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RIPARIAN VEGETATION AND STREAM CONDITION IN A TROPICAL AGRICULTURE–SECONDARY FOREST MOSAIC

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Abstract. Changes in land cover from forest to agriculture often alter riparian vegetation, which modifies the physical conditions of streams. To understand the impacts of different categories of land cover on riparian and stream habitats, we sampled riparian vegetation and stream conditions in three adjacent watersheds in southeastern Puerto Rico. Land cover categories (pasture, mixed, and forest) were determined using aerial photographs. Vegetation structure and composition and characteristics of streams were assessed for 35 riparian sites. Sites were located along first-order streams, at 400–600 m elevation in the wet-forest life zone. Understory vegetation in the forest sites was mainly shrubs, herbs, and ferns, whereas the mixed and pasture sites were dominated by grasses, vines, and bare soil. *Syzygium jambos* and *Spathodea campanulata*, nonnatives, and *Guarea guidonia*, a native, were the most common tree species in the riparian areas. Surrounding land cover explained >60% of the variation among stream sites. There was a positive relationship between tree cover and percentage of dissolved oxygen, and a negative relationship between tree cover and percentage of substrata covered by sediments from eroded soil. The amount of woody debris in the streams tended to increase with forest cover. Overall, land cover is a landscape feature that effectively characterized riparian understory cover, tree species composition, and stream condition.

Key words: first-order streams; land cover; montane watersheds; Puerto Rico; riparian vegetation; secondary forest; tropical agriculture; tropical streams; watersheds.

Introduction

Riparian vegetation is an important feature of the landscape because it connects terrestrial and aquatic systems and can function as corridors (Tabacchi et al. 1990, Malanson 1993, Machtans et al. 1996, Naiman and Décamps 1997). Deforestation, agriculture, and urban development alter the extent and connectivity of vegetation patches in the riparian zone. These activities often result in elimination of native riparian plant species, colonization by invasive species, and alteration of stream banks and substrata (Allan and Flecker 1993, Hunsacker and Levine 1995, Nilsson 1995, Roth et al. 1996, Boutin and Jobin 1998, Bunn et al. 1998, Carpenter et al. 1998, Tabacchi et al. 1998, Wissmar and Beschta 1998). Fragmentation affects biotic and abiotic conditions within watersheds and riparian areas. Breaks in the continuous forest cover of riparian areas restrict movement of organisms and affect temperature and light conditions, which can lead to the local loss of plant and animal species (Malanson 1993, Forman 1995, Machtans et al. 1996, Poff et al. 1997, Wissmar and Beschta 1998, Debinski and Holt 2000).

Changes in riparian vegetation also affect structure and processes within streams (Sweeney 1992, Bunn et al. 1998, Wear et al. 1998). When riparian vegetation is removed, stream bank stability is lost, resulting in an increase in light and sediment load, which alters stream-reach microhabitats (Roth et al. 1996, Allan et al. 1997, Tabacchi et al. 1998). Riparian vegetation influences stream processes by acting as a sink and/or source of matter and energy. As a sink, riparian vegetation dissipates the energy of flowing water while it retains and absorbs particles from upland areas (Turner 1989, Fisher et al. 1998, Kindler 1998). As a source, production of leaf litter contributes matter to the stream ecosystem and woody debris contributes to structure (Hawkins et al. 1993, Tabacchi et al. 1998). The contribution of leaf litter and woody debris is a particularly important resource for organisms in first-order streams, which depend mainly on allochthonous (outside) sources of energy (Allan 1995, Nilsson 1995, Tabacchi et al. 1998, Crowl et al. 2001).

Land use change, including urban development and regeneration of secondary forests, create a complex land cover mosaic that affects landscape features such as riparian vegetation (Aide et al. 1995, 2000, Zimmerman et al. 1995, Roth et al. 1996, Allan et al. 1997, Wissmar and Beschta 1998). Large-scale landscape assessments, such as mapping land cover, serve as a first step in the development of sustainable management plans for watersheds. To understand how changes in land cover affect riparian vegetation and their associ-

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ated freshwater systems, we addressed the following questions: (1) What is the land cover composition of three adjacent watersheds, and what is the extent and connectivity of riparian cover? (2) How do patterns of land cover and tree species composition vary in riparian areas of first-order streams? (3) Are characteristics of first-order streams predicted by land cover in riparian or watershed areas? These questions were answered by studying the land cover patterns of three montane watersheds in southeastern Puerto Rico, and documenting the riparian vegetation and stream conditions of 35 first-order streams.

Methods

Study area

The study area included the Usabón, Matón, and Guavate river watersheds of the La Plata River system in Puerto Rico (Fig. 1). These rivers occur within the subtropical wet-forest life zone (Ewel and Whitmore 1973). Elevation in the three watersheds ranges from 250 to 905 m, and precipitation varies from 2000 to 4000 mm/yr (Ewel and Whitmore 1973). The landscape of these watersheds is a mosaic of secondary forests and rural areas, including low-density housing, small-scale agriculture, abandoned coffee plantations, and urban areas with subdivisions. Soils are derived from limestone parent material and are prone to soil compaction (Ewel and Whitmore 1973). The southeast part of the Guavate River watershed is located within the Carite Commonwealth Forest.

Land cover in the watersheds, subwatersheds, and riparian areas

Land cover composition and riparian forest connectivity in the three watersheds were determined using 1:20 000-scale aerial photographs from 1995. Land cover categories were determined based on tree canopy cover and density of houses or other buildings. The land cover categories were urban, pasture, mixed, and forest cover (Table 1). In the aerial photographs, we identified all polygons of each land cover category with a minimum mapping unit of 1 ha. We digitized polygons and transformed the resulting land cover to the State Plane coordinate system for Puerto Rico with PC ARC/INFO 3.5 software (ESRI 1996). Topography and hydrology cover data were obtained from U.S. Geological Survey (USGS) 1:20 000-scale Digital Line Graphs (DLG). To make further analyses and overlays possible, these data were combined to generate a Geographic Information System (GIS) in ArcView Version 3.1 (ESRI 1996). Topographic 7.5-min maps were used for field observations and location of sampling sites (USGS). The distribution of land cover categories was determined for the three watersheds and provided the basis for generating subwatershed and riparian land cover data. Riparian buffer zones of 5, 25, and 50 m on each side of the stream were generated in ARC/INFO around all stream channels within each watershed. To determine connectivity, forest cover fragments were quantified in the 50-m riparian buffers along all tributaries of the three watersheds. The length of each fragment and distance between fragments were measured along the stream channel to assess the extent of continuous riparian habitat within the three watersheds. The distribution of land cover was determined for the drainage area of each study site. First-order stream drainage areas, termed ‘‘subwatersheds,’’ were delineated using 1988 USGS 1:20 000 topographic maps.

Riparian vegetation sampling and data analysis

To determine how land cover and riparian species composition varied across the landscape, we sampled a total of 35 sites in the three watersheds between May and July 1999. All sites were located from 400 to 600 m elevation in first-order streams (as identified in USGS 1:20 000 topographic maps). In each watershed, we sampled four replicate sites of each of the three nonurban land cover categories. Streams in the urban land cover category were not included because of channelization and the disturbed condition of the stream banks and substrata. Sites were sampled in pasture ($n = 12$), mixed ($n = 12$), and forest ($n = 11$) cover categories. We were only able to sample three forest cover sites in the Usabón watershed. At each site, one transect (1×30 m) was randomly established on one side of the stream, 2 m meters away from the stream bank. We measured stem diameter at 130 cm (dbh) and identified all trees and shrubs ($\geq$1 cm dbh). Percent cover of understory composition, vines, shrubs, ferns, grasses, herbs, and bare ground was estimated in 30 1-m^2 plots along the transect. The quantity of accumulated leaf litter was estimated in each 1-m^2 plot by piercing the litter at three different points across the plot with a thin metal skewer. All leaves, or recognizable leaf pieces (>5 cm in length), pierced by the skewer were counted.

The understory composition was first compared among watersheds and then among land cover categories, using a Kruskal-Wallis test (KW, H). Riparian tree species richness and diversity (Shannon-Weaver diversity index, H') were compared with estimated diversity indices using randomizations (Colwell 1997). The relationship of species composition among sites was determined by two multivariate ordination analyses (Nonmetric Multidimensional Scaling, NMDS), one based on species abundance and the other based on basal area (PC ORD 1997). For each NMDS analysis, a dissimilarity matrix was generated using Bray-Curtis distance. We used ANOSIM to test for differences among riparian areas of different land cover categories (one-way analysis), and another test using watershed and land cover as the main factors (two-way analysis). These analyses were done by calculating KW following the procedure described in Philippi et al. (1998) and Clarke (1993), using SAS Version 8 (SAS

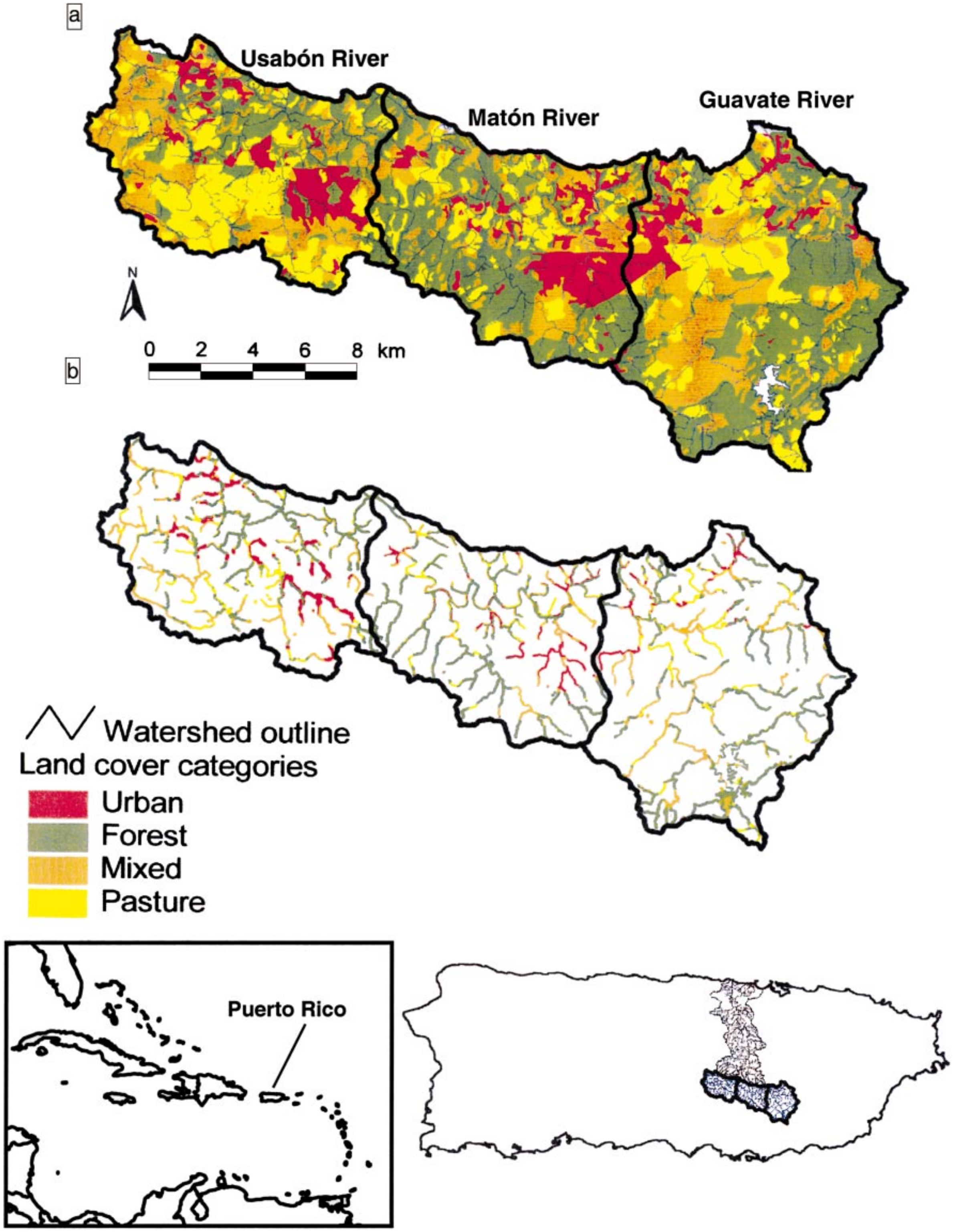

FIG. 1. Study area within the La Plata river system, Puerto Rico. Land cover categories are shown for (a) the three study watersheds and (b) a 50-m buffer zone around riparian corridors of all stream channels, including first-order streams.

TABLE 1. Land cover categories used in aerial photo interpretation for site classification.

Category	Characteristics
Urban	subdivisions and high-density buildings
Pasture	<25% tree cover, shrubs, and isolated housing
Mixed cover	25–75% tree cover, scattered and low-density housing, small-scale agriculture
Forest	>75% tree cover, closed canopy

Institute 1999). The accepted level of significance was $P < 0.05$ for all statistical tests.

Stream sampling and data analysis

Stream characteristics were assessed using both abiotic and biotic parameters of the stream substrata. The abiotic parameters were: presence of boulders (>1 m diameter), rocks (<1–0.25 m diameter), pebbles (<0.25 m), presence of sand and silt, and the presence of fine sediments from eroded soil (observed from an adjacent collapsed and eroded bank). Temperature and dissolved oxygen were measured using a YSI meter (YSI, Yellow Springs, Ohio, USA). To characterize the biotic component of the stream, we assessed presence/absence of algae/subaquatic vegetation, coarse woody debris, and leaf litter. These variables were quantified at 1-m intervals across the channel. Transects were established randomly until 50 points were described at each stream site, by visual and tactile assessment of particles (Marcus et al. 1995). Temperature and dissolved oxygen were measured once at each site. Additional temperature data were obtained with data loggers (StowAway Tidbit Temperature Logger, Onset Computer, Bourne, Massachusetts, USA), which were left for 21 d in three streams of the Matón River watershed. Stream slope was calculated for each site by dividing the elevation change along the stream reach by the length of the stream reach.

To determine if streams varied among sites with different land cover, an ordination analysis (Principal Component Analysis, PCA) was done on a variance–covariance matrix with transformed data (arcsine square-root; PC ORD 1997). In addition, we compared the amount of forest cover present in the riparian areas and in the subwatersheds with stream characteristics. To establish the scale at which land cover influenced stream characteristics, we used linear regressions to determine the relationship between percent forest cover at two spatial scales (riparian and subwatershed) and stream characteristics (sediments from eroded soil, woody debris, and dissolved oxygen).

RESULTS

Land cover in the watersheds and riparian areas

The distribution of land cover categories was similar among the three watersheds (Table 2). Within each watershed, the composition of land cover among the 5-, 25-, and 50-m riparian buffer corridors remained the same. In addition, land cover patterns among riparian areas and the whole watershed also had similar distributions. Forest cover was the dominant category within the riparian areas in the three watersheds (Table 2). In the Matón watershed, there was more urban cover in the riparian areas (>13.1%) than in the other watersheds.

Most forest fragments that occupied both banks of the riparian area in the 50-m buffer areas were <600 m in length and few fragments were >2000 m (Fig. 2). Fragment length varied among the riparian areas of the three rivers (Kruskal-Wallis statistic $H = 6.80$, $P = 0.03$); the Usabón riparian area had the shortest forest fragments. Median lengths of riparian forest fragments in the Usabón, Matón, and Guavate were 262, 413, and 439 m, respectively (Fig. 2). The distance between adjacent forest fragments did not differ among the three watersheds ($H = 0.49$, $P = 0.78$). The median distance between fragments was 600 m, but 25% of the fragments were isolated by >1000 m (Fig. 2).

Land cover in the first-order riparian areas at 400–600 m

The distribution of land cover did not vary with buffer width (5, 25, or 50 m) within watersheds (Table 3). There was no difference between whole-watershed land cover patterns and riparian buffers around first-order streams within the Matón and Guavate. However, in the Usabón watershed, the 50-m riparian buffer differed in mixed- and pasture-cover composition from the whole watershed. Forest, followed by mixed cover, dominated the first-order riparian areas in the Guavate and Matón watersheds (Table 3). In the Usabón watershed, forest (>42.7%) and pasture (>20.0%) were the most abundant land covers in the first-order riparian areas. In the Matón riparian zone, area covered by forest decreased from 59.3% to 54.8% when buffer width was increased from 5 to 50 m. Urban cover in the

TABLE 2. Total area and percent cover of land cover categories in watersheds and riparian zones of different widths.

Watershed	Total area (km^2)	Land cover categories (%)			
		Forest	Mixed	Pasture	Urban
Guavate	102.3	45.8	23.9	15.4	14.9
Riparian zones					
5 m	2.1	57.2	26.8	10.2	5.8
25 m	8.2	51.8	29.6	12.5	6.1
50 m	15.4	50.1	30.2	13.1	6.6
Usabón	99.3	34.8	37.7	16.7	10.8
Riparian zones					
5 m	1.4	41.5	32.1	15.0	11.4
25 m	7.1	41.0	32.2	15.7	11.1
50 m	13.6	38.8	33.2	16.3	11.7
Matón	94.8	46.3	24.8	11.4	17.5
Riparian zones					
5 m	1.3	57.4	18.6	9.3	14.7
25 m	6.4	57.4	19	10.2	13.4
50 m	13.7	62.3	16.3	8.3	13.1

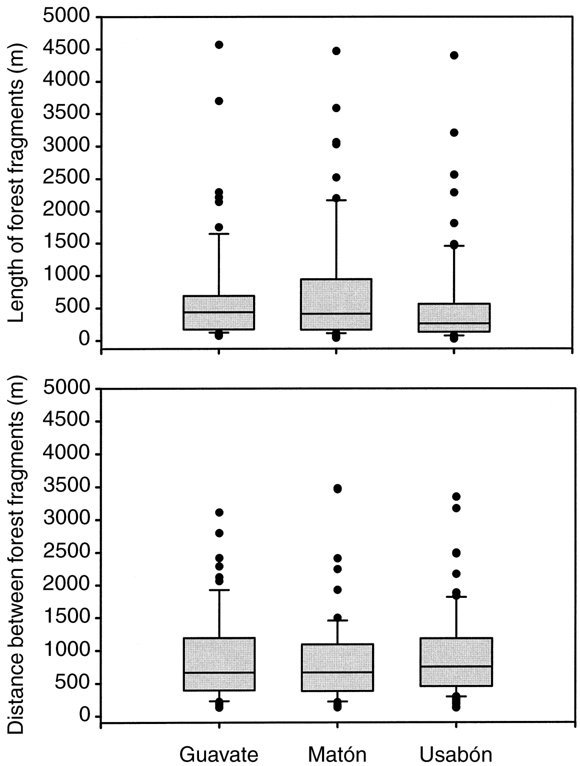

FIG. 2. Box plots of the length of forest-cover fragments and the distance between the fragments. The horizontal line in the box represents the median, the box represents the 25th to 75th percentiles, the extensions represent the 10th and 90th percentiles, and solid circles represent the outliers.

TABLE 3. Percentage of the area occupied by the land cover categories in the riparian zones of first-order streams 400–600 m.

Watershed	Total area (km^2)	Land cover categories (%)			
		Forest	Mixed	Pasture	Urban
Guavate riparian zones					
5 m	0.4	54.1	24.3	8.1	13.5
25 m	1.8	53.6	22.9	8.9	14.5
50 m	3.5	51.9	22.8	9.4	16.0
Usabón riparian zones					
5 m	0.2	45.0	20.0	20.0	15.0
25 m	1.0	43.4	19.2	22.2	15.2
50 m	1.9	42.7	18.3	23.6	15.4
Matón riparian zones					
5 m	0.3	59.3	18.5	7.4	14.8
25 m	1.5	58.0	18.8	7.3	15.9
50 m	3.1	54.8	20.2	7.3	17.7

riparian areas increased in relative area with an increase in buffer size from 5 to 50 m in all three watersheds (Table 3). The greatest increase occurred in the Matón watershed, where urban cover increased from 14.8% to 17.7%.

Riparian vegetation structure and composition of first-order streams

There was no effect of watershed on understory vegetation cover; consequently, the data were combined for further analyses by land cover categories. There were differences in understory vegetation among the land cover categories (Fig. 3). Forest sites had greater understory cover of ferns ($H = 0.08$, $P = 0.04$) and shrubs ($H = 6.59$, $P = 0.03$), accumulated more leaf litter ($H = 12.23$, $P = 0.002$), and had the lowest cover of grasses ($H = 14.65$, $P = 0.001$) and bare soil ($H = 12.21$, $P = 0.003$). Riparian sites associated with pasture cover had the lowest herb cover ($H = 6.64$, $P = 0.03$). Vine and log cover ($H = 3.59$, $P = 0.166$) did not differ among the land cover categories.

The number of woody species in the riparian vegetation ranged from zero (in a mixed-cover and a pasture site) to 22 species (in a forested site, Fig. 4a). In total, 67 tree species were found in the 35 sites. Only 27 species occurred in more than two sites (Appendix). The sampled area in each site appeared to be adequate, given that the diversity of each site did not differ from the estimated diversity indices (Colwell 1997) based on abundance or basal area. Species richness ($H = 15.98$, $P < 0.001$) and diversity index values ($H' = 6.33$, $P = 0.042$) were higher for forest sites than for mixed and pasture sites, but there was no effect of land cover on the number of nonnative species ($H' = 2.02$, $P = 0.360$). The dominant nonnative tree species were *Spathodea campanulata* and *Syzygium jambos*. The dominant agricultural species were *Musa* sp. and *Coffea arabica*. The most abundant native tree species in forest-cover sites were *Guarea guidonia* and *Ocotea leucoxylon*. In mixed-cover sites, *Eugenia biflora* and *Guarea guidonia* were the most abundant native trees, whereas in the pasture sites, the dominant native tree species was *Casearia sylvestris* (see the Appendix). Stem density and basal area were lower in the pasture sites (density, $H = 9.72$, $P = 0.008$; basal area, $H = 8.21$, $P = 0.017$) than in mixed and forest sites (Fig. 4b–c). Vegetation size class structure was not signifi-

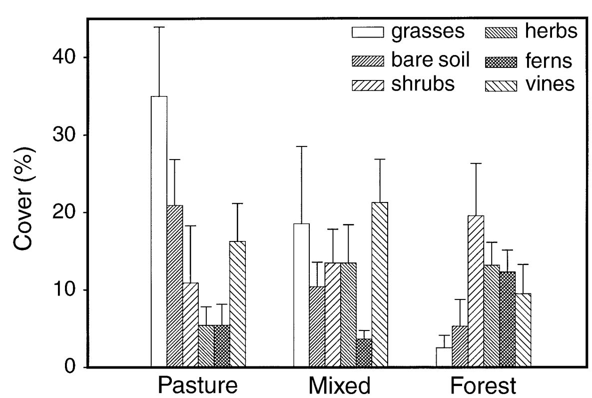

FIG. 3. Percent cover of understory composition (mean + 1 SE) for riparian corridors in the three land cover categories. Data were combined for the three watersheds.

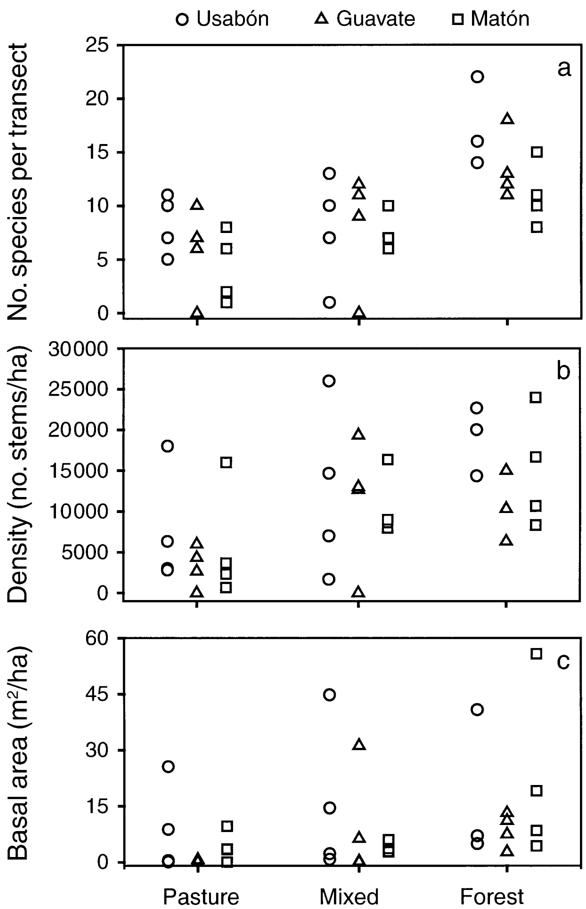

FIG. 4. Species richness, stem density, and basal area of vegetation ≥1 cm dbh in riparian corridors of each land cover category in the three watersheds.

cantly different among land cover categories and watersheds (Kolmogorov-Smirnov, KS > 0.09, $P = 1.00$). In all sites, stem density was highest in the 1–5 cm dbh class.

Riparian species composition was not significantly different among the three watersheds (two-way ANOSIM, KW, $H = 5.02$, $P = 0.37$); *Casearia sylvestris*, *Eugenia biflora*, *Guarea guidonia*, *Trichillia pallida*, and *Piper* spp. were common species found in all land covers among the three watersheds (Appendix). There was a significant difference in species composition among land cover categories (two-way ANOSIM, KW, $H = 9.88$, $P = 0.0003$). Species composition was different between the mixed and forest sites (ANOSIM KW, $H = 7.49$, $P = 0.0018$), and between pasture and forest sites (ANOSIM, KW, $H = 13.49$, $P = 0.0009$). There was no difference in species composition between mixed and pasture sites (ANOSIM, KW, $H = 0.6245$, $P = 0.2578$). In particular, *Zanthoxylum martinicense*, *Myrcia deflexa*, and *Schefflera morototoni* occurred in forest sites, but not in mixed or pasture sites (Appendix). *Miconia prasina* and *Citharexylum fruticosum* were common in pasture and mixed-cover sites, but did not occur in any forest site.

Stream characteristics

There was no difference in stream slope among watersheds ($F = 1.71$, $P = 0.19$), but there was a difference among land covers. Pasture sites occurred on lower slopes than mixed and forest sites ($F_{2,32} = 3.80$, $P = 0.033$). Dissolved oxygen ($F = 0.14$, $P = 0.87$) and percentage of the substrata covered with sediments from eroded soil ($F = 2.39$, $P = 0.11$) did not differ

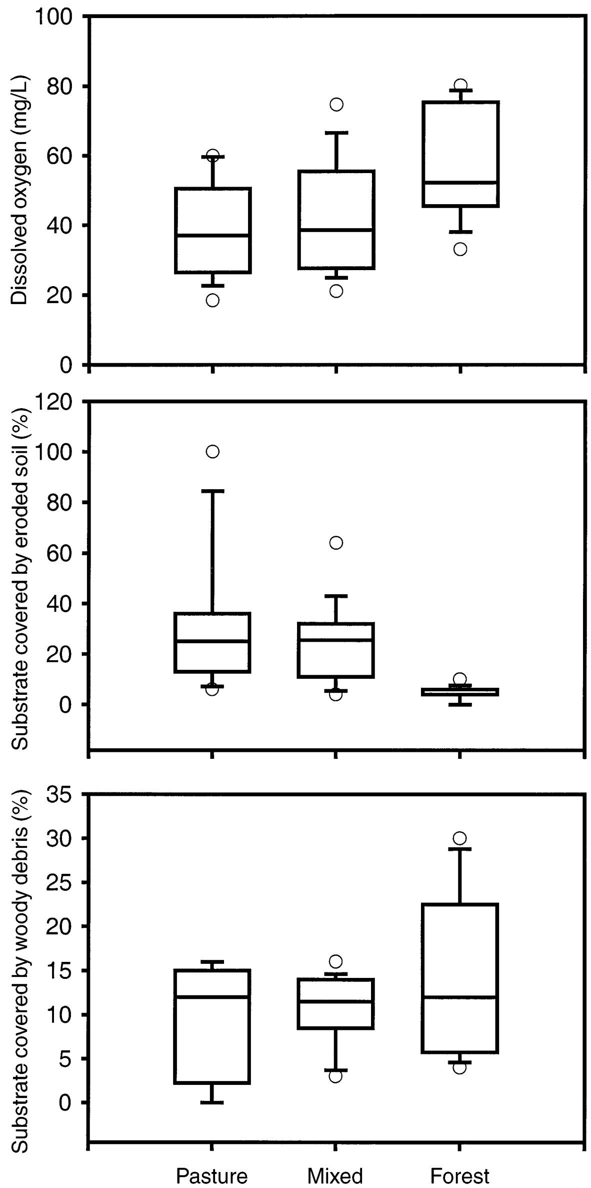

FIG. 5. Percentages of substrate covered by woody debris and bare soil, and concentration of dissolved oxygen (mg/L) in the three land cover categories. Data were combined for the three watersheds. For a description of the box plot, see the Fig. 2 legend.

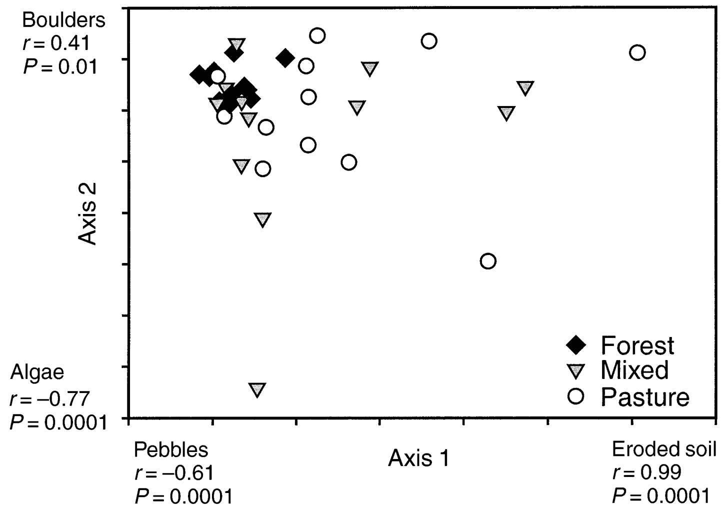

FIG. 6. Plot of ordination analysis (PCA) based on substrate characteristics of streams from pasture-, mixed-, and forest-cover categories. Data were combined for the three watersheds.

among the watersheds, but varied among the land cover categories. Dissolved oxygen had a large range of values within the same land cover sites (Fig. 5), but there was a trend for forest sites to have the highest values ($F = 2.94$, $P = 0.06$). The amount of sediments from eroded soil was highest in pasture sites ($F_{2,32} = 6.42$, $P = 0.005$) and decreased as forest cover increased. The range of values for sediments from eroded soil in mixed cover overlapped with the pasture cover values (Fig. 5), even though these land covers had different slope values. There was less woody debris cover in the Usabón watershed than in the Matón and Guavate ($F_{2,32} = 7.97$, $P = 0.002$). Although coarse woody debris tended to increase with tree cover in the riparian area, the relationship was not significant ($F = 2.15$, $P = 0.130$, Fig. 5).

Stream sites with forest cover were separated from mixed and pasture stream sites based on substrata characteristics in the PCA plot (Fig. 6). In the PCA (Table 4, Fig. 6), Axis 1 explained 49.3% of the variation in stream substrata characteristics, giving high positive weighting to sediments from eroded bank soil ($r = 0.988$, $P = 0.001$) and high negative weighting to pebbles ($r = 0.611$, $P = 0.001$). Axis 2 explained 14.1% of the variation (63.4%, cumulatively), giving high positive weightings to boulders ($r = 0.412$, $P = 0.02$) and high negative weighting to algae ($r = 0.773$, $P < 0.01$).

Temperature measurements taken at 15-min intervals for 21 d in the Matón watershed ranged from 21.7°C to 23.6°C in the forest site and from 22.2°C to 25.0°C in the mixed sites. Pasture sites had the highest values and largest range of temperatures (22.6°–26.5°C). The peak in daily temperature was reached earlier in the day in pasture cover sites, compared with mixed- and forest-cover sites.

The percentage of forest cover in each site accounted for the variability in stream characteristics. There was a positive relationship between dissolved oxygen and the percentage of forest cover at the riparian and subwatershed scale (Table 5). Eroded soil was negatively related to forest cover at both scales. There was no relationship between these variables and wood debris (Table 5). Land cover at both the riparian 50-m buffer and subwatershed scale influenced stream characteristics.

DISCUSSION

Land cover in the watersheds and riparian areas

Forest was the dominant land cover in the watersheds and riparian areas, and within the forest category there were various land uses: protected forest, secondary forests, abandoned shade coffee plantations, and small-scale subsistence farming of tubers and fruits in the forest understory. Land cover patterns were similar among the watersheds, and reflect the economic development patterns of the island. Industry and business have replaced most agricultural activities, and forest has regenerated on abandoned agricultural areas (Thomlinson et al. 1996, Aide et al. 2000), particularly

TABLE 4. Pearson correlation coefficients for stream substrate characteristics ($n = 35$).

Stream characteristic	Axis 1 r_S	Axis 1 P	Axis 2 r_S	Axis 2 P
Eroded soil	0.988	<0.01	0.128	NS
Leaf litter	−0.343	<0.05	0.176	NS
Woody debris	−0.048	NS	0.201	NS
Algae	0.165	NS	−0.773	<0.01
Boulders	−0.432	<0.05	0.412	<0.05
Rocks	−0.431	<0.05	0.257	NS
Pebbles	−0.611	<0.01	0.242	NS
Sand	−0.480	<0.01	0.175	NS
Silt	−0.357	<0.05	−0.117	NS

Notes: For Axis 1, the percentage variance is 49.3%; for Axis 2, the variance is 14.1%. Nonsignificant P values are denoted by NS.

TABLE 5. Linear regressions of stream characteristics with percentage of forest cover in riparian corridors and subwatersheds ($n = 35$).

Stream characteristic	Riparian corridor			Subwatershed		
	r^2	F	P	r^2	F	P
Dissolved oxygen (%)	0.18	6.21	0.02	0.12	4.62	0.04
Eroded soil	−0.17	6.98	0.01	−0.12	4.62	0.03
Woody debris	0.07	2.55	0.12	0.04	1.49	0.23

Note: Eroded soil and woody debris are based on percentage of the substrate covered.

in upland areas, where forest cover and mixed cover were most abundant.

Forest cover in the riparian areas was highly fragmented, and the lack of continuous riparian forest decreases the effective riparian habitat. To maximize conservation of this habitat, priority should be given to establishing connectivity (minimum distance between forest patches), and to increasing the minimum riparian forest width. Because first-order streams contribute water flow and organic matter to the network of tributaries along the river, protection of forest cover in the headwaters would improve many river ecosystem processes (Crowl et al. 2001).

Riparian vegetation

Understory vegetation composed of shrubs and herbaceous cover is common in riparian forests of the wet-forest life zone, and herbaceous cover is a defining characteristic of the riparian zones (Scatena 1990). Understory vegetation is a good predictor of soil erosion potential (Lyon and Sagers 1998, Wear et al. 1998), and we found that areas with minimum forest cover (e.g., pasture sites) had low herbaceous cover ($<$10%) and the highest percentage of eroded soil in the streams.

The original vegetation in these riparian areas was probably similar to the *Dacryodes–Sloanea* vegetation type found at a similar altitude in wet forests in the protected Luquillo mountains (Ewel and Whitmore 1973, Taylor 1994). Most of the species found in the *Dacryodes–Sloanea* vegetation type were represented by a single individual in a single site. Based on their large size, these individuals seem to be remnants, rather than recent colonists. The most abundant species in riparian areas were the same native and nonnative generalist species that dominate secondary forests throughout moist and wet life zones in Puerto Rico (Aide et al. 1995, 2000, Zimmerman et al. 1995). The high density of these generalist species may be due to the effects of frequent disturbance in and around the riparian forest areas, and may explain why pasture and mixed sites shared many species and had a distinct composition in comparison with the forest sites.

Stream characteristics

Land cover was an effective predictor of stream condition. Stream sites associated with pasture cover had the lowest amount of coarse organic matter and high fluctuations of stream water temperatures. Pebble and boulder cover were characteristics that separated streams of different land cover categories, in particular, forest cover from mixed and pasture cover (Fig. 6). This difference could be due to variation in stream slopes, but forest and mixed-cover sites had different stream characteristics. Although the mixed and forest sites occurred on steeper slopes than did pasture sites, other characteristics (algae cover, eroded soil) were more important in separating the sites in the multivariate analysis. Few of the forest and mixed-cover sites had low slope gradients, which could be the result of historical logging and land conversion on the most accessible sites. However, there was a great range in the substrata characteristics of streams with pasture and mixed cover, when compared to forest sites.

In addition, the riparian vegetation associated with a particular land cover influences stream characteristics. Grasses were abundant in the riparian vegetation associated with pasture sites, and they can provide effective ground cover. However, riparian vegetation associated with pastures is often trampled by cattle, and this can increase bare soil areas and bank erosion (T. Heartsill-Scalley, *personal observation*). When riparian vegetation is reduced or eliminated by changes in land use or land cover, streams may change from terrestrial-based productivity (allochthonous) to algal-driven productivity (autochthonous), which will affect the stream biota (Vannote et al. 1980, Roth et al. 1996, Bunn et al. 1998, Fisher et al. 1998). The lack of riparian vegetation in pastures and agricultural areas increases erosion and runoff, which increases nutrient input into the streams and, in areas of high light, leads to excess algal growth (Carpenter et al. 1998, Wear et al. 1998). Lack of canopy and vegetation cover has the additional effect of providing much less buffering protection against large ranges in temperature, such as those observed in pasture-cover sites. Among the three watersheds, there was a large range of dissolved oxygen, and few sites had values $>$5 mg/L. These values are much lower than expected for headwater streams (Allan 1995), and could lead to changes in the aquatic communities and loss of diversity (Allan and Flecker 1993, Roth et al. 1996).

Implications of land cover on riparian and stream environments

Forested riparian areas within a nonforest land cover are important landscape features that can help to maintain species diversity in disturbed habitats by serving as refugia for mature forest species. Furthermore, these forest patches greatly influence the conditions of the riparian understory vegetation and stream substrata characteristics. In contrast to higher order streams, first-order streams receive pulse inputs of organic matter from the riparian vegetation and have narrow temperature ranges, making them vulnerable to the effects of changes in land cover (Tabacchi et al. 1998). A decrease in forest cover will result in a decrease in woody debris input into streams, contributing to the degradation of the stream habitat, which extends to the rest of the river ecosystem (Johnson et al. 1995, Johnson and Covich 1997). This study suggests that not only land cover in the riparian areas, but also land cover at the drainage area or subwatershed scale are important factors affecting stream conditions. The amount of woody species and vegetative cover surrounding stream channels at these scales should be considered when managing streams and freshwater communities.

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Literature Cited

Aide, T. M., J. K. Zimmerman, L. Herrera, M. Rosario, and M. Serrano. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. Forest Ecology and Management **77**:77–86.

Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology **8**:328–338.

Allan, J. D. 1995. Stream ecology, structure and function of running waters. Chapman and Hall, London, UK.

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology **37**:149–161.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. BioScience **43**:32–43.

Boutin, C., and B. Jobin. 1998. Intensity of agricultural practices and effects on adjacent habitats. Ecological Applications **8**:544–557.

Bunn, S. E., P. M. Davies, D. M. Kellaway, and I. P. Prosser. 1998. Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. Freshwater Biology **39**:171–178.

Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorous and nitrogen. Ecological Applications **8**:559–568.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117–143.

Colwell, R. K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. Version 5. [Online, URL: ⟨http://viceroy.eeb.uconn.edu/EstimateS⟩.]

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology **82**:775–783.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**:342–355.

ESRI. 1996. ARC/INFO version 3.5, and ArcView version 3.1. Environmental System Research Institute, Redlands, California, USA.

Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA U.S. Forest Service Research Paper **ITF-18**.

Fisher, S. G., N. B. Grimm, E. Martí, R. M. Holmes, and J. B. Jones, Jr. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. Ecosystems **1**:19–34.

Forman, T. T. 1995. Land mosaics. Cambridge University Press, Cambridge, UK.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries **18**:3–12.

Hunsaker, C. T., and D. A. Levine. 1995. Hierarchical approaches to the study of water quality in rivers. BioScience **45**:193–203.

Johnson, B. L., W. B. Richardson, and T. J. Naimo. 1995. Past, present and future concepts in large river ecology. BioScience **45**:134–141.

Johnson, S. L., and A. P. Covich. 1997. Scales of observation of riparian forests and distributions of suspended detritus in a prairie river. Freshwater Biology **37**:163–175.

Kindler, J. 1998. Linking ecological and development objectives: trade-offs and imperatives. Ecological Applications **8**:591–600.

Lyon, J., and C. L. Sagers. 1998. Structure of herbaceous plant assemblages in a forested riparian landscape. Plant Ecology **138**:1–16.

Machtans, C. S., M. A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology **10**:1366–1379.

Malanson, G. P. 1993. Riparian landscapes. Cambridge University Press, Cambridge, UK.

Marcus, W. A., S. C. Ladd, J. A. Stoughton, and J. W. Stock. 1995. Pebble counts and the role of user-dependent bias in documenting sediment size distributions. Water Resources Research **31**:2625–2631.

McCune, B., and M. J. Mefford. 1997. Multivariate analysis of ecological data. PC ORD Version 3.01. Glenenden Beach, Oregon, USA.

Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics **28**:621–658.

Nilsson, C. 1995. The fragility of ecosystems: a review. Journal of Applied Ecology **32**:677–692.

Philippi, T. M., P. M. Dixon, and B. E. Taylor. 1998. Detecting trends in species composition. Ecological Applications **8**:300–308.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaar, B. D. Richter, R. E. Sparks, and J. C. Stromberg.

1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience **47**:769–784.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology **11**:141–156.

SAS Institute. 1999. SAS. Version 8.0. SAS Institute, Cary, North Carolina, USA.

Scatena, F. N. 1990. Selection of riparian buffer zones in humid tropical steeplands. Research needs and applications to reduce erosion and sedimentation in tropical steeplands. Proceedings of the Fiji Symposium, June 1990. IASH-AISH Publication number 192.

Sweeney, B. W. 1992. Streamside forests and the physical, chemical, and trophic characteristics of piedmont streams in Eastern North America. Water Science and Technology **26**:2653–2673.

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

Tabacchi, E., A. M. Planty-Tabacchi, and O. Décamps. 1990. Continuity and discontinuity of the riparian vegetation along a fluvial corridor. Landscape Ecology **5**:9–20.

Taylor, C. M. 1994. Annotated checklist of the flowering plants of the El Verde Field Station, Puerto Rico. Report to the Terrestrial Ecology Division, University of Puerto Rico, Rio Piedras, Puerto Rico.

Thomlinson, J. R., M. I. Serrano, T. del M. López, and T. M. Aide. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). Biotropica **28**:525–536.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**:171–197.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130–137.

Wear, D. N., M. G. Turner, and R. J. Naiman. 1998. Land cover along an urban–rural gradient: implications for water quality. Ecological Applications **8**:619–630.

Wissmar, R. C., and R. L. Beschta. 1998. Restoration and management of riparian ecosystems: a catchment perspective. Freshwater Biology **40**:571–585.

Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. Forest Ecology and Management **77**:65–76.

APPENDIX

A table listing woody species used in the NMS and ANOSIM, by family, type, and land cover, is available in ESA's Electronic Data Archive: *Ecological Archives* A013-004-A1.