Dudgeon, D. (1994): The influence of riparian vegetation on macroinvertebrate community structure and functional organization in six New Guinea streams. *Hydrobiologia* **294**:65-85.

Dudgeon, D. (2000): The Ecology of Tropical Asian Rivers and Streams in Relation to Biodiversity Conservation.- *Annual Review of Ecology & Systematics*. **31**:239-263.

Dudgeon, D; Arthington, A.H; Gessner, M.O; Kawabata, Z; Knowler, D.J; Leveque, C; Naiman, R.J; Prieur-Richard, A; Soto, D; Stiassny, M.L.J & Sullivan, C.A. (2006): Freshwater Biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*. **81**:163-182.

England, L.E. & Rosemond, A.D. (2004): Small reductions in forest cover weakens terrestrial-aquatic linkages in headwater streams.- *Freshwater Biology*. **49**:721-734.

Fearnside, P.M. (2005): Deforestation in Brazilian Amazonia: History, Rates and Consequences. *Conservation Biology* **19 (3)**: 680-688.

Fisher, R.A; Corbet, A.S. & Williams, C.B.(1943): The relation between the number of species and number of individuals in a random sample of animal population. *Journal of Animal Ecology*. **12**: 42-58.

Gibert, J. & Deharveng, L. (2002): Subterranean ecosystems: a truncated functional biodiversity. *BioScience* **52**: 473–481.

Graça, M. A. S; Cressa, C; Gessner, M. O; Feio, M. J; Callies, K. A. & Barrios, C. (2001): Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. – *Freshwater Biology*. **46:** 947– 957.

Harding, J.S; Benfield, E.F; Bolstad, P.V; Helfman, G.S. & Jones, E.B.D. (1998): Stream Biodiversity: Ghost of Land Use Past.- *Proceedings of the National Academy of Sciences of the United States of America*. **95**:14843-14847.

Heino, J; Muotka, T. & Paavola, R. (2003): Determinants of macroinvertebrate diversity in headwater streams: Regional and local influences. *Journal of Animal Ecology*. **72(3)**: 425-434.

Iwata, T; Inoue, M; Nakano, S; Miyaska, H; Doi, A. & Covich, A.P. (2003): Shrimp abundance and habitat relationships in tropical rainforest streams, Sarawak, Borneo.- **19:4**: 387-395.

Iwata, T; Nakano, S. & Inoue, M. (2003): Impacts of past deforestation on stream communities in a tropical forest in Borneo. *Ecological Applications*. **13(2)**: 461-473.

Jacobsen, D. (2008): Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia.* **154**:795-807.

Jacobsen, D; Schultz, R. & Encalada, A. (1997): Structure and diversity of stream invertebrate assemblages: The influence of temperature with altitude and latitude.- *Freshwater Biology.* **38**:247-261.

Jost, L. (2007): Partitioning diversity into independent alpha and beta components. *Ecology*. **88(10)**: 2427-2439.

Lake, P.S. (2000): Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*. **19(4)**; 573-592.

Lamouroux, N; Doledec, S. & Gayraud, S. (2004): Biological traits of stream macroinvertebrate communities: Effects of microhabitat, reach and basin filters. *Journal of the North American Benthological Society*. **23(3)**: 449-466.

Lorion, C.M. & Kennedy, B.P. (2009): Relationships between deforestation, riparian forest buffers and macroinvertebrates in neotropical headwater streams.- *Freshwater Biology*. **54**: 165-180.

Lorion, C.M. & Kennedy, B.P. (2009): Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams.-*Ecological Applications*. **19(2)**:468-479.

McCabe, D.J. & Gotelli, N.J. (2000): Effects of disturbance frequency, intensity and area on assemblages of stream macroinvertebrates. *Oecologia*. **124(2)**: 270-279.

McTammany, M.E; Benfield, E.F. & Webster, J.R. (2007): Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society.* **26(3)**: 532-545.

Merritt, R.W. & Cummins, K.W. (1984): Introduction to the Aquatic Insects of North America. *Kendall/Hunt Publishing Company.*

Outridge, P.M. (1987): Possible causes of high species diversity in tropical Australian freshwater macrobenthic communities. *Hydrobiologia*. **150**: 95-107.
Palmer, M.W. (1989). Variation in species richness: Towards a unification of hypotheses. *Folia Geobotanica & Phytotaxonomica*. **29(4)**: 511-530.

Petraitis, P.S; Latham, R.E. & Niesenbaum, R.A. (1989). The maintenance of species diversity by disturbance. *Quarterly Review of Biology*. **64(4)**: 393-418.

Pfankuch D.J. (1975): Stream reach inventory and channel stability evaluation. USDA Forest Service Northern Region, Montana.

Rahel, F.J. (2002): Homogenisation of freshwater faunas. *Annual Review of Ecology and Systematics*. **33**:291-315.

Ramirez, A. & Pringle, C.M. (1998); Invertebrate drift and benthic community dynamics in lowland neotropical stream, Costa Rica. *Hydrobiologia.* **386**:19-26.
Ricciardi, A. & Rasmussen, J.B. (1999): Extinction rates of North American freshwater Fauna.- *Conservation Biology*. **13(5)**: 1220-1222.

Sala, O. E; Chapin, F. S; Armesto, J. J; Berlow, R; Bloomfield, J; Dirzo, R; Huber-Sanwald, E; Huenneke, L. F; Jackson, R. B; Kinzig, A; Leemans, R; Lodge, D; Mooney, H. A; Oesterheld, M; Poff, N. L; Sykes, M. T; Walker, B. H; Walker, M. & Wall, D. H. (2000): Global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1774.

Sanchez-Azofeifa, G.A; Harriss, R.C. & Skole, D.L. (2001): Deforestation in Costa Rica: a quantitative analysis using remote sensing imagery. *Biotropica*, **33**: 378–384.

Simpson, E. H. (1949): Measurement of diversity. – *Nature* **163**: 688.

Sweeney, B.W; Bott, T.L; Jackson, J.K; Kaplan, L.A; Newbold, J.D; Standley, L.J;

Hession, W.C; Horwitz, R.J & Wolman, M.G. (2004): Riparian Deforestation, Stream Narrowing, and Loss of Stream Ecosystem Services.- *Proceedings of the National Academy of Sciences of the United States of America*. **39**: 14132-14137.

Tabacchi, E; Correll, D.L; Hauer, R; Pinay, G; Planty-Tabacchi, A.M. & Wissmar, R.C. (1998): Development, maintenance and role of vegetation in the river landscape. *Freshwater Biology*. **40**: 497-516.

Townsend, C.R; Scarsbrook, M.R. & Doledec, S. (1997): Quantifying disturbance in streams: Alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*. **16(3)**: 531-544.

Velasquez, S.M. & Miserendino, M.L. (2003): Habitat type and macroinvertebrate assemblages in low order Patagonian streams. *Arch. Hydrobiol.* **158(4)**: 461-483.

Vinson, M.R. & Hawkins, C.P. (1998): Biodiversity of Stream Insects: Variation at local, basin, and regional scales. *Annual Review of Entomology*. **43**:271-293.

Wilson, M. V. & Schmida, A. (1984): Measuring beta diversity with presence-absence data. – *Journal of Ecology.* **72:** 1055 –1064.

Wright, M.S. & Covich, A.P. (2005): The effect of macroinvertebrate exclusion on leaf breakdown rates in a tropical headwater stream. *Biotropica*, **37(3)**: 403-408.