IMPACTS OF AGRICULTURAL LAND USE ON STREAM ECOSYSTEMS OF THE COFFEE-GROWING REGION OF COLOMBIA

by

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Abstract

The pressures of a growing population and a fluctuating economy have caused extensive land use transformations in the Andean region of Colombia, as more than 63% of the natural land cover has been replaced by cattle pastures and crop fields. To date, the specific consequences of this development for stream ecosystems remain unclear. In this study, land use, habitat, and macroinvertebrate community characteristics were measured in 30 first order streams of the coffee-growing region of Colombia. This information was analyzed using structural equation modeling to evaluate effects of agriculture on macroinvertebrate community acting indirectly through effects on riparian condition and instream habitat characteristics.

Landform and land use were measured in catchments and riparian zones of the 30 streams using digital elevation models and QuickBird satellite imagery. Stream habitat was evaluated in a 100-meter reach using water physicochemical characteristics, discharge, channel morphology, substrate, and type of flow. Macroinvertebrate tolerance was measured using a version of the Biological Monitoring Working Party adapted for the region (BMWP-Univalle).

The results supported the hypothesis that agricultural land use has strong negative impacts on stream ecosystems, as reflected in the aquatic macroinvertebrate community. These negative impacts occurred indirectly, appearing to act through a reduction of riparian forest width and availability of coarse substrates, and an increase in the percent of slow-flowing habitats and the ammonia nitrogen concentration in the water. The extent of riparian forest had a positive indirect influence on the macroinvertebrate community by reducing the percent of slow-flowing habitats in the reach. Furthermore, the percent of slow-flowing habitats in stream reaches proved to be an important indicator of habitat deterioration in the studied systems.

These results indicate that local farming practices such as elimination of the riparian forest, excess application of fertilizers, and cattle grazing in riparian zones are responsible for most of the impacts of agriculture on stream habitat and communities. Land management practices such as establishment of riparian forest buffer strips, control of grasses in the riparian zone, and fences to prevent the access of cattle to the stream channel are recommended to mitigate the negative effect of agriculture on these systems. The results also highlight the importance of local studies of

land use, given that the effects of agriculture are strongly affected by local farming practices and environmental conditions.

Key words:

Land use, agriculture, the Andes, tropical streams, aquatic macroinvertebrates, riparian forest buffer, instream habitat.

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Introduction

In the Andean region of Colombia, the pressures of a growing population and a fluctuating economy have driven extensive land cover transformations in recent decades. These transformations have included the deforestation of large areas of mid-elevation forest to establish pastures and crop fields (Etter & Wyngaarden, 2000). Presently, more than 63% of the natural land cover has been replaced by agriculture in the region (Etter et al., 2006). The repercussions of this trend are so important that the tropical Andes have been designated a conservation priority, as one of the 25 most species rich and exceptionally threatened areas of the world (Myers et al., 2000). However, despite the obvious importance of agriculture as a potential cause of environmental degradation in the Andean region, there is little information about the mechanisms through which it impacts specific ecosystems such as low order streams.

The impacts of agriculture on running waters are diverse and complex, involving multiple physical and chemical factors acting at different scales (Allan & Johnson, 1997; Allan, 2004; Maloney & Weller, 2011; Riseng et al., 2011). Numerous studies conducted in the temperate region document that agricultural land use increases the input of sediments, nutrients and pesticides into streams, alters the flow regime, and causes degradation of riparian and stream channel habitat (Allan, 2004; Johnson & Host, 2010). These physical and chemical modifications of stream ecosystems often impair habitat quality and alter resource availability for biologic communities, causing shifts in their trophic structure and composition (Allan, 2004; Diana et al., 2006; Johnson & Host, 2010; Riseng et al., 2011).

The response of stream ecosystems to agricultural land use is strongly affected by local conditions such as landscape position along the regional flow path, bedrock characteristics, surficial geology, climate, regional hydrologic regime, and geographic location (Allan & Johnson, 1997; Munn et al., 2009; Johnson & Host, 2010). For example, Riseng et al. (2011) demonstrated that different regions of the United States showed important variation in the sensitivity of stream ecosystems to agricultural land use. Furthermore, they found that the geographic context also affected the relative importance of the causal pathways through which agriculture affected stream biological integrity. Therefore, regional studies are desirable in order to understand how local agricultural practices influence stream ecosystems under the local environmental conditions.

Few investigations address the specific effects of agriculture for tropical Andean stream ecosystems. In terms of water quality, Mesa (2010) reported that streams in agricultural catchments in northwestern Argentina had higher conductivity, nitrate, pH, and water temperature when compared to forested catchments. On the other hand, the relationship between agricultural land use and stream condition has not always been clear in previous studies conducted in the region. In high altitude streams of Ecuador, Ordóñez (2011) found that agriculture did not have significant effects on macroinvertebrate community tolerance scores, relative diversity or taxonomic richness, and attributed this result to geological conditions and the low intensity of agricultural practices in the region. Similar results were reported for streams of the coffee-region of Colombia, where agriculture was not strongly correlated with fish and macroinvertebrate community measures (Chará 2003). However, that study found agriculture to be strongly associated with degradation of instream habitat quality, which in turn was strongly correlated to biological measures. Chará (2003) concluded that agricultural land use may have indirect effects on biological integrity through degradation of habitat in these ecosystems, following a pattern that has been observed in a number of studies conducted in other regions (e.g. Allan & Johnson, 1997; Allan, 2004; Waite et al., 2010; Malloney & Weller, 2011; Riseng et al., 2011).

To better understand how local agricultural practices affect stream communities in the landscape context of the tropical Andes and to formulate mechanisms to improve those practices, it is important to identify specific direct and indirect causal paths linking agriculture to the observed condition of habitat and biological communities. The present study used structural equation modeling (SEM) to explore the complex cause and effect pathways by which agricultural land use interacts with macroinvertebrate communities of Colombian Andean streams. The overall working hypothesis of this study was that agriculture affects the macroinvertebrate community indirectly through effects on riparian condition and instream habitat characteristics.

Methods

Study area

La Vieja River basin is located on the western flank of Colombia's Central Andes and covers an area of 2,880 km^2 (Figure 1). The basin is characterized by steep to gently undulating topography with altitudes ranging from 889 to 4,802 meters above sea level (masl). La Vieja River basin is part of the coffee-growing region of Colombia, an area that has experienced rapid landscape transformations in recent decades. Due to soil quality and climate, the land located between 1,200 and 1,800 m of altitude in this region was the center of Colombian coffee production during the 1970's through to the 1990's. However, following the world coffee crisis in the mid 1990's, a large proportion of these coffee plantations were replaced by other types of agriculture as well as pastures for livestock production (Chará, 2003). As a result, this basin is currently a rural landscape dominated by cattle pasture land and various types of crops, with only sparse patches of native forest.

The region has a tropical climate with stable daily mean temperatures throughout the year and a bimodal increase in precipitation occurring from March to May and from October to December. Due to the altitudinal gradient, annual mean temperature varies throughout the basin, ranging from 3.75°C above 3000 masl to 18°C below this elevation. Similarly, annual precipitation has a mean of 2,400 mm above 1,300 m and averages 1,900 mm below that altitude.

Within La Vieja River basin, 30 micro-basins of first order streams were selected for the study (Figure 1). To minimize differences due to elevation, all the streams were located between 990 and 1720 masl. Catchment area upstream of sampling sites ranged from 15,026 to 822,131 m^2 with an average of 175,832 m^2.

Landform and land use variables

Landform and land use characteristics were measured for the whole catchment and for a riparian buffer of 15 m from each side of the stream channel (Table 1). The catchment upstream of each sampling reach was delineated from a 30-m resolution Digital Elevation Model (DEM) using the ArcGIS Hydrology tools: fill, flow direction, flow accumulation, stream link, and watershed.

Streams were defined using a flow accumulation value of 10,000 in order to capture small first order drainages. Catchment polygons obtained through this process were overlaid on 60-cm resolution QuickBird Satellite imagery and brought to field to verify their precision.

Land use was manually classified due to the small size of the studied catchments and the lack of high resolution land cover information for the region. Land use polygons for each catchment were digitalized in ArcMap 9.3 (ESRI, 2009) using 60-cm resolution QuickBird Satellite imagery of 2003 and ground-truth information collected in the field during summer 2011. Identified land uses included bare soil, cropland, cattle pastures, forest, early secondary vegetation (shrubs), and urban land. Some of these categories were further divided in order to investigate possible differential effects of regional land use practices, such as intensive coffee plantations and forests dominated by the neotropical bamboo species *Guadua angustifolia* (Guadua forest). Furthermore, the land uses related to agricultural activities (cropland and cattle pastures) were grouped together in the "agriculture" category to test for combined effects of different types of agricultural practices in these rural landscapes.

Habitat and macroinvertebrate sampling

This investigation used combined biological and reach characterization data from a number of different survey data sets provided by the Centre for Research in Sustainable Agricultural Production Systems (CIPAV). Most of the surveys were completed from November of 2002 through February of 2003. All sites were re-visited during summer 2011 to collect additional data and validate previous sampling. A reach of 100 m was selected in each stream to measure habitat characteristics, water quality, and aquatic biota.

Methods for physical habitat sampling were adapted for Andean streams by Chará (2004) from the "Rapid Bioassessment Protocols for use in streams and wadeable rivers of the United States" (Barbour et al., 1999). In each study reach, three equally spaced transects perpendicular to stream flow were established. At each transect, bankfull width was recorded and water depth was measured at three equidistant points. Percentage of canopy cover was quantified in the middle of each transect with a spherical crown densiometer. The proportion of the reach represented by different stream morphological types (riffles, runs, pools, slow currents) and substrate components (bedrock, boulder, cobble, pebble, gravel, sand, silt, mud, detritus, fine particulate organic matter) was visually estimated.

Water quality was measured using the following parameters: temperature, dissolved oxygen, pH, turbidity, ammonia nitrogen, total phosphate, total suspended solids, dissolved solids, total solids, alkalinity, total coliforms, and faecal coliforms. Temperature and pH were measured in the field using portable equipment (Hanna HI 991300). Water samples were transported to the laboratory to measure the remaining parameters according to Standard Methods (American Public Health Association, 1995).

Aquatic macroinvertebrate samples were collected from each reach using a D-frame (500 µm mesh). A total of 20 sweeps were taken from all major habitat types of the reach in proportion to their representation of surface area. Invertebrates were preserved and transported to the laboratory for identification. Approximately 92.5% of the sample was identified to genus level; the remaining percentage was identified to family level. Due to the lack of identification keys for the neotropical region, individuals belonging to Bivalvia, Gastropoda, Oligochaeta, Decapoda, Tricladida, Amphipoda, Culicidae, and Chironomidae were identified only to class or family level in all samples.

Community descriptors such as total macroinvertebrate abundance, taxa richness, and Fisher's alpha diversity were calculated for each sampled stream to describe variation in macroinvertebrate community structure. An adaptation of the Biological Monitoring Working Party index (BMWP), the BMWP-Univalle, was calculated using family-level scores of tolerance to organic pollution that were adjusted for the region by Zúñiga & Cardona (2009). In this system, family scores range from 1 to 10, with the maximum scores given to the most sensitive families. Site indices are then expressed as the sum of the scores of the families present in the sample. The richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa was also used as an indicator of sensitivity to pollution.

Data analysis

A total of 54 variables were recorded; 48 explanatory variables and 6 response variables (Table 1). Percentages were arcsin-transformed and positively skewed data were log-transformed prior to analysis. The explanatory variables were organized in three separate matrices according to the scale of the measurement: catchment-scale variables, riparian-scale variables, and habitat-scale variables. The correlation structure of the data within each matrix was examined with principal component analyses (PCA) and Spearman correlations in order to select non-redundant variables that represented most of the variation among sites and were strongly correlated to the response variables.

Structural equation modeling (SEM) was used to examine direct and indirect effects of land use and natural landscape factors on the aquatic macroinvertebrate community. SEM is an extension of factor analysis and general linear modeling that enables a researcher to test a hypothetical set of linear causal equations simultaneously (Schumacker & Lomax, 1996). It provides estimates of both direct and indirect effects of exogenous factors on endogenous response variables based on a specified conceptual model. The general conceptual model used in this study was based on the hypothesis that land use and natural landscape variables at the catchment scale affect the stream community only indirectly through effects on the riparian condition and the instream habitat characteristics (Figure 2).

Spearman correlations were used to examine how the different community descriptors correlated with each other and with land use and habitat variables. The BMWP-Univalle index was selected as the most suitable measure of macroinvertebrate community condition due to the high number of significant correlations with explanatory variables and other community descriptors (Table 2). Scores for other macroinvertebrate community metrics are presented in Appendix A.

Because the relatively small number of sites (30) of this study would preclude the construction of complex structural equation models, preliminary multiple regression analyses were used to explore the most important variables representing the main paths of the conceptual model. First, regression models were developed to find good predictor variables for stream community tolerance at the catchment, riparian, and habitat scales. Subsequently, the same approach was used to find the land cover and land use variables with most influence on the important habitat-scale factors. Fit of the multiple linear regression models was measured using multiple R^2 (R^2), adjusted R^2 (Adj-R^2), and residual standard error (RSE).

A SEM linking the most important catchment, riparian, and habitat variables with macroinvertebrate community tolerance was developed to help identify a causal structure consistent with the conceptual model. Model fit was evaluated using the chi-square statistic ($\mathcal{X}^2$), the root mean square error approximation (RMSEA), the comparative fit index (CFI), and the Tucker-Lewis index (TLI). The $\mathcal{X}^2$ is used to measure correspondence between observed and predicted covariance matrices. Therefore, low $\mathcal{X}^2$ values which result in significance levels greater than 0.05 are desirable, because they indicate that there are no significant differences between the model and the data (Schumacker & Lomax, 1996; Hoe, 2008). The RMSEA estimates data fit to the causal hypothesis and is not affected by sample size. It ranges from 0 to 1, with values up to 0.08 indicating reasonable fit (Hoe, 2008). The CFI is a noncentrality, parameter-based index robust to small sample size and non-normal data distributions. It ranges from 0 to 1, with 0.90 or greater representing an acceptable fit (Schumacker & Lomax, 1996; Hoe, 2008). The TLI compares the model's fit and parsimony with a null model. It is also resilient to sample size and is expected to have values of 0.90 or greater (Schumacker & Lomax, 1996; Hoe, 2008).

The statistical analyses described in this section were implemented using a combination of the R statistical program (R Development Core Team, 2012), SPSS statistics (SPSS Inc., an IBM Company, 2010), and Amos software (Arbuckle, 2010).

Results

Land use characteristics

Agriculture was the most important land use in the overall study area, comprising 76% of the total surveyed land. Of this agricultural land, 61% was dedicated to cattle pastures and 38% to croplands. Forest was another important land cover in the region, representing 16% of the overall study area, whereas urban land was one of the least important land uses, covering only 4%.

Within the studied catchments, total agricultural land cover ranged from 13 to 100%, with an average of 76% (Table 1). The mean proportion of cattle pastures in these catchments was 52%, ranging from 0 to 100%, and the mean proportion of cropland was 23%, ranging from 0 to 90%. However important the agricultural land cover, the studied catchments exhibited considerable variation in the proportion of forest, with an average of 15% and values ranging from 0 up to 86%. Within the forest category, the Guadua-dominated forests represented only 30% of the forest in the overall study area, and had little average coverage in the studied catchments (7%).

Agriculture was also the most important land use at the riparian buffer scale, averaging 57% of buffer area in the studied streams. At this scale most agricultural land use was represented by cattle pastures, which on average covered 44% of riparian buffer area. Forest also was a significant feature, covering an average of 36% of the riparian buffer in the studied streams. The width of riparian forest varied markedly, ranging from 0 to 124 m, with an average of 21 m (Table 1).

Habitat characteristics

The studied streams presented some variation in size but in general were small systems, with an average discharge of 8.8 l/s, an average bankfull width of 3.2 m, and a mean water depth of 15 cm (Table 1). The most common stream morphological type was slow currents, which covered on average 53% of the studied reaches, riffles covered in average 32%, and pools only 10%. Mud was the most common streambed substrate on the studied reaches averaging 64%, whereas coarse substrates covered on average 19%. An interesting field observation was the high incidence of streambed invasion by pasture grass, as 63% of the studied streams had a substantial section of the sample reach invaded by pastures. Most of the streams in this condition presented streambeds dominated by muddy substrates.

Physicochemical characteristics of the water varied markedly among the streams, with temperatures ranging from 18 to 27.4°C, oxygen concentrations from 0.5 to 9.7 mg/l, specific conductance from 41 to 378 µs/cm, and ammonia nitrogen concentrations from 0 to 1.6 mg/l. Total and fecal coliforms also exhibited a wide range among the studied systems, with values ranging from 0.20 to 7000 NPM/ml.

Macroinvertebrate assemblage

A total of 46,039 macroinvertebrates belonging to 9 classes, 21 orders, 79 families and 133 genera were collected in the sampled streams. The most abundant taxa were Chironomidae (Diptera), making up 49% of the organisms, followed by Hydrobiidae (Gastropoda) and Sphaeriidae (Bivalvia) which made up 11% and 9% respectively. *Atrichopogon* (Diptera: Ceratopogonidae), *Forcipomyia* (Diptera: Ceratopogonidae), Culicidae (Dipera), *Heterelmis* (Coleoptera: Elmidae), *Physa* (Gastropoda), and *Smicridea* (Trichoptera: Hydropsychidae) were also common and in combination made up 21% of all organisms collected.

Total numbers of macroinvertebrates per stream ranged from 76 to 13,245 and total taxa richness from 16 to 51 (Table 1). Estimates of the BMWP-Univalle index ranged greatly from a low score of 27, which indicates very contaminated waters, to a high of 190 which indicates waters of excellent quality. Similarly, richness of taxa sensitive to organic pollution (EPT richness) showed considerable variation among the studied streams, ranging from 0 to 14.

Variable selection

The PCA for catchment variables identified four main components that together explained 70% of the variation among the 30 sites (Table 3). The first component represented 24% of the variance and was mainly determined by productive land uses such as pastures, total cropland and coffee crops. The percent of pastures was negatively correlated with cropland in the catchment and, as expected, the latter variable was positively correlated with the percent of coffee crops (Table 4). The percent of catchment in pasture and the percent as agriculture were both retained for further analyses, due to their predominance in the region and their relevance to the research questions addressed in this study. The second component represented 19% of the variation and was mainly related to the total percent of agricultural land in the catchment. This category was retained for the analysis due to its importance for the research question. The third component explained 15% of the variation and was associated to the slope of the channel and the area and the elevation of the catchment. All of these variables were retained for the analysis to represent some of the natural landscape characteristics of the catchments. The fourth component explained 12% of the variance and was mainly determined by the percent of shrubs, bare soil, and forest in the catchment. Only the percent of forest was retained for the analysis due to its strong correlation to the response variable.

The PCA ordination of riparian land use variables produced two main components that represented 58% of the variation among sites (Table 5). The first component explained 40% of the variance and was associated to the width of the riparian buffer, the percent of pastures, the percent of forest, the percent of Guadua forest, and the percent of agriculture, all of which were highly correlated with each other (Table 6). The width of the riparian buffer and the percent of agriculture in the buffer were the only retained variables of this group due to their importance for the research question and correlation to the response variable. The second component explained 19% of the variation and was mainly determined by the percent of riparian cropland and the percent of coffee crops. These two variables were redundant, thus only the percent of cropland was retained for the analysis given its larger contribution to variation among the studied systems. The third component, which explained 12% of the variance, was mainly determined by the percent of bare soil, shrubs and Guadua forest. Only the percent of Guadua forest was retained because the other two land uses had a very low representation within the studied riparian buffers.

The PCA ordination of the habitat variables revealed the high collinearity of the parameters measured at this scale. The first component explained 28% of the variation among sites and was related to bankfull width, most of the substrate variables, most of the flow type variables and some physicochemical measures (Table 7). In general, habitat characteristics such as bankfull width, percent of slow currents, percent of mud, temperature, and concentration of fecal coliforms were negatively correlated to the percent of coarse substrates, the percent of riffles, and the concentration of dissolved oxygen in the streams. As most of these variables were collinear, only the percent of slow currents and the percent of coarse substrates were retained for the analysis, given their high contribution to the variation among sites and their strong correlation to the response variable (Table 8). The second component was mainly represented by discharge, conductivity, concentration of NH_3-N, and fecal coliforms. Only the concentration of ammonia nitrogen was selected for further analysis due to its strong correlation with the BMWP-U index and its large contribution to variation among sites. The third component was strongly correlated only to pH, which was discarded because it was not significantly correlated to the response variable. The fourth component was mainly determined by depth, discharge, percent of pools, and concentration of total solids and total coliforms. Due to the high collinearity of some of these variables with previously selected habitat parameters, only the concentration of total solids was retained.

Exploratory multiple regression models

The exploratory multiple regression analyses at the catchment scale found that the percent of agriculture had marginally significant negative effects on the BMWP.U index ($p = 0.05$, $R^2 = 0.13$; Table 9). Conversely, the percent of forest in the catchment had a significant positive effect on this macroinvertebrate metric ($p < 0.001$, $R^2 = 0.33$). Consistent with these results, both the width of the forest buffer and the percent of riparian agriculture were good riparian-scale predictors of BMWP, explaining 20% and 16% of the variance respectively when evaluated independently. At the habitat-scale, the percent of slow currents, the percent of coarse substrates, and the concentration of ammonia nitrogen were the best predictors, explaining 51% of the variation of the macroinvertebrate community tolerance in the studied streams. The percent of slow currents and the concentration of ammonia nitrogen had significant negative effects on BMWP.U ($p < 0.05$), whereas the percent of coarse substrates had a marginally significant positive effect on the macroinvertebrate metric ($p = 0.06$).

Based on the above results, multiple linear regressions were developed to explore the relationships of landscape-scale and riparian-scale variables with the best habitat-scale predictors of BMWP.U (Table 9). At the catchment scale, the elevation of the catchment and the percent of forest were good predictors of the presence of slow currents, accounting for 34% of the variance of this parameter. At the riparian scale, the width of the forest buffer, the percent of pastures, and the percent of total agricultural cover were all found to have significant effects on the percent of slow currents, accounting for 30, 27 and 21% of the variation of this habitat measure respectively.

The proportion of coarse substrates in the studied reaches was best explained by the percent of forest and the slope of the channel at the catchment scale (50% of the variance explained). However, the percent of agriculture in the catchment was also found to have marginally significant effects on the proportion of coarse substrates ($p < 0.1$, $R^2 = 0.11$). At the riparian scale, both the width of the forest buffer and the percent of agriculture were good predictors of the percent of coarse substrates in the reach, explaining 52 and 41% of the variance respectively. On the other hand, the concentration of NH3-N was best predicted by the percent of cropland and total agricultural land at both catchment and riparian scales, and cropland accounted for a larger percent of the variance in both scales.

Structural equation model development

The SEM (Figure 3) was developed based on results of the PCA, exploratory regression analyses, and literature evidence. It included one catchment land use variable (percent of agriculture), two natural landscape variables (slope of the channel and channel elevation), one variable representing the condition of the riparian zone (width of the forest buffer), and three habitat characteristics of importance for the macroinvertebrate community (percent of slow currents, percent of coarse substrates, and concentration of ammonia nitrogen). In the model, agricultural land use, which included the percent of cropland and cattle pastures, was hypothesized to directly reduce the width of the riparian forest buffer, decrease the percent of coarse substrates and increase the concentration of ammonia nitrogen in the stream water. In turn, the possible consequences of the reduction of the riparian forest width were represented in the model through effects of this variable on the percent of slow currents, the concentration of ammonia nitrogen, and the percent of coarse substrates.

According to the exploratory analyses, the percent of slow currents was one of the habitat characteristics with greatest negative influence on the macroinvertebrate community. High percentages of slow currents in the studied reaches were associated with low discharge and degraded banks (Table 8). Therefore, wider riparian forests were expected to reduce the percent of slow currents through improved hydrologic regulation, bank stabilization, and protection from livestock trampling. The elevation of the catchment was also included as a factor affecting the percent of slow currents in the streams because average annual precipitation decreases with altitude in the studied region. Thus, lower elevation catchments are expected to be more susceptible to reductions in discharge and consequently an increase in slow flow habitats. The slope of the channel was another natural factor included in the model as a regulator of the percent of slow currents and the percent of coarse substrates, since high gradient streams should have more coarse substrates and less predominance of slow-flowing habitats. On the other hand, as the deposition of sediments is favored in slow-flowing habitats, the percent of slow currents was hypothesized to have a negative effect on the percent of coarse substrates.

Structural equation model results

The SEM model was found to be a good representation of the data set based on all measures of fit (Table 10). Additionally, the model satisfied univariate and multivariate normality assessments of Amos (skewness <2.0, kurtosis <7.0, Mardia's critical ratio <5.0). The model explained 50% of the variation in the BMWP.U index across sites, as well as 39% of the variation in the percent of slow currents, 48% of the variation in the percent of coarse substrates, 20% of the variation in NH_3-N concentration in the streams, and 23% of the variation in width of the riparian forest buffer (Figure 3).

The fitted model suggests that agriculture in the catchment had a significant negative impact (standardized total effect (STE) = -0.322, p = 0.014) on the BMWP.U index (Table 11, Figure 3). This negative impact occurred because agricultural land use had strong total negative effects on the width of the riparian forest buffer (STE = -0.482, p = 0.021), and positive effects on the percent of slow currents (STE = 0.219, p = 0.004) and the concentration of NH_3-N (STE = 0.436, p = 0.015). In turn, the width of the riparian forest had a positive indirect influence on the macroinvertebrate community (STE = 0.204, p = 0.057). This positive effect of the riparian forest was mainly due to its strong negative effects on the percent of slow currents (STE = -0.453, p = 0.004) because, contrary to expectations, the width of the forest buffer only had marginal total effects on the percent of coarse substrates (STE = 0.243, p = 0.120) and no effects on the concentration of NH_3-N (STE = 0.092, p = 0.672). As expected, the percent of slow currents (STE = -0.476, p = 0.008) and the concentration of NH_3-N (STE = -0.358, p = 0.018) had strong negative effects on BMWP.U. However, the SEM only detected marginal effects of the percent of coarse substrates on the macroinvertebrate community tolerance index (STE = 0.305, p = 0.140).

To determine the relative strength of the multiple pathways through which agriculture in the catchment and the width of the riparian forest affect BMWP.U, the total effect of these two variables was partitioned into relative indirect effects mediated by habitat variables. As shown in Table 12, almost 50% of the negative effect of agriculture was mediated through the increase of ammonia nitrogen in the water, 27% through the decrease in the percent of coarse substrates and 24% through the increase in the percent of slow flowing habitats. Conversely, most of the positive effect of the riparian forest buffer was mediated by the decrease in the percent of slow currents (60%), 27% was mediated by the increase in coarse substrates, and 12% through the decrease in NH3-N. However, the last two pathways were not statistically significant.

Discussion

Overall, these results support the hypothesis that agricultural land use in the coffee-growing region of Colombia has negative impacts on the condition of stream ecosystems, as reflected in the aquatic macroinvertebrate community. Furthermore, the SEM analysis successfully identified several plausible causal pathways through which such effects take place in the region. The results indicate that agriculture in these Andean catchments affects the invertebrate community indirectly by increasing the concentration of ammonia nitrogen in the water and decreasing the width of the riparian forest. Moreover, through the reduction of the riparian forest, agriculture increased the percent of slow currents and decreased the availability of coarse substrates in the reach, which also had important effects on the macroinvertebrate community. Although pathways identified from exploratory analyses and found significant in the SEM may identify surrogate rather than causal relationships, results are supported by numerous studies showing the adverse effects of agricultural land use on the biota through degradation of riparian and stream habitat (e.g. Sponseller et al., 2001; Chará, 2003; Allan, 2004; Diana et al., 2006; Riseng et al., 2011).

Direct effects of agriculture on in-stream habitat

Increased sedimentation and increased input of nitrogen compounds are two of the most commonly reported effects of agriculture on stream ecosystems (Quinn et al., 1997; Neill et al., 2001; Gergel et al., 2002; Allan, 2004; Scanlon et al., 2007). These impacts were included in the conceptual model of this study as direct effects of agriculture on the concentration of ammonia nitrogen and the percent of coarse substrates, and indirect effects on both measures through the deforestation of the riparian corridor. Even though the fitted SEM indicated that the agricultural land use did have total effects on both habitat characteristics, the results only supported the presence of significant direct effects on the concentration of ammonia nitrogen, suggesting that most of the influence of agriculture on the availability coarse substrates took place indirectly.

According to the SEM, the direct increase of ammonia nitrogen concentration in the water accounted for almost 50% of the negative impacts of agriculture on the macroinvertebrate community. This is not surprising because high concentrations of ammonia may have severe effects on the aquatic biota due to its high toxicity (USEPA, 2009). Furthermore, many studies have reported high concentrations of nitrogen compounds in agricultural streams (Mesa, 2010; Vázquez et al., 2011; Riseng et al., 2011; Gücker et al., 2009). Higher inputs of nitrogen in agricultural catchments are attributed to the effect of fertilizers, nitrogen-fixing crops, and animal wastes (Allan & Castillo, 2007; USEPA, 2009). In this investigation, the results of the linear regressions also indicate that croplands are contributing larger inputs of ammonia than cattle pastures. This corresponds with the findings of a study in Mexican tropical streams (Vázquez et al., 2011), and may suggest the need for better cropland management practices in the region.

The augmented input of sediments in agricultural catchments has been documented in several studies conducted in both temperate and tropical regions (e.g. Quinn et al., 1997; Allan et al. 1997; Niyogi et al., 2007; Mesa, 2010; Vázquez et al., 2011). In the present study the percent of coarse substrates was used to measure sedimentation under the premise that increased sedimentation would be reflected on low availability of coarse substrates. Although exploratory analyses suggested a direct negative effect of agriculture on this habitat measure, the SEM did not support this causal pathway, indicating that most of the negative effect of agriculture on the availability of coarse substrates was transmitted indirectly through reduction of the riparian forest and the consequent increase of slow-flowing habitats in the stream. This result may indicate that the expected increase in sedimentation is only noticeable in streams dominated by slow-flowing habitats. However, interpretation regarding substrate composition must be considered with caution because there are many natural factors that may regulate this characteristic of the streambed (e.g. geology of the catchment, position on the drainage network; Allan & Castillo, 2007), and the model only accounted for the slope of the channel.

Indirect effects of agriculture through forest buffer degradation

The reduction or elimination of the forest buffer is considered one of the most important negative impacts of intensive agriculture on stream ecosystems. Reduction of the width of the riparian forest may affect important functions such as hydrologic regulation and sediment and nonpoint pollutant sequestration (Osborne & Kovacic, 1993; Schmitt, 1999; Hook, 2003; Allan, 2004). These possible indirect effects of the agricultural land use were represented in the SEM through effects of the riparian forest width on the percent of slow currents, the concentration of ammonia nitrogen, and the percent of coarse substrates.

This study finds that agricultural land use had a significant negative impact on the width of the riparian forest buffer, which in turn significantly reduced the incidence of slow-flowing habitats and increased the percent of coarse substrates in the reach. Moreover, the elevation of the catchment had a negative effect on the percent of slow currents, indicating that lower elevation catchments, which receive less mean annual precipitation, were more susceptible to the development of slow-flowing conditions. In this respect, the results are consistent with a number of studies documenting that, under certain conditions, increases in agricultural land use in the catchment and elimination of the forest buffer can cause changes in stream hydrology, lowering base flows due to low infiltration and more episodic export of water. This decrease may result in less stable flows, less variability in channel morphology, increased area of shallow slow-flowing habitats, and higher water temperature (Allan, 2004; Diana et al., 2008; Duehr et al., 2008). Some of these habitat transformations associated with the prevalence of slow currents in the studied streams were evident in the correlation structure of the habitat variables. Reaches dominated by slow-flowing habitats had large bankfull cross-section widths, low discharge, low representation of riffle and pool habitats, high percentages of fine substrates, low presence of detritus in the streambed, high temperatures, high pH, high concentrations of total coliforms, and low dissolved oxygen concentrations.

Contrary to expectations, the results of the SEM suggested that the width of the riparian buffer did not have strong direct effects on the percent of coarse substrates or the concentration of ammonia nitrogen. Riparian vegetation buffers are considered an effective measure to reduce anthropogenic inputs of nitrogen to aquatic ecosystems, and wider riparian buffers should transform and remove more nitrogen from the water (Mayer et al., 2007). However, the type of vegetation, the depth of the root zone, and patterns of subsurface hydrology and subsurface biogeochemistry are important factors regulating nitrogen removal in buffers (Mayer et al., 2007; Young & Briggs, 2007). These factors were not measured in this study and may result in important variation in the capacity of buffers to regulate ammonia nitrogen concentrations, thereby making the influence of riparian buffer on ammonia concentrations difficult to detect. A previous investigation in similar catchments of the coffee-growing region suggested that riparian zones were more effective in reducing experimental nitrogen inputs than were cattle pastures, due to their increased regulation of superficial runoff (Chará et al., 2012). This contrasting evidence highlights the need for future research addressing functional aspects of nitrogen removal effectiveness in riparian forest buffers of the region.

The ability of riparian forests to trap sediments has been widely accepted (Sweeney, 1993; Allan, 2004; Vondracek et al., 2005; Johnson et al., 2007) and their efficiency has been related to buffer width and vegetation characteristics (Schmitt, 1999; Hook, 2003). Therefore, a direct positive effect of the riparian forest width on the percent of coarse substrates was expected as a result of the reduced sedimentation in the reach. However, the SEM did not identify strong significant direct effects of the width of the riparian forest on the percent of coarse substrates, even though these two measures were highly correlated. This is likely due to the fact that most of the effect of the riparian forest on the substrate was mediated through the reduction of slow currents in the studied streams.

Some investigations have associated reduced riparian forest cover and cattle grazing and trampling with degradation of stream banks and increases in bank angle and bankfull cross section width (Townsend et al., 2004; Herbst et al., 2012). Conversely, other studies have reported increased incision and channel narrowing in small streams where the riparian forest has been replaced by pastures, which can inhibit channel erosion with their deep and dense root system (Davies-Colley, 1997; Lyons et al., 2000), and some have even recommended the establishment of grass along the margin of narrow streams to protect water quality and channel characteristics (Vondracek et al., 2005). In this study, large bankfull widths were clearly related to the negative habitat transformations occurring in streams with high percentages of slow currents, and both characteristics were associated with low channel stability and streambed invasion by grass. These patterns, added to the significant positive regression between the percent of slow currents and the percent of cattle pastures in the riparian corridor, suggest that the physical impact of cattle on the stream channel was another important factor increasing the occurrence of slow-flowing habitats.

The high incidence of streambed invasion by pasture grasses in streams dominated by slow-flowing conditions was an interesting tendency in the studied systems. The streambed invasion by grass was not included in statistical analyses due to the qualitative nature of the measure, but field observations indicated that nearly two-thirds of the streams with more than 50% of the reach in slow currents experienced grass invasion of the streambed. The growth of grasses belonging to the family Poaceae is an unusual habitat transformation affecting the streambed that has only been reported in a few studies conducted in the coffee-growing region of Colombia (Pedraza et al., 2008) and Western Australia (Clarke et al., 2004; Loo et al., 2009). In both regions, severe instream habitat degradation was associated with this condition and the recuperation of the riparian forest was recommended as an effective preventive measure.

Model limitations

In this investigation, an SEM was used to test hypothesized causal relationships within a number of variables representing stream ecosystem condition, environmental characteristics and anthropogenic impacts. As with every model, the SEM developed in this study is a simplification of a more complex reality because it was not feasible to consider all possible factors relating land use to stream characteristics and biological responses. Therefore, selected variables may represent surrogate measures and the conceptual model may fail to include all possible relationships. Nonetheless, the model was useful to measure the relative strengths of interactions among a set of important variables in the studied systems, and it is broadly consistent with similar studies.

There is little consensus on the recommended sample size for SEM development. However, this type of analysis typically requires large data sets (Hoe, 2008). Even though the sample size in this study was below the recommended threshold, there were no latent variables evaluated and the distribution of the sample was strictly normal, which generally improves the consistency of results. Furthermore, a number of fit statistics robust to small sample sizes were used and indicated good model fit. However, increasing the sample size in the study region and further testing of this model clearly is desirable.

Implications for stream management and research

The findings of this investigation indicate that local farming practices in the coffee-growing region of Colombia, including the elimination of riparian forest, excess application of fertilizers, and cattle grazing in riparian zones, likely are responsible for most of the physical impacts of agriculture on the stream habitat and biological communities. Therefore, land management practices such as establishment of riparian forest buffer strips, fences to control the access of cattle to the stream channel, and active control of grass growth in the riparian zone and stream channel may mitigate the negative effect of agriculture on these stream ecosystems.

Habitat responses identified in these Andean streams, including the unusual colonization of the streambed by grasses, highlight the importance of studying the impacts of agriculture at the local scale in the tropics. Even though the impacts of land use on tropical streams have received increased attention in recent years (e.g. Neill et al., 2001; Gücker et al., 2009; Miserendino & Masi, 2010; Mesa, 2010; Uriarte et al., 2011; Vázquez et al., 2011), a full understanding of how tropical stream ecosystems function and how they may respond to disturbance is still lacking in poorly studied regions such as the Andes. Further research into the causal pathways relating land use practices to stream condition is essential to formulate better management practices that are relevant to the local context.

Tables

Table 1. Mean, standard deviation (SD), minimum (Min.) and maximum (Max.) values for each explanatory and response variable registered in 30 small streams of the coffee-growing region of Colombia.

Variable	Abbreviation	Mean	SD	Min.	Max.
Catchment scale					
Mean catchment elevation (masl)	CatchElev	1274.5	154.7	1067	1709.3
Catchment area (m^2)	CatchArea	175,832.2	168,958.9	15,025.8	822,131
Channel slope	ChanSlope	0.1	0.1	0	0.2
% Bare soil catchment	BareCat	1.1	2.8	0	11.7
% Coffee crop catchment	CoffeeCat	11.4	25.5	0	90.3
% Cropland catchment	CropCat	23.8	28.1	0	90.0
% Cattle pastures catchment	PastCat	52.0	30.9	0	100.0
% Agriculture catchment	AgCat	75.8	22.9	13.2	100.0
% *Guadua* forest catchment	GuaCat	6.9	9.8	0	34.9
% Forest catchment	ForstCat	15.9	19.1	0	86.7
% Shrubs catchment	ShruCat	3.5	8	0	29.5
% Urban catchment	UrbCat	1.8	5.4	0	29.5
Riparian Scale					
Mean width of the riparian forest (m)	BuffWid	20.9	25.1	0	124.3
% Riparian bare soil	RipBar	0.6	2.9	0	15.7
% Riparian coffee agriculture	RipCoffee	6	14.9	0	70.2
% Riparian cropland	RipCrop	12.7	20.7	0	70.2
% Riparian pastures	RipPast	44.4	38.6	0	100.0
% Riparian agriculture	RipAg	57.1	35.1	0.6	100.0
% Riparian Guadua forest	RipGua	15.9	26.8	0	99.2
% Riparian forest	RipForst	35.6	35.4	0	99.4
% Riparian Shrubs	RipShru	6.6	13.1	0	49.4
% Riparian Urban	RipUr	0.1	0.6	0	3
Habitat scale					
Bankfull width (m)	Bankfull	3.2	3	0.7	12.5
Water depth (cm)	Depth	15.2	9.4	3.6	46.2
Discharge (l/s)	Disch	8.8	10.2	0.5	42
% Riffles	Riffl	32.5	36.6	0.0	100.0
% Slow currents	SlowCur	53.4	40.6	0	100
% Pools	Pool	9.8	18.5	0	60
% Bedrock	Bedr	7.3	17.2	0	70
% Coarse substrates (boulder, cobble, pebble and gravel)	Coar	18.7	30.1	0	95.0
% Sand	Sand	3.9	8.2	0	30
% Mud	Mud	64.5	42.3	0	100.0
% Detritus	Det	22.4	21.5	0	60
% Fine Particulate Organic Mater	FPOM	66.8	31.1	10	100
% Canopy cover	Canopy	54.5	32.8	0	96.7

Variable	Abbreviation	Mean	SD	Min.	Max.
pH	pH	6.6	0.5	5.9	8.1
Temperature (°C)	Temp	21.8	2	18	27.4
Total solids (mg/l)	TotSol	153.3	83.3	28	422
Dissolved oxygen (mg/l)	DO	4.7	2.4	0.5	9.2
Total alkalinity (mg/l)	Alk	63.3	45	16.3	188.6
Specific conductance (µs/cm)	Cond	138.9	94.8	41	378
Ammonia Nitrogen NH_3-N (mg/l)	NH3-N	0.6	0.6	0	1.6
Total coliforms (NPM/100ml)	TotCol	57072.7	140438.4	200	700000
Fecal coliforms (NPM/100ml)	FeCol	37904.8	134919.5	20	700000
Macroinvertebrate community metrics					
Abundance	Abnd	1534.6	2550.2	76	13245
Richness	Rich	32.4	9.8	16	51
Alpha	Alpha	7.3	2.6	2.5	12.6
EPT Richness	RichEPT	7	4.5	0	14
% EPT	PerEPT	15.5	14	0	38.9
BMWP-Univalle	BMWP.U	98.5	41.5	27	190

Table 2. Spearman correlations of macroinvertebrate community metrics.

Variables	1	2	3	4
LogAbnd	-			
Richn	0.334	-		
Alpha	-0.393*	0.616**	-	
RichEPT	-0.131	0.558**	0.483**	-
BMWP.U	0.138	0.725**	0.858**	0.852**

*p<0.05, **p<0.01

Table 3. Factor loadings and total variance explained for the principal component analysis of catchment-scale variables. Larger loadings are in boldface.

Variable	Component 1	Component 2	Component 3	Component 4
CatchElev*	0.33	0.21	**-0.43**	-0.07
CatchArea*	0.16	-0.11	**0.61**	-0.08
ChanSlope*	0.19	-0.13	**0.48**	0.22
BareCat	0.22	-0.14	-0.31	**-0.42**
CropCat*	**0.44**	0.35	0.06	0.04
CoffeeCat	**0.45**	0.3	0.05	0.12
PastCat*	**-0.53**	0.12	-0.02	0.04
AgCat*	-0.18	**0.6**	0.08	0.07
ForstCat*	0.13	**-0.45**	-0.18	**0.48**
GuaCat	0.14	-0.2	-0.2	0.39
ShruCat	0.06	-0.27	0.06	**-0.57**
UrbCat	0.17	-0.08	0.14	-0.20
% Total variance	24.23	18.6	15.15	11.74

*****Retained variable

Table 4. Spearman correlations of catchment-scale variables.

Variables		1	2	3	4	5	6	7	8	9	10	11	BMWP.U
1.	CatchElev	-											0.044
2.	CatchArea	-0.219	-										0.006
3.	ChanSlope	-0.093	-0.028	-									0.315
4.	BareCat	0.276	0.057	0.044	-								0.074
5.	CropCat	0.509**	0.248	-0.084	0.158	-							0.113
6.	CoffeeCat	0.612**	0.102	0.190	0.105	0.677**	-						0.112
7.	PastCat	-0.375*	-0.397*	0.009	-0.250	-0.603**	-0.504**	-					-0.258
8.	AgCat	0.005	-0.256	-0.073	-0.343	0.228	0.082	0.496**	-				-0.319·
9.	ForstCat	-0.022	0.061	0.392*	0.133	-0.102	-0.124	-0.264	-0.643**	-			0.562**
10.	GuaCat	0.132	-0.169	0.355	0.096	0.126	0.045	-0.234	-0.331	0.542**	-		0.284
11.	ShruCat	-0.089	0.193	-0.177	0.114	-0.074	0.000	-0.159	-0.417*	-0.087	0.110	-	-0.091
12.	UrbCat	0.166	0.177	0.327	0.481**	0.053	0.125	0.016	-0.208	0.138	0.340	0.244	0.249

·p<0.1, *p<0.05, **p<0.01

Table 5. Factor loadings and total variance explained for the principal component analysis of riparian-scale variables. Larger loadings are in boldface.

Variable	Component 1	Component 2	Component 3
BuffWid*	**0.43**	-0.19	0.16
RipBare	0.13	-0.08	**0.56**
RipForest	**0.46**	-0.23	-0.10
RipGua	0.31	0.09	**-0.48**
RipCrop*	0.13	**0.64**	-0.02
RipCoffee	0.17	**0.61**	0.01
RipPast*	**-0.47**	-0.19	-0.07
RipAg	**-0.46**	0.20	-0.15
RipShru	-0.03	0.18	**0.50**
RipUrb	-0.08	0.08	0.38
% Total variance	39.56	18.69	11.58

***Retained variable

Table 6. Spearman correlations of riparian-scale variables.

Variable	1	2	3	4	5	6	7	8	9	BMWP-U
1. BuffWid	-									0.394*
2. RipBare	0.259	-								0.034
3. RipForest	0.885**	0.216	-							0.409*
4. RipGua	0.300	0.072	0.456*	-						0.143
5. RipCrop	0.062	0.317	0.065	0.287	-					0.081
6. RipCoffee	0.098	0.112	0.133	0.314	0.604**	-				0.112
7. RipPast	-0.733**	-0.292	-0.769**	-0.470**	-0.509**	-0.500**	-			-0.309
8. RipAg	-0.881**	-0.219	-0.907**	-0.353	-0.075	-0.187	0.838**	-		-0.356
9. RipShru	-0.134	0.008	-0.278	-0.198	0.109	0.195	-0.051	-0.077	-	-0.081
10. RipUrb	-0.050	0.341	-0.117	-0.088	-0.002	0.196	0.072	0.115	0.081	-0.120

*p<0.05, **p<0.01

Table 7. Factor loadings and total variance explained for the principal component analysis of habitat-scale variables. Larger loadings are in boldface.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Bankfull	**0.26**	0.08	-0.11	0.16
Depth	-0.13	0.26	-0.19	**0.43**
Disch	-0.01	**-0.30**	0.23	**0.42**
Riffl	**-0.26**	0.14	0.20	-0.04
SlowCur*	**0.35**	-0.08	-0.06	0.02
Pool	-0.19	-0.05	-0.04	**0.36**
Coar*	**-0.24**	0.25	0.21	-0.06
Detr	**-0.26**	0.17	0.07	-0.20
Sand	**-0.26**	0.15	-0.11	0.04
Mud	0.19	-0.26	-0.01	0.12
FPOM	0.15	0.16	-0.31	-0.15
Canopy	-0.09	-0.10	0.16	0.16
Temp	**0.33**	-0.01	0.08	0.28
pH	0.06	-0.01	**0.54**	-0.14
TotSol*	0.22	0.26	0.09	**0.32**
DO	**-0.26**	0.26	0.06	0.13
Alk	0.22	0.29	0.39	0.03
Cond	0.21	**0.33**	0.34	0.04
NH3-N*	-0.06	**-0.40**	0.26	-0.18
TotCol	**0.25**	0.04	0.01	**-0.31**
FecCol	0.21	**0.32**	-0.16	-0.17
% Total variance	28.15	16.98	10.73	8.11

*Retained variable

Table 8. Spearman correlations of habitat-scale variables.

Variable	1	2	3	4	5	6	7	8	9	10	BMWP.U
1. Bankfull	-										-0.018
2. Depth	-0.056	-									0.363*
3. Discharge	0.044	0.404*	-								0.184
4. Riffles	-0.415*	0.272	0.526**	-							0.287
5. SlowCur	0.415*	-0.342	-0.458*	-0.703**	-						-0.498**
6. Pools	-0.332	0.283	-0.110	0.157	-0.244	-					-0.021
7. Bedrock	-0.306	0.041	0.105	0.186	-0.335	0.270	-				-0.002
8. Coar	-0.315	0.177	0.182	0.348	-0.527**	0.357	0.474**	-			0.435*
9. Sand	-0.156	0.497**	0.538**	0.457*	-0.581**	0.263	0.416*	0.465**	-		0.510**
10. Mud	0.223	-0.283	0.010	-0.238	0.368*	-0.295	-0.550**	-0.717**	-0.586**	-	-0.449*
11. Det	-0.317	0.154	0.318	0.469**	-0.505**	0.162	0.655**	0.489**	0.369*	-0.395*	0.113
12. FPOM	0.347	0.016	-0.239	-0.376*	0.376*	-0.128	0.093	-0.084	0.037	-0.009	-0.032
13. Canopy	-0.277	0.152	0.144	0.048	-0.030	0.022	0.108	0.036	0.176	-0.231	-0.077
14. pH	-0.151	-0.477**	-0.006	0.151	0.061	-0.121	0.120	0.014	-0.197	0.193	-0.303
15. Temp	0.443*	-0.118	-0.114	-0.417*	0.672**	-0.219	-0.510**	-0.430*	-0.457*	0.402*	-0.358
16. TotSol	0.444*	0.148	0.185	-0.104	0.331	-0.126	-0.180	-0.107	-0.031	-0.030	-0.042
17. DO	-0.193	0.490**	0.578**	0.715**	-0.657**	0.246	0.311	0.514**	0.497**	-0.341	0.445*
18. Alk	0.244	-0.092	-0.174	-0.142	0.495**	-0.286	-0.364*	-0.104	-0.352	0.124	-0.146
19. Cond	0.265	-0.044	-0.222	-0.157	0.518**	-0.254	-0.271	-0.083	-0.322	0.073	-0.213
20. NH3-N	-0.293	-0.578**	-0.118	-0.101	0.090	0.064	0.012	-0.090	-0.372*	0.235	-0.499**
21. TotCol	0.216	-0.299	-0.297	-0.319	0.498**	-0.481**	-0.354	-0.293	-0.281	0.086	-0.170
22. FecCol	0.512**	0.077	-0.105	-0.257	0.362	-0.525**	-0.339	-0.297	-0.126	0.028	0.018

*p<0.05, **p<0.01

Table 8 Continuation. Spearman correlations of habitat-scale variables.

Variable	11	12	13	14	15	16	17	18	19	20	21	BMWP.U
11. Det	-											0.113
12. FPOM	0.116	-										-0.032
13. Canopy	-0.081	-0.242	-									-0.077
14. pH	0.053	-0.115	0.112	-								-0.303
15. Temp	-0.584**	0.052	0.097	0.063	-							-0.358
16. TotSol	-0.175	0.063	-0.096	0.041	0.582**	-						-0.042
17. DO	0.570**	-0.200	-0.063	-0.055	-0.522**	0.054	-					0.445*
18. Alk	-0.226	0.268	-0.118	0.244	0.651**	0.683**	-0.240	-				-0.146
19. Cond	-0.112	0.293	-0.094	0.214	0.612**	0.703**	-0.188	0.952**	-			-0.213
20. NH3-N	-0.080	-0.393*	0.219	0.511**	-0.066	-0.401*	-0.339	-0.252	-0.284	-		-0.499**
21. TotCol	-0.514**	0.128	0.140	0.123	0.357	0.233	-0.501**	0.434*	0.410*	0.166	-	-0.170
22. FecCol	-0.259	0.338	-0.109	-0.161	0.435*	0.626**	-0.274	0.530**	0.555**	-0.363	0.668**	0.018

*p<0.05, **p<0.01

Table 9. Exploratory multiple regression models to predict macroinvertebrate community tolerance and habitat characteristics of small streams of the coffee-growing region of Colombia.

Response Variable	Regression model	Standardized coefficient	R^2	Adj-R^2	RSE
Catchment scale					
BMWP-Univalle	% Forest catchment	0.57***	0.33	0.30	0.42
BMWP-Univalle	% Agriculture catchment	-0.36·	0.13	0.10	0.47
% Slow currents	Elevation	-0.45**	0.34	0.29	0.42
	% Forest catchment	-0.35*			
% Coarse substrates	Channel slope	0.47**	0.50	0.47	0.36
	% Forest catchment	0.46**			
% Coarse substrates	% Agriculture catchment	-0.33·	0.11	0.07	0.48
NH3-N	% Cropland catchment	0.55**	0.30	0.27	0.43
NH3-N	% Agriculture catchment	0.43*	0.18	0.15	0.46
Riparian scale					
BMWP-Univalle	Forest buffer width	0.45*	0.20	0.17	0.45
BMWP-Univalle	% Riparian agriculture	-0.41*	0.16	0.13	0.47
% Slow currents	Forest buffer width	-0.55**	0.30	0.27	0.43
% Slow currents	% Riparian pastures	0.52**	0.27	0.24	0.43
% Slow currents	% Riparian agriculture	-0.45*	0.21	0.18	0.45
% Coarse substrates	Forest buffer width	0.52**	0.28	0.25	0.43
% Coarse substrates	% Riparian agriculture	-0.41*	0.17	0.14	0.46
NH3-N	% Riparian cropland	0.47**	0.22	0.19	0.45
Habitat scale					
BMWP-Univalle	% Slow currents	-0.38*	0.51	0.45	0.37
	NH3-N	-0.36*			
	% Coarse substrates	-0.31·			

·p<0.1, *p<0.05, **p<0.01, ***p<0.001

Table 10. Fit statistics of the structural equation model

χ^2	DF	χ^2 *P* value	RMSEA	TLI	CFI
12.352	12	0.418	0.032	0.986	0.994

Table 11. Standardized direct, indirect and total effects of catchment, riparian and habitat variables on dependent factors of the structural equation model

		Catchment scale			Riparian scale	Habitat scale		
Variables	**Effect**	**AgCat**	**ChanElev**	**ChanSlope**	**BuffWid**	**SlowCur**	**Coar**	**NH3-N**
BuffWid	Direct	-0.482*	0	0	0	0	0	0
	Indirect	0	0	0	0	0	0	0
	Total	-0.482*	0	0	0	0	0	0
SlowCur	Direct	0	-0.435*	-0.108	-0.453**	0	0	0
	Indirect	0.219**	0	0	0	0	0	0
	Total	0.219**	-0.435*	-0.108	-0.453**	0	0	0
Coar	Direct	-0.168	0	0.422**	0.069·	-0.384*	0	0
	Indirect	-0.117·	0.167·	0.042	0.174*	0	0	0
	Total	-0.285*	0.167·	0.464*	0.243	-0.384*	0	0
NH3-N	Direct	0.481*	0	0	0.092	0	0	0
	Indirect	-0.044	0	0	0	0	0	0
	Total	0.436*	0	0	0.092	0	0	0
BMWP.U	Direct	0	0	0	0	-0.359*	0.305·	-0.358*
	Indirect	-0.322*	0.207*	0.180	0.204·	-0.117·	0	0
	Total	-0.322*	0.207*	0.180	0.204·	-0.476**	0.305·	-0.358*

·p=0.1, *p<0.05, **p<0.01, ***p<0.001

Table 12. Relative indirect effects of agriculture and forest buffer width on BMWP.U as mediated by habitat variables

	AgCat		BufWid	
Mediating variable	**Relative effect**	**% Contribution**	**Relative effect**	**% Contribution**
SlowCur	-0.079	24.4	0.163	60
Coar	-0.087	27.0	0.074	27
NH3-N	-0.156	48.5	-0.033	12

Figures

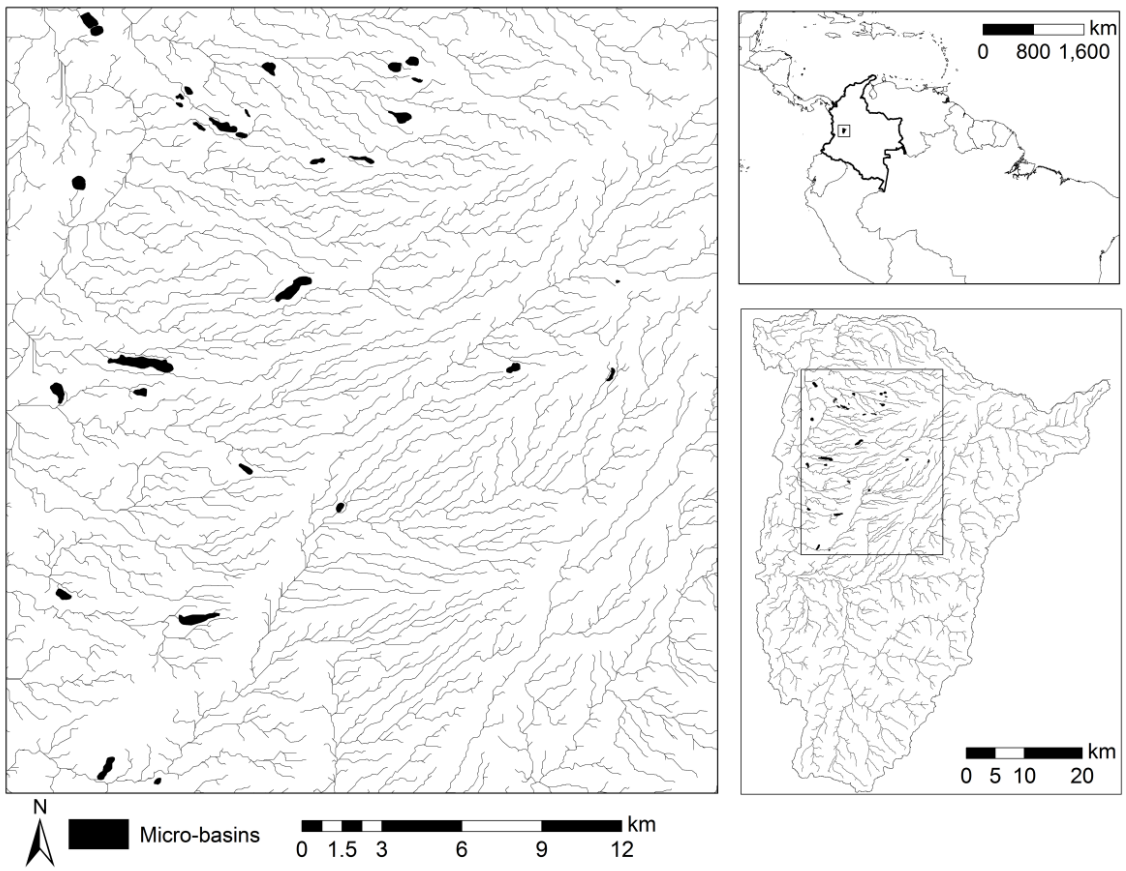

Figure 1. Location of the 30 micro-basins (left) in western Colombia (top right) and La Vieja River Basin (bottom right).

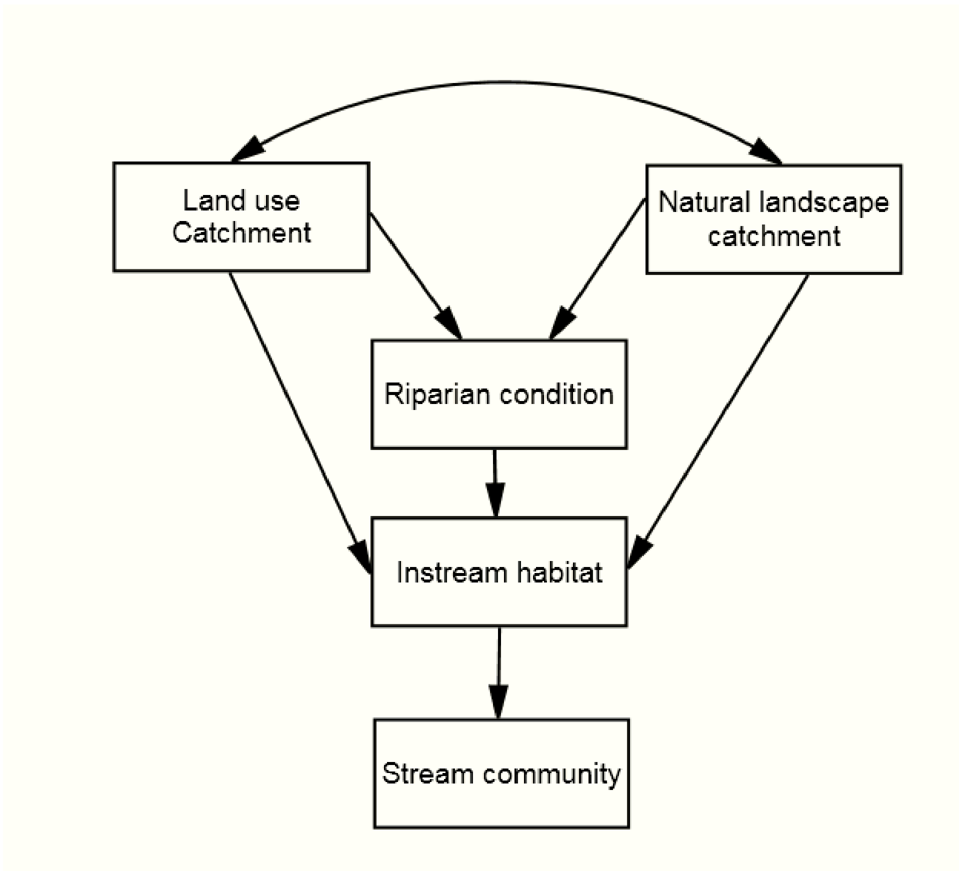

Figure 2. General conceptual model of the possible pathways through which natural and anthropogenic factors affect stream ecosystems

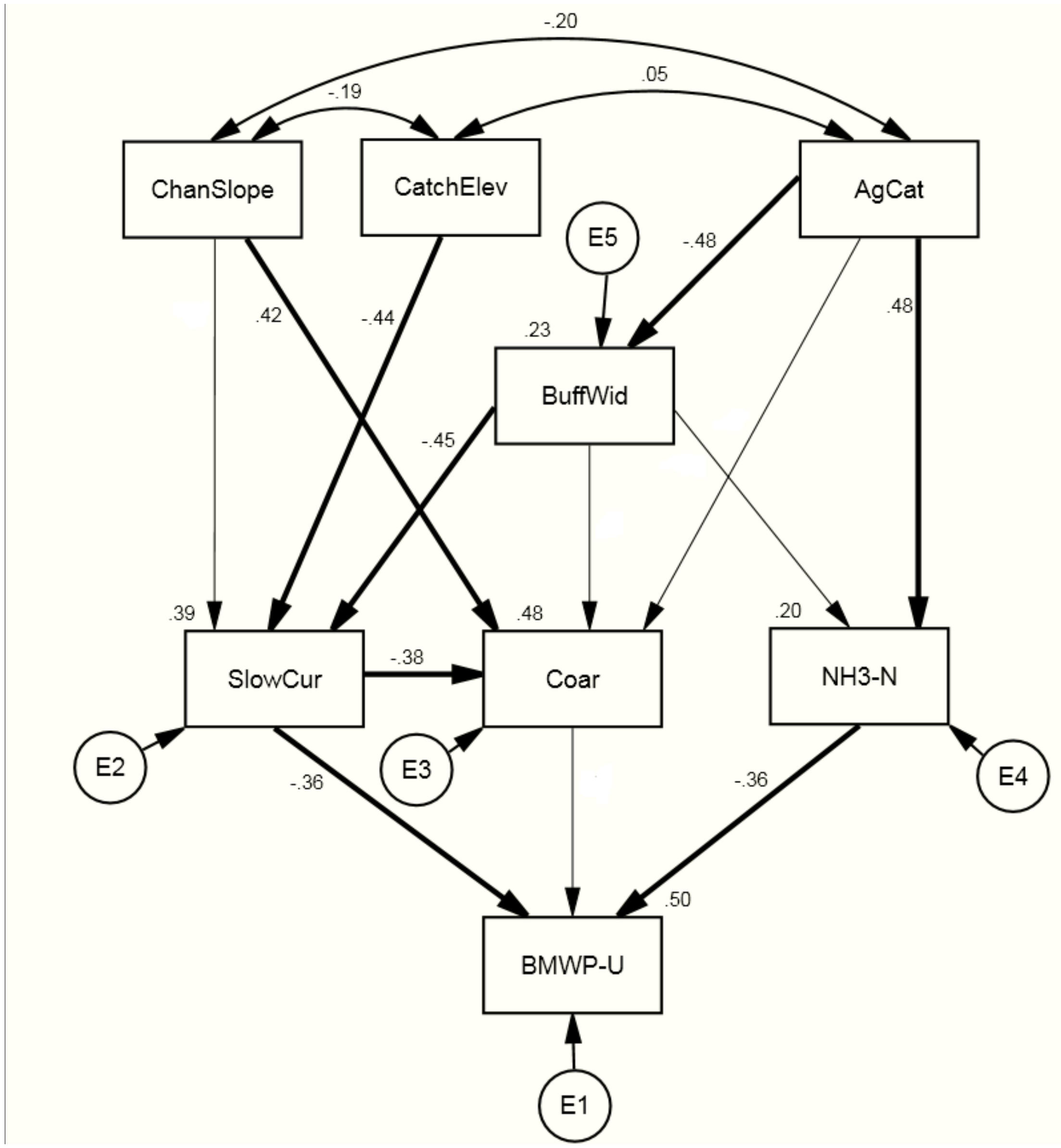

Figure 3. Structural equation model to describe the influence of catchment, riparian and habitat variables on macroinvertebrate community tolerance. Large arrows indicate significant direct effects (p<0.05). Standardized regression coefficients are presented only with significant paths in the model. R^2 values for the dependent variables are printed above the variable.

References

Allan J.D. & Johnson L.B. (1997) Catchment-scale analysis of aquatic ecosystems. *Freshwater Biology* **37**, 107-111.

Allan J.D. (2004) Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **35**, 257-284.

Allan J.D. & Castillo M.M. (2007) Stream Ecology, structure and function of running waters. *Springer*, Dordrecht, Netherlands, 436 pp.

American Public Health Association (1995). Standard methods for the examination of water and wastewater*. American Public Health Association, American Waterworks Association, and Water Pollution Control Federation,*Washington, USA.

Arbuckle J. L. (2010). Amos version 2.0. *Amos Development Corporation*, Meadville, USA.

Barbour M.T., Gerritsen J., Snyder B.D. & Stribling J.B. (1999) Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. EPA 841-B-99-002, U.S. *Environmental Protection Agency, Office of Water*, Washington D.C., USA.

Chará J. (2003) Interactions between biodiversity and land use in low-order stream catchments of the Colombian Andes. Ph. D. Thesis. *Institute of Aquaculture. University of Stirling*, UK, 217 pp.

Chará J. (2004) Manual de evaluación biológica de ambientes acuáticos en microcuencas ganaderas. 2 ed. *Fundación Cipav*, Cali, Colombia 52 pp.

Chará J., Giraldo L.P., Chará-Serna A.M. & Pedraza G.L. (2012) Beneficios de los corredores ribereños de Guadua angustifolia en la protección de ambientes acuáticos en la Ecorregión Cafetera de Colombia. 2. Efectos sobre la escorrentía y captura de nutrientes*. Revista recursos naturales y ambiente* **61**, 60-66.

Clarke A., Lake P.S. & O'Dowd D.J. (2004) Ecological impacts on aquatic macroinvertebrates following upland stream invasion by a ponded pasture grass (*Glyceria maxima*) in southern Australia. *Marine and Freshwater Research* **55**, 709-713.

Davies-Colley R.J. (1997) Stream channels are narrower in pasture than in forest. *New Zealand Journal of Marine and Freshwater Research* **31**, 599-608.

Diana M., Allan J.D. & Infante D. (2006) The Influence of Physical Habitat and Land Use on Stream Fish Assemblages in Southeastern Michigan. *American Fisheries Society Symposium* **48**, 359-374.

Duehr J.P., Siepker M.J., Pierce C.L. & Isenhart T.M. (2008) Relation of Riparian Buffer Strips to In-Stream Habitat, Macroinvertebrates and Fish in a Small Iowa Stream. *Journal of the Iowa Academy of Science* **113**, 101-107.

Environmental Systems Resource Institute –ESRI. (2009). ArcMap 9.3. *ESRI*, Redlands, USA.

Etter A. & Wyngaarden W.V. (2000) Patterns of Landscape Transformation in Colombia, with Emphasis in the Andean Region. *Ambio* **29**, 432-439.

Etter A., McAlpine C., Wilson K., Phinn S. & Possingham H. (2006) Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, Ecosystems & Environment* **114**, 369-386.

Gergel S.E., Turner M.G., Miller J.R., Melack J.M. & Stanley E.H. (2002) Landscape indicators of human impacts to riverine systems. *Landscape* **64**, 118– 128.

Gücker B., Boëchat I.G. & Giani A. (2009) Impacts of agricultural land use on ecosystem structure and whole-stream metabolism of tropical Cerrado streams. *Freshwater Biology* **54**, 2069-2085.

Herbst D.B., Bogan M.T., Roll S.K. & Safford H.D. (2012) Effects of livestock exclusion on in-stream habitat and benthic invertebrate assemblages in montane streams. *Freshwater Biology* **57**, 204-217.

Hoe S.L. (2008) Issues and procedures in adopting structural equation modeling technique. *Quantitative Methods Inquires* **3**, 76-83.

Hook P.B. (2003) Sediment retention in rangeland riparian buffers. *Journal of environmental quality* **32**, 1130-7.

Johnson T.E., Mcnair J.N., Srivastava P. & Hart D.D. (2007) Stream ecosystem responses to spatially variable land cover: an empirically based model for developing riparian restoration strategies. *Freshwater Biology* **52**, 680-695.

Johnson L.B. & Host G.E. (2010) Recent developments in landscape approaches for the study of aquatic ecosystems. *Journal of the North American Benthological Society* **29**, 41-66.

Loo S.E., Mac Nally R., O'Dowd D.J. & Lake P.S. (2009) Secondary Invasions: Implications of Riparian Restoration for In-Stream Invasion by an Aquatic Grass. *Restoration Ecology* **17**, 378-385.

Lyons J., Trimble S.W. & Paine L.K. (2000) Grass versus trees: managing riparian areas to benefit streams of central North America. *Journal of the American Water Resources Association*, **36,** 919–30.

Maloney K.O. & Weller D.E. (2011) Anthropogenic disturbance and streams: land use and land-use change affect stream ecosystems via multiple pathways. *Freshwater Biology* **56**, 611-626.

Mesa L.M. (2010) Effect of spates and land use on macroinvertebrate community in Neotropical Andean streams. *Hydrobiologia* **641**, 85-95.

Miserendino M.L. & Masi C.I. (2010) The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. *Ecological Indicators* **10**, 311-319.

Munn M.D., Waite I.R., Larsen D.P. & Herlihy A. (2009) The relative influence of geographic location and reach-scale habitat on benthic invertebrate assemblages in six ecoregions. *Environmental monitoring and assessment* **154**, 1-14.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-8.

Mayer P.M., Reynolds S.K., McCutchen M.D. & Canfield T.J. (2007) Meta-analysis of nitrogen removal in riparian buffers. *Journal of environmental quality* **36**, 1172-80.

Neill C., Deegan L.A., Thomas S.M. & Cerri C.C. (2001) Deforestation for pasture alters nitrogen and phosphorus in small Amazonian streams. *Ecological Applications* **11**, 1817–1828.

Niyogi D.K., Koren M., Arbuckle C.J. & Townsend C.R. (2007) Stream communities along a catchment land-use gradient: subsidy-stress responses to pastoral development. *Environmental management* **39**, 213-25.

Ordóñez M.V. (2011) Influencia del uso de suelo y la cobertura vegetal natural en la integridad ecológica de los ríos altoandinos al noreste del Ecuador. M.S. Thesis. *Universidad San Francisco de Quito*, 45 pp.

Osborne L.L. & Kovacic D.A. (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology* **29**, 243-258.

Pedraza G.X., Giraldo L.P. & Chará J.D. (2008) Efecto de la restauración de corredores ribereños sobre características bióticas y abióticas de quebradas en zonas ganaderas de la cuenca del río La Vieja, Colombia. *Zootecnia tropical* **26**, 1-4.

Quinn J.M., Cooper A.B., Davies-Colley R.J., Rutherford J.C. & Williamson R.B. (1997) Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research* **31**, 579-597.

R Development Core Team (2012) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria.

Riseng C.M., Wiley M.J., Black R.W. & Munn M.D. (2011) Impacts of agricultural land use on biological integrity: a causal analysis. **21**, 3128-3146.

Scanlon B.R., Jolly I., Sophocleous M. & Zhang L. (2007) Global impacts of conversions from natural to agricultural ecosystems on water resources: Quantity versus quality. *Water Resources Research* **43**.

Schumacker R.E. & Lomax, R.G. (1996) A beginner's guide to structural equation modeling. *Lawrence Erlbaum associates, publishers*. Mahwah, USA 288 pp.

Sponseller R. a., Benfield E.F. & Valett H.M. (2001) Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* **46**, 1409-1424.

SPSS Inc., an IBM Company. (2010) IBM SPSS Statistics, version 19.0. *IBM*, Armonk, USA.

Schmitt T.J., Dosskey M.G. & Hoagland K.D. (1999) Filter Strip Performance and Processes for Different Vegetation, Widths, and Contaminants. *Journal of Environmental Quality* **28**, 1479-1489.

Sweeney B.W. (1993) Streamside forests and the physical, chemical, and trophic characteristics of piedmont streams in eastern North America. *Water Science and Technology* **26**, 2653-2673.

Townsend C.R., Downes B.J., Peacock K. & Arbuckle C.J. (2004) Scale and the detection of land-use effects on morphology, vegetation and macroinvertebrate communities of grassland streams. *Freshwater Biology* **49**, 448-462.

U.S. Environmental Protection Agency –USEPA. (2009) Draft 2009 update aquatic life ambient water quality criteria for ammonia – Freshwater. *USEPA, Office of Water and Office of Science and Technology,* Washington D.C., USA.

Vázquez G., Aké-Castillo J. A. & Favila M.E. (2011) Algal assemblages and their relationship with water quality in tropical Mexican streams with different land uses. *Hydrobiologia* **667**, 173-189.

Vondracek B., Blann K.L., Cox C.B., Nerbonne J.F., Mumford K.G., Nerbonne B. A, Sovell L.A. & Zimmerman J.K.H. (2005) Land use, spatial scale, and stream systems: lessons from an agricultural region. *Environmental management* **36**, 775-791.

Waite I.R., Brown L.R., Kennen J.G., May J.T., Cuffney T.F., Orlando J.L. & Jones K.A. (2010) Comparison of watershed disturbance predictive models for stream benthic macroinvertebrates for three distinct ecoregions in western US. *Ecological Indicators* **10**, 1125-1136.

Young E.O. & Briggs R.D. (2007) Nitrogen dynamics among cropland and riparian buffers: soil-landscape influences. *Journal of environmental quality* **36**, 801-14.

Zúñiga M. del C & Cardona W. (2009) Bioindicadores de calidad de agua y caudal ambiental. pp 167-197. In: Cantera J.R., Carvajal, Y & Castro, L.M. (eds), Caudal ambiental. Conceptos, experiencias y desafíos. *Programa Editorial de la Universidad del Valle*. Santiago de Cali, Colombia.

Appendix

Appendix A. Complete list of macroinvertebrate community descriptors calculated for 30 small streams of the coffee-growing region of Colombia

Metric	**Mean**	**SD**	**Min.**	**Max.**
Abundance	1534.6	2550.2	76	13245
Richness	32.4	9.8	16	51
Shannon H' Log Base 10.	0.9	0.3	0.2	1.4
Shannon J'	0.6	0.2	0.1	0.9
Alpha	7.3	2.6	2.5	12.6
Simpson's Diversity	0.3	0.2	0.1	0.8
EPT Richness	7	4.5	0	14
% EPT	15.5	14	0	38.9
Diptera abundance	920.1	2422.8	3	12261
% Diptera	38.7	26.5	0.1	93.2
Mollusca abundance	353.9	562	0	2181
% Mollusca	23.9	32	0	97.3
BMWP-Univalle	98.5	41.5	27	190