Influence of land use on water quality in a tropical landscape: a multi-scale analysis

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Abstract

There is a pressing need to understand the consequences of human activities, such as land transformations, on watershed ecosystem services. This is a challenging task because different indicators of water quality and yield are expected to vary in their responsiveness to large versus local-scale heterogeneity in land use and land cover (LUC). Here we rely on water quality data collected between 1977 and 2000 from dozens of gauge stations in Puerto Rico together with precipitation data and land cover maps to (1) quantify impacts of spatial heterogeneity in LUC on several water quality indicators; (2) determine the spatial scale at which this heterogeneity influences water quality; and (3) examine how antecedent precipitation modulates these impacts. Our models explained 30–58% of observed variance in water quality metrics. Temporal variation in antecedent precipitation and changes in LUC between measurements periods rather than spatial variation in LUC accounted for the majority of variation in water quality. Urbanization and pasture development generally degraded water quality while agriculture and secondary forest re-growth had mixed impacts. The spatial scale over which LUC influenced water quality differed across indicators. Turbidity and dissolved oxygen (DO) responded to LUC in large-scale watersheds, in-stream nitrogen concentrations to LUC in riparian buffers of large watersheds, and fecal matter content and in-stream phosphorus concentration to LUC at the sub-watershed scale. Stream discharge modulated impacts of LUC on water quality for most of the metrics. Our

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findings highlight the importance of considering multiple spatial scales for understanding the impacts of human activities on watershed ecosystem services.

Keywords

Forest transition; Urbanization; Watershed ecosystem services; Agricultural abandonment; Puerto Rico

Introduction

Watershed ecosystem services are essential for most societies so there is a pressing need to understand the ecological and social processes that can safeguard these services (Brauman et al. 2007). Humans influence watersheds through multiple pathways. They directly affect land use and land cover change (LUCC) (Lambin and Geist 2006) while substantial indirect effects occur via the atmosphere and hydrosphere (IPCC 2007). These changes interact with socio-economic and political factors to determine the vulnerability of places and people to perturbations in their water resources (Turner et al. 2003). In order to minimize vulnerability, one must begin to disentangle these varied human impacts, which are often confounded over temporal and spatial scales.

Of the many land-cover changes tropical landscapes are experiencing, two of the most significant to watershed ecosystem service provisioning and human well-being are the large increases in the extent of secondary forests and urban areas (Brown and Lugo 1990; Grimm et al. 2008). The area of degraded and secondary forests in the tropics was recently estimated at 850 million hectares (ITTO 2002). In spite of their increasing extent, dominance, and prevalence in tropical countries, second growth forests remain undervalued and underused for their capacity to provide environmental services and enhance human well-being. More information is needed on the capacity of regenerating secondary forests to provide many of the services attributed to primary forests including regulation of water flow and quality (ITTO 2002).

In addition to extensive forest re-growth, many tropical regions are undergoing rapid urbanization. The percent of the global population living in cities increased from 10% in the 1990s to more than 50% in 2008, and is expected to reach 60% by 2030 (Grimm et al. 2008). The majority of this increase is occurring in cities in tropical regions of the developing world (UNPD 2006). Urban expansion poses direct and indirect threats to the integrity of streams and watersheds (Paul and Meyer 2001). Increases in the extent of impervious surfaces alter the hydrological cycle while the discharge of pollutants into streams, rivers, and lakes leads to pollution of downstream waters and eutrophication. By placing demands on the provisioning capacities of upstream watersheds, urban dwellers also pose indirect threats to watershed ecosystems.

In addition to its direct impacts, changes in land use/land cover interact with other anthropogenic drivers such as climate variability to affect the provisioning capacities of watersheds (Meyer et al. 1999). Global circulation models currently project an increase of surface temperature in tropical regions of 1–2°C during the next century (IPCC 2007), and

precipitation is expected to decline as much as 50% in some regions and seasons (Neelin et al. 2006). Any attempt to understand the impact of future climate change on watersheds and water delivery systems must take into account the compounded effects of land use/land cover change and climate variability on watershed ecosystem services, and the temporal and spatial scales over which these effects are manifest (Allan 2004; Bruijnzeel 2004).

Recognizing domains of scale for existing natural variation in ecological patterns and processes is often difficult (Wiens 1989; Levin 1992). Yet, choosing the appropriate scales of study and understanding the links among scales is crucial not only to predict the response of watershed ecosystem services to LUCC and climate variability but also to develop adequate indicators of the effects of human activities on stream conditions and consequently, effective management plans (Hunsaker and Levine 1995; Gergel et al. 2002; Allan 2004). For instance, experimental evidence collected to date suggests that increases in vegetation cover lead to more consistent and less extreme water yields, less erosion, and improved water quality relative to other non-vegetated land covers, but in the tropics, most of these results come from small (<1 km^2) catchments (Bruijnzeel 2004). The effects of LUCC on stream yields and condition may be harder to detect at larger scales particularly if rainfall exhibits strong spatial variability within the watershed or if larger areas contain a greater variety of land covers (Gergel et al. 1999). Different environmental and anthropogenic stressors are likely to exert their influence on water quality at different spatial and temporal scales (Gergel et al. 2002; Allan 2004). There is a need to expand research efforts to establish the effects of LUCC at multiple spatial scales on downstream waters and to observe how changes in watersheds have affected stream conditions through long-term analysis (Bruijnzeel 2004).

Our goal in this paper is to investigate how historical shifts in land use and land cover (LUC) in Puerto Rico between 1977 and 2000 in combination with temporal variability in antecedent short-term precipitation have influenced water quality in the island. We also examine the spatial scales at which these changes impact water quality. To do so, we employ USGS water quality data from dozens of gauge stations throughout the island together with three land cover maps (1977, 1991, 2000) and detailed precipitation data from an island-wide network of weather stations. We address the following questions:

1. How does spatial and temporal variation in LUC within and across watersheds influence stream water quality metrics in Puerto Rico?

2. At what spatial scale does landscape heterogeneity act to influence water quality?

3. How does variation in antecedent precipitation modulate the effects of LUC on stream water quality?

Methods

Study area

Puerto Rico is a Caribbean island (17°45′–18°30′N; 66°15′–67°15′W) stretching 160 km E–W and 55 km N–S. Its mountainous terrain creates barriers to northeasterly trade winds, resulting in a distinct precipitation gradient with areas in the southwest receiving less than

half the annual rainfall (~750 mm) as areas in the northeast (~1,500–2,000 mm). Mean annual temperatures range between 19.4 and 29.7°C with cooler temperatures occurring at higher elevations (Daly et al. 2003).

Puerto Rico is densely populated and to date, has lacked effective governmental land use planning and natural resources management (Dietz 1986; Hunter and Arbona 1995). Socioeconomic changes in the island during the past 50 years have resulted in dramatic landscape and demographic transformations. The introduction of a government-sponsored industrialization program in the late 1940s shifted attention away from agricultural activities to manufacturing, leading to abandonment of agriculture and increases in the extent of secondary forests and urban areas (Fig. 1, Appendix I in ESM) (Rudel et al. 2000; Grau et al. 2003). An influx of federal funds in the form of subsidies, health spending, and social security further encouraged rural–urban migration (Weisskoff 1985). Forest cover rose from less than 10% of the island area in the 1930s to approximately 57% in 2003 (Brandeis et al. 2007). Recent studies coupling remote sensing images with population census data have shown that over 40% of the island is in some degree of urban sprawl (Martinuzzi et al. 2007). Urban sprawl can degrade water quality, while the observed increase in forest cover has the potential to regulate water flow and improve water quality (Allan 2004; Bruijnzeel 2004).

Land use/cover maps

Three land use/cover maps from 1977 to 1978, 1991 to 1992, and 2000 were used to quantify LUC during our study period. The earliest map was created using aerial photographs from 1977 and 1978 at 1:20,000 resolutions (Ramos and Lugo 1994) and digitized to polygons at a 1:24,000 scale. The other two LUC maps were based on Landsat TM and ETM + mosaics of images taken in 1991–1992 and 2000 with 30 × 30 m resolution (Helmer et al. 2002; Kennaway and Helmer 2007).

All map manipulations and spatial analyses were performed using ESRI ArcGIS 9.2. All maps were rasterized to 30 × 30 m resolution (a 30 m cell size was assigned to the 1977–1978 map by majority rule) to a common geographic projection system. For all maps, LUC classifications were simplified from their original classification to six categories: urban (including sub-urban), agriculture, pasture, forest, wetland, and water. We further classified forests into young (~7–35 years old) and closed canopy, older forests (≥35 years old) (Fig. 1) (Brown and Lugo 1990). Because of the merging of LUC classes and the source of the 1977–1978 maps, it is difficult to evaluate the overall accuracy of the three maps. Accuracy of the 1991 and 2000 maps is ca. 80%, slightly higher than reported elsewhere (Kennaway and Helmer 2007) due to aggregation from 27 to eight land cover classes. Details on the classification methods are provided in Appendix I in ESM.

Stream flow and water quality data

Water quality and stream flow data for Puerto Rico were obtained from the U.S. Geological Services (USGS) National Water Information System (http://nwis.waterdata.usgs.gov/pr/nwis/qwdata). We obtained daily stream discharge and water quality data for 105 stations that were actively collecting between 1977 and 2000, and had a total of 50 or more data

points within this period. We only used data collected in streams, and avoided stations that were located directly downstream from dams. These criteria brought the total number of stations included in the analyses to a range of 55–57 depending on the water quality metric (Table 1; Fig. 2).

We examined several water quality metrics. Turbidity is a measure of light penetration, which is usually positively correlated with sediment erosion and in-stream production (Eaton and Franson 2005). The concentration of dissolved oxygen (DO) in the water column is a measure of aeration and photosynthetic activity. We also used data for in stream concentration of total phosphorus and nitrogen. Concentrations of these nutrients reflect inputs from draining watersheds (e.g., fertilizers, sewage) and in-stream biogeochemical activity (Downing et al. 1999). Fecal coliform (FC) and fecal streptococci (FS) concentrations have been used throughout the world as indicators for water contamination by feces (Meays et al. 2004). Since they can influence biogeochemical transformation, erosion, or fecal content, stream discharge, water pH, temperature, and streambed geology data collected at the study sites were used as covariates in the analyses.

Watershed delineation

To calculate LUC proportions for each water station, we delineated point-based watersheds. Only watershed areas upstream of stations were considered. Given the steep topography of the island, we delineated watersheds using the AGREE surface reconditioning system, a procedure that generates minimal watershed distortions (Hellweger 1997). The AGREE method uses known vector water networks to alter the surface elevation values of a Digital Elevation Map (DEM), within a given buffer distance from the vectors. After pre-processing the data, the AGREE algorithm was run on a 30 × 30 m DEM obtained from USGS (http://seamless.usgs.gov/).

Using the adjusted DEM, we employed standard hydrology and watershed tools in ArcGIS to delineate all watersheds and sub-watersheds based on the location of the USGS stations. Watersheds were delineated according to U.S. federal standards at a 10 digit (5th basin level, 10,000–40,000 acres) hydrologic unit and the sub-watershed at a 12 digit (6th level, 40,000–250,000 acres) unit (FGDC 1998). A unique watershed was drawn for each of the water stations. To assess the accuracy of the boundaries of these station-based watersheds, we visually matched them to area-based watershed and sub-watershed boundaries from USGS and USDA (USGS 2002). Boundaries were largely consistent across all watersheds. Watersheds with noticeable distortions were usually distorted because of slight pixel misalignment along vector networks and could be redrawn more accurately by realigning pixels. Sub-watersheds were delineated by matching and intersecting existing USGS 12-digit sub-watershed boundaries with our stations-based delineations. All sub-watersheds were either a subset of the stations-based delineations or were approximately the same in boundary extent and area. We retained our stations-based delineations in areas where both USGS sub-watershed and stations-based delineations boundaries overlapped. In areas where USGS sub-watershed boundaries sub-divided a larger stations-based boundary, we used the USGS sub-watershed delineations. In a few instances where boundaries did not entirely

match, delineations were manually drawn using a flow accumulation layer from the adjusted DEM as guidance. We included only the areas that directly drained into our point of interest.

Since we were interested in investigating the impact of LUC on water quality at multiple spatial scales, we first calculated the proportion of each of the LUC categories at two spatial scales: watersheds and sub-watersheds draining into each of the water collection points. LUC at the watershed scale, however, may be less critical to water flow or quality than the characteristics of the riparian buffers (Hunsaker and Levine 1995; Heartsill-Scalley and Aide 2003, but see Silva and Williams 2001). For instance, riparian buffers often act as nutrient sinks (Weller et al. 1998). To assess the effects of LUC in riparian zones on water quality, we selected a 60 m buffer along all stream and river networks (USGS vector coverage) and calculated proportions for each LUC class in this buffer. The four spatial scales over which these proportions were calculated are depicted in Fig. 3. These proportions were assigned to each water station data as follows: 1977 LUC values were assigned to 1977–1984 water quality data, 1991–1992 LUC values to 1985–1995 data, and 2000 LUC values to the 1996–2001 data (Fig. 4).

Precipitation

Daily precipitation data for the study period were obtained from the Puerto Rico and U.S. Virgin Islands Climate Office at the University of Puerto Rico, Mayagüez (http://atmos.uprm.edu/stations.html). We matched each USGS water station with precipitation data from the closest climate station. To control for antecedent conditions (e.g., soil saturation), precipitation data was summed for a 2-day period prior to each water quality, or stream flow measurement date. Preliminary analyses using a 7-day index of precipitation prior to measurement had worse fits to the data so we settled on the 2-day index.

Statistical analyses

Data for all water quality measures were initially screened for clear outliers. For some sites on some days, water quality measures fell below the level at which commonly used field devices are capable of precise measurements and were recorded only as a measure that was less than a specified threshold (e.g., >0.01) (http://water.epa.gov/drink/contaminants/index.cfm#1). Rather than ignoring these data or simply using the threshold value, we chose to use half the threshold (e.g., 0.005).

For all water quality measures, we analyzed the data using generalized linear mixed models and began by comparing four "full" models. These models included as covariates the percentage of pasture, mature forest, young forest, agriculture, and urban cover types, with mature forest acting as the intercept or baseline. The four models differed in the area over which these percentages were calculated, either the whole watershed, the sub-watershed, or the 60 m buffers within the two whole watershed scales (Fig. 3). All models included the log of stream discharge as a predictor. We settled on the log of discharge after initial analyses suggested that it was generally a better predictor of water quality than the inverse of discharge, discharge itself, or antecedent precipitation. Based on previous findings, models for water quality also included pH, temperature, and streambed geology as covariates (McDowell and Asbury 1994). We also considered a model of discharge as a function of

precipitation and drainage area. The latter did not influence stream discharge but we established a link with precipitation in the 2 days prior to the date water quality was assessed (Table 2). We also ran "control" models for discharge and water quality metrics that excluded all LUC covariates. The effects of LUC on water quality may be mediated by water availability which influences the residence time of water in the soil matrix and the "flashiness" of inputs (Neill et al. 1999). For this reason, we also examined interactions between the extent of different LUC types and the log of discharge.

For lognormal-distributed data we used the lmer function in the lme4 package of the statistical software R (R Development Core Team 2008). Gamma-distributed data were analyzed using WinBugs Bayesian statistical software (Table 1). Models were compared using BIC for gamma-distributed data or DIC lognormal-distributed data (Spiegelhalter et al. 2002). After using model comparison to determine which full model was best for each water quality metric, we used backwards step-wise removal of predictors to assess which individual predictors were important drivers for each metric.

We calculated model goodness of fit as the proportion of explained variance (R^2) at the sample (data) and site levels using methods modified from Gelman and Pardoe (2006). At, at the sample, or data level, R^2 was calculated as:

$$R^2_{\text{sample}} = 1 - \frac{E\left(V_{j=1}^{j=N_{\text{sample}}}\left(\log(y_j) - \beta X_j - \omega_{\text{site}(j)}\right)\right)}{E\left(V_{j=1}^{j=N_{\text{sample}}}\left(\log(y_j)\right)\right)} \quad (1)$$

where N_{sample} is the number of samples, E is the expected value, V is the variance, y_j is the water quality measure for the jth sample, βX_j is the sum of the products of the estimated coefficient and the predictors, and $\omega_{\text{site}(j)}$ is the random effect associated with the site of the sample. The expected value of the variance was calculated by averaging the value of the variance obtained from 1,000 independent draws from the joint posterior distribution of the fixed and random effects. At the site, or random effect level, R^2 was calculated as:

$$R^2_{\text{site}} = 1 - \frac{E(V_{k=1}^{k=N_{\text{site}}}(\omega_k))}{E(V_{k=1}^{k=N_{\text{site}}}(\beta \overline{X_k} + \omega_k))} \quad (2)$$

where N_{site} is the number of sites, ω_k is the random effect for the kth site, and $\beta \overline{X_k}$ is the product of the estimated coefficients and the mean value of the predictors within the kth site.

Greater R^2 values at the data (sample) level indicate that the patterns are driven by temporal variation in covariates (i.e., changes in antecedent precipitation or land cover within a site over time) while a greater R^2 at the site level suggests that spatial variability in covariates among sites accounts for variation in response variables. This is an important consideration because often, comparisons across LUC categories implicitly substitute space (i.e., comparisons of stream condition indicators across watersheds of contrasting land uses) for time.

Results

Land use/cover underwent considerable changes in the majority of watersheds during the study period. Total forest cover increased dramatically from 1977 to 1991 but only slightly from 1991 to 2000 (Fig. 1, Appendix I in ESM). To some degree, the extent of agriculture largely mirrored these trends. Analysis of deforestation patterns between 1977 and 2000 indicates that forest was most likely to be replaced by pasture, followed by urban land cover (Appendix Table A3 in ESM). The extent of urban cover increased steadily throughout the island during our study period (Fig. 1).

Our models explained from 30 to 58% of the observed variance in water quality metrics (Table 2). In general, R^2 was higher at the data level suggesting that temporal variation in antecedent precipitation and LUC rather than spatial variation between sites drives the observed results for the majority of water quality metrics (Table 2). For instance, discharge and LUC explained 58% of the variance in in-stream phosphorus concentration at the sample level but only 15% of the variance at the site level. The only exception were FC/FS ratios for which spatial variation in LUC among sites accounted for almost twice as much of the observed variation as temporal variation in covariates within sites (Table 2).

Effects and spatial scaling of land cover/land use on stream water quality

LUC composition can influence stream water quality via multiple processes operating at different spatial scales. For this reason, we ran four models that made different assumptions about the spatial area of influence of landscape composition on several water quality metrics (Fig. 3).

The spatial scale over which LUC influenced water quality differed across metrics included in the analyses (Table 1). Turbidity and DO, responded to the composition of LUC in the large scale drainage watersheds. In contrast, models that only considered LUC of the riparian areas buffering the streams in larger catchments were better predictors of in-stream concentration of nitrogen. Lastly, FC/FS ratios and in-stream phosphorus concentrations were best explained by LUC composition at the smaller sub-watershed scale (Fig. 3). Despite strong effects of LUC on all water quality metrics, stream discharge was only affected by precipitation in the 2 days preceding a sampling event (Table 1).

After determining the spatial scale over which LUC influenced water quality, we used stepwise backwards regression for variable selection at the spatial scale which best fitted the data (Table 1).

Turbidity and DO—Using mature forests as the baseline (intercept), the extent of urban and pasture cover in larger watersheds increased turbidity, a measure of soil runoff, fine particulate organic matter inputs, and in-stream production and morphology (Table 2). Not surprisingly, turbidity also increased with stream discharge. The concentration of DO in the water column, a measure of water aeration and photosynthetic activity, was lower in watersheds draining urban areas relative to those draining older forests. DO concentrations were greater in watersheds dominated by agriculture or young forest re-growth than in those draining older forests. The negative effects of urban cover on DO, as evidence by the

standardized regression coefficients, decreased DO concentrations threefold relative to the positive effects of pasture or young forest. As expected, DO concentrations increased with stream discharge (Table 2).

Biogeochemical metrics—LUC in the riparian buffer zones in Puerto Rico had strong effects on nitrogen concentrations in stream water. Total nitrogen concentrations were higher in catchments draining riparian zones dominated by pastureland and urban development (Table 2). Lower stream pH and temperature, and greater discharge were associated with higher concentrations of total nitrogen. Forest age also influenced total N concentrations in the stream, with lower N concentrations from watersheds draining young than mature forests. In contrast, phosphorus concentrations increased for all LUC categories when evaluated relative to an older forest baseline (Table 2). The highest P levels were observed in streams draining watersheds dominated by pasture followed by those dominated by agriculture, urban cover, and young forests. Greater stream discharge led to higher in-stream P concentrations.

Biological metrics—FC and FS are indicators of fecal waste. Greater FC/FS ratios typically indicate a greater contribution of human relative to animal waste (Meays et al. 2004). FC/FS ratios exhibited a fine gradient of responses to LUC with highest values in streams draining sub-watersheds dominated by urban development, followed by pastureland, agriculture, and young forest (Table 2). FC/FS ratios, however, were unaffected by stream discharge.

Interactive effects of discharge and LUC on stream water quality

The influence of LUC on water quality metrics may be mediated by water availability. For this reason, we also examined interactions between the extent of different LUC types at the relevant spatial scale and the log of discharge. The reduction in DO with increasing urban development in the watershed was more marked at higher stream discharge rates (Table 2). In contrast, the positive effect of the extent of pasture and young forest cover in the watershed on DO concentrations intensified at lower discharge levels. We also found significant negative interactions between stream discharge and land cover composition on total P and N concentrations and stream turbidity. Specifically, the extent of pastureland in stream buffers of the watershed draining area increased turbidity as well as nitrogen and phosphorus concentrations but this effect was more marked during periods of lower stream discharge (Table 2). We also observed greater effects of urban cover on in-stream nitrogen at lower stream discharge. Finally, the effects of forest age on in-stream N and P were stronger at lower discharge levels.

Discussion

Our goal in this paper was to investigate how historical changes in land cover and land use in Puerto Rico from 1977 to 2000 together with temporal variability in precipitation influenced stream water quality. Our approach allowed us to quantify the importance of spatial variation in LUC on stream conditions relative to changes in LUC over time, an important consideration given that, often, comparisons of water quality across LUC

categories implicitly substitute space (i.e., comparisons across watersheds of contrasting land uses or covers) for time (i.e., tracking changes in stream conditions as land cover or use in the watershed changes through time) (Allan 2004). Our models accounted for 30–58% of the observed variance in water quality metrics. This percentage was higher at the data relative to the site level. This is an expected result given the lack of site level predictors (predictors that were constant throughout the study within sites) compared to the large observed temporal changes in landscape composition and discharge during the study period. The exception to this pattern—that is, greater variation at the site than at the data level observed for FC/FS ratios—may be driven by the absence of a discharge effect on this variable and large spatial heterogeneity in urban development, rural dwellings, and black water leakages from septic tanks and farm animals in small watersheds (e.g., Roth et al. 1996).

LUC in watersheds influenced all water quality indicators but these effects were idiosyncratic for each metric. Urbanization and pasture expansion in watershed catchments led to greater turbidity, and higher nutrient concentrations and FC/FS ratios relative to forested watersheds. An increase in turbidity and FC/FS ratios in stream draining pasturelands is not surprising given the potential for soil erosion and high animal fecal inputs in these watersheds. Similarly, the extent of impervious surfaces in urban area and the potential for pollutant inputs are likely to increase stream turbidity and FC/FS ratios (Paul and Meyer 2001). Our results also corroborate previous studies that found urbanized watersheds had higher N yields while forested watersheds had considerable lower yields (Paul and Meyer 2001; Ortiz-Zayas et al. 2006). Surprisingly, the extent of agricultural land use affected DO, phosphorus concentrations, FC/FS ratios but not nitrogen or turbidity. The absence of an impact of agriculture on other water quality metrics in our study may be the result of non-linearities. Streams in agricultural catchments usually remain in good condition until the extent of agriculture is relatively high, typically a threshold of 30–50% of the upstream catchment area (Allan 2004). In our study watersheds, agriculture accounted for only a small proportion of land area (median <3% at all spatial scales). The relatively minor extent of agriculture and its highly spatially clustered distribution may have also minimized the likelihood of finding an island-wide effect of agricultural land use on some water quality. Nevertheless, the extent of agricultural land use increased turbidity, in-stream P, and FC/FS ratios. Turbidity and P may simply indicate greater levels of soil erosion in these watersheds relative to a mature forest baseline. Large spatial heterogeneity in urban development, rural dwellings, and black water leakages from septic tanks and farm animals in agricultural watersheds may have contributed to greater FC/FS levels from watersheds with a high proportion of agricultural land cover (Roth et al. 1996). This spatial heterogeneity may also explain the greater FC/FS ratios observed in streams draining younger forests relative to those draining more spatially homogeneous watersheds dominated by mature forests. Finally, we detected an effect of forest age on in-stream nutrient concentrations. Watersheds draining younger, successional forests had greater outputs of stream phosphorus and lower nitrogen levels than those draining older forests. Documenting changes in soil properties and biogeochemistry through succession has received a fair amount of attention in tropical regions (e.g., Reiners et al. 1994; Zarin and Johnson 1995; Schlessinger et al. 1998; Bautista-Cruz and del Castillo 2005). Walker and

Syers (1976) first proposed that P limitation should increase through succession and long-term soil development as demands from growing vegetation increase and P becomes bound to secondary minerals and SOM (Aerts and Chapin 2000). The generality of this pattern, however, may depend on geological substrate, past land use, and mean precipitation levels (Bautista-Cruz and del Castillo 2005). Lower levels of nitrogen in watersheds draining younger forest relative to those from mature forests are expected given greater nitrogen demands from growing vegetation in younger stands (Reiners et al. 1994).

DO also responded strongly to gradations in land cover. DO was lower in urbanized watersheds, an expected result given that eutrophication is a common outcome of urbanization (Paul and Meyer 2001; Ortiz-Zayas et al. 2006). In contrast, DO concentrations in watersheds dominated by pastureland were similar to those dominated by mature forests. In a study of 35 riparian sites representing a range of pastureland and forest cover, Heartsill-Scalley and Aide (2003) uncovered a positive relationship between tree cover and stream DO in first order streams. The majority of streams in our study were 4th order or above, possibly hampering our ability to detect fine scale effects on stream DO. Differences in the range of tree cover in the watersheds between the two studies may also have contributed to these apparently contrasting findings. In our study, streams draining watersheds dominated by younger successional forests had greater DO than those draining areas dominated by older forests. A more fully developed canopy in older forests could have resulted in greater light interception, lower streambed irradiance, and lower stream photosynthetic activity (Hill et al. 2001). We also found that streams draining catchments dominated by agriculture had greater DO levels than those from watersheds dominated by older forests, an unexpected result. Agricultural land use in the island may not be representative of agriculture in other regions. At the start of the study period, agricultural land use was dominated by coffee, a crop which decreased dramatically between 1977 and 1991. Structurally, coffee agroforests and plantations may resemble younger successional forests (Perfecto and Vandermeer 2008).

Numerous studies have established statistical associations between LUC and stream condition (reviewed in Allan 2004). Developing tropical regions are experiencing rapid urbanization, a phenomenon which is likely to degrade water quality (Paul and Meyer 2001). Puerto Rico exemplifies how increased population and changes in land cover associated with industrial development can affect water quality (Santos-Román et al. 2003). The present drivers of forest recovery and urbanization in Puerto Rico reflect general processes at work in other tropical regions undergoing development (Rudel et al. 2005). Unlike other tropical regions, however, Puerto Rico imports most of its food (Weisskoff 1985). Countries with high intensity agriculture are unlikely to undergo the extensive reforestation observed in Puerto Rico; rather food demands from expanding urban centers may lead to higher deforestation rates (DeFries et al. 2010), and greater fertilizer use. Regulation and enforcement of water quality standards in Puerto Rico is also likely to differ from other tropical regions. In the 1980s, legal pressure from the US EPA forced the local water authority to build and upgrade sewage treatment plants across the island and to remove many septic systems and raw discharges (Hunter and Arbona 1995). These actions probably reduced N and P and fecal matter concentrations in some areas even though land use did not change. The negative effects of development in urban areas may not be ameliorated by

landscape level reforestation or enforcement of water quality standards, at least in the initial stages of urbanization (Downing et al. 1999).

Land use/cover in catchments had no impact of discharge in the study streams in contrast to a recent study in NE Puerto Rico (Wu et al. 2007). Apparently contradictory results are not surprising given that LUC impacts on stream discharge depend on geological substrate in the catchment area, levels of groundwater reserves, the degree of soil erosion and compaction, the age/biomass of growing vegetation, non-linear responses and threshold effects, spatial variability in precipitation, density of human populations, water withdrawals in the catchment area, and perhaps most critical to our study, the temporal and spatial scale of sampling (reviewed in Bruijnzeel 2004). Like in many other regions, the frequency and scheme of stream sampling in Puerto Rico hinges on a number of logistical considerations. For instance, many stations have flow limits and are unlikely to be representative of the extreme precipitation events that typically accompany severe tropical storms. As such, our inability to detect an effect of land use on discharge may not be indicative of the full range of interactive effects of land use and climate variability on stream flow.

River and streams are hierarchical systems (Allan 2004). Different metrics of stream condition are expected to vary in their responsiveness to large versus local-scale factors (Allan et al. 1997). The spatial extent over which LUC patterns influence water quality remains an unresolved question (reviewed in Gergel et al. 2002; Allan 2004). This is in part because the spatial scale at which an effect is detected depends on how closely riparian land cover parallels that of the whole watershed, data resolution, the specific spatial configuration of land covers, and the interplay of anthropogenic and natural gradients (Hunsaker and Levine 1995; Gergel et al. 1999; Allan 2004). For instance, variation in land cover is often greater at the riparian than at the watershed scale which likely contributes to the greater influence attributed to the riparian land use relative to regional effects in many studies (e.g., Stauffer et al. 2000). This was certainly the case in our study: the coefficient of variation in urban cover at the small watershed scale is 0.94, at the large watershed 1.01, and at the buffer (watershed scale) 1.37. These trends were also observed for forest, pasture, and agricultural cover. As a result of these differences, effects of this local heterogeneity may be averaged at greater spatial scales (Wiens 1989). Studies like ours that have examined the response of several water condition metrics to variation in LUC at multiple scales, including both riparian zones and whole watersheds, have encountered mixed effects. For instance, Gergel et al. (1999) found similar support for models that explained dissolved organic carbon in lakes as a function of the proportion of wetlands in the total watershed and models using only proportion in riparian buffers. A synthetic understanding of the impact of LUC on water metrics at different spatial scales will require a mechanistic understanding of the biophysical and hydrological factors that influence water quality.

Understanding water quality responses to the interplay between anthropogenic and natural factors remains an important challenge. The effects of heterogeneity of LUC on water quality can vary daily, seasonally, and annually (Gergel et al. 1999). In our study, greater rates of stream discharge lead to higher turbidity, DO, and nutrient concentrations. Temporal variation in discharge interacted with spatial heterogeneity in land cover to influence water quality. Increases in stream nutrient concentration and turbidity associated with pastureland

dominance were ameliorated at lower levels of discharge. This effect may be driven by lower soil–water contact at high levels of precipitation (Neill et al. 1999). In a parallel fashion, the increases in DO, total N, and phosphorus observed in watersheds dominated by young forests and agriculture were lessened at higher discharge. We previously hypothesized that the difference in stream DO between these land covers and older forest was driven by variation in light incidence in the stream and litter inputs. The interaction between discharge and land cover found for agriculture and young forest is consistent with this interpretation if we assume that wetter periods with more discharge also have higher cloudiness and lower solar irradiance levels (Zimmerman et al. 2007). Finally, higher discharge exacerbated the negative effect of urban cover on DO but ameliorated impacts of in-stream N. Urban streams tend to be "flashier" and carry sewage and other pollutants which in turn can lead to eutrophication and low DO levels (Paul and Meyer 2001; Ramírez et al. 2009). Effects of nutrients, however, may hinge on the degree of dilution that accompanies changes in discharge.

Our findings highlight the importance of considering multiple spatial and temporal scales for understanding the impacts of human activities on watershed ecosystem services. Scale-sensitive analyses are needed to determine the effects of ongoing natural and anthropogenic disturbances on water quality and flow. A first step is to collect high quality data that captures the range of variability in anthropogenic and natural drivers, a task that may require innovative and flexible sampling schemes. Such an approach would allow for a deeper understanding of the spatial and temporal scales over which human activities influence water quality and how these scales vary along physical, environmental, and governance gradients.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

References

Aerts R, Chapin FS. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res. 2000; 30:1–67.

Allan J. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu Rev Ecol Evol Syst. 2004; 35:257–284.

Allan JD, Erickson DL, Fray J. The influence of catchment land use on stream integrity across multiple spatial scales. Freshw Biol. 1997; 37:149–161.

Bautista-Cruz A, del Castillo RF. Soil changes during secondary succession in a tropical montane cloud forest area. Soil Sci Soc Am J. 2005; 69:906–914.

Brandeis, TJ.; Helmer, EH.; Oswalt, SN. Resour Bull SRS-119. US Department of Agriculture Forest Service, Southern Research Station; Asheville: 2007. The status of Puerto Rico's forests, 2003; p. 72

Brauman KA, Daily GC, Duarte TK, Mooney HA. The nature and value of ecosystem services: an overview highlighting hydrologic services. Annu Rev Environ Re-sour. 2007; 32:67–98.

Brown S, Lugo AE. Tropical secondary forests. J Trop Ecol. 1990; 6:1–31.

Bruijnzeel LA. Hydrological functions of tropical forests: not seeing the soil for the trees? Agric Ecosyst Environ. 2004; 104:185–228.

Daly C, Helmer EH, Quinones M. Mapping the climate of Puerto Rico, Vieques and Culebra. Int J Climatol. 2003; 23:1359–1381.

DeFries R, Rudel TK, Uriarte M, Hansen J. Pressures on tropical forests in the 21st century. Nat Geosci. 2010; 3:178–181.

Dietz, JL. Economic history of Puerto Rico: institutional change and capitalist development. Princeton University Press; Princeton: 1986.

Downing JA, McClain M, Twilley R, Melack JM, Elser J, Rabalais NN, Lewis WM, Turner RE, Corredor J, Soto D, Yanez-Arancibia A, Kopaska JA, Howarth RW. The impact of accelerating land-use change on the N-cycle of tropical aquatic ecosystems: current conditions and projected changes. Biogeochemistry. 1999; 46:109–148.

Eaton, AD.; Franson, MAH. Standard methods for the examination of water & wastewater. 21. American Public Health Association; Washington, D.C: 2005.

Federal Geographic Data Committee (FGDC). FGDC content standard for digital geospatial metadata. Version FGDC-STD-001-1998. 1998.

Gelman A, Pardoe L. Bayesian measures of explained variance and pooling in multilevel models. Technometrics. 2006; 48:241–251.

Gergel SE, Turner MG, Kratz TK. Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers. Ecol Appl. 1999; 9:1377–1390.

Gergel SE, Turner MG, Miller JR, Melack JM, Stanley EH. Landscape indicators of human impacts to riverine systems. Aquat Sci. 2002; 64:118–128.

Grau HR, Aide TM, Zimmerman JK, Thomlinson JR, Helmer EH, Zou X. The ecological consequences of socioeconomic and land use changes in post-agriculture Puerto Rico. Bioscience. 2003; 53:1159–1168.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. Global change and the ecology of cities. Science. 2008; 319:756–760. [PubMed: 18258902]

Heartsill-Scalley T, Aide TM. Riparian vegetation and stream condition in a tropical agriculture-secondary forest mosaic. Ecol Appl. 2003; 13:225–234.

Hellweger, F. [Accessed Aug 2009] AGREE—DEM surface reconditioning system. 1997. http://www.ce.utexas.edu/prof/maidment/gishydro/ferdi/research/agree/agree.html

Helmer EH, Ramos O, del MLópez T, Quinones M, Diaz W. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. Caribb J Sci. 2002; 38:165–183.

Hill WR, Mulholland PJ, Marzolf ER. Stream ecosystem responses to forest leaf emergence in spring. Ecology. 2001; 82:2306–2319.

Hunsaker CT, Levine DA. Hierarchical approaches to the study of water quality in rivers. Bioscience. 1995; 45:193–203.

Hunter JM, Arbona SI. Paradise lost: an introduction to the geography of water pollution in Puerto Rico. Soc Sci Med. 1995; 40:1331–1355. [PubMed: 7638643]

IPCC. Core Writing Team. Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change. In: Pachauri, RK.; Reisinger, A., editors. Climate change 2007: synthesis report. IPCC; Geneva: 2007.

ITTO. International Tropical Timber Organization, ITTO Policy Development Series No 13. 2002. Guidelines for the restoration, management, and rehabilitation of degraded and secondary tropical forests.

Kennaway T, Helmer EH. The forest types and ages cleared for land development in Puerto Rico. GISci Remote Sens. 2007; 44:356–382.

Lambin, EF.; Geist, H. Land-use and land-cover change: local processes and global impacts. Springer-Verlag; Berlin: 2006.

Levin SA. The problem of pattern and scale in ecology. Ecology. 1992; 73:1943–1967.

Martinuzzi S, Gould WA, Gonzalez OMR. Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. Landsc Urban Plan. 2007; 79:288–297.

McDowell WH, Asbury CE. Export of carbon, nitrogen, and major ions from three tropical montane watersheds. Limnol Oceanogr. 1994; 39:111–125.

Meays CL, Broersma K, Nordin R, Mazumder A. Source tracking fecal bacteria in water: a critical review of current methods. J Environ Manag. 2004; 73:71–79.

Meyer JL, Sale MJ, Mulholland PJ, Poff NL. Impacts of climate change on aquatic ecosystem functioning and health. J Am Water Resour Assoc. 1999; 35:1373–1386.

Neelin JD, Münnich M, Su H, Meyerson JE, Holloway CE. Tropical drying trends in global warming models and observations. Proc Natl Acad Sci USA. 2006; 103:6110–6115. [PubMed: 16606851]

Neill C, Piccolo MC, Melillo JM, Steudler PA, Cerri CC. Nitrogen dynamics in Amazon forest and pasture soils measured by N-15 pool dilution. Soil Biol Biochem. 1999; 31:567–572.

Ortiz-Zayas JR, Cuevas E, Mayol-Bracero OL, Donoso L, Trebs I, Figueroa-Nieves D, McDowell WH. Urban influences on the nitrogen cycle in Puerto Rico. Biogeochemistry. 2006; 79:109–133.

Paul M, Meyer J. Streams in the urban landscape. Annu Rev Ecol Syst. 2001; 32:333–365.

Perfecto I, Vandermeer J. Spatial pattern and ecological process in the coffee agroforestry system. Ecology. 2008; 89:915–920. [PubMed: 18481515]

R Development Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing; Vienna: 2008.

Ramírez A, De Jesus-Crespo R, Martino-Cardona DM, Martinez-Rivera N, Burgos-Caraballo S. Urban streams in Puerto Rico: what can we learn from the tropics? J North Am Benthol Soc. 2009; 28:1070–1079.

Ramos OM, Lugo AE. Mapa de la vegetación de Puerto Rico. Acta Cientifica. 1994; 8:63–66.

Reiners WA, Bouwman AF, Parsons WF, Keller M. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecol Appl. 1994; 4:363–377.

Roth NE, Allan JD, Erickson DL. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecol. 1996; 11:141–156.

Rudel TK, Perez-Lugo M, Zichal H. When fields revert to forest: development and spontaneous reforestation in post-war Puerto Rico. Prof Geogr. 2000; 52:386–397.

Rudel TK, Coomes OT, Moran E, Achard F, Angelsen A, Xu J, Lambin E. Forest transitions: towards a global understanding of land use change. Glob Environ Change. 2005; 15:23–31.

Santos-Román DM, Warner GS, Scatena F. Multivariate analysis of water quality and physical characteristics of selected watersheds in Puerto Rico. J Am Water Resour Assoc. 2003; 39:829–839.

Schlessinger WH, Bruijnzeel LA, Bush MB, Klein EM, Mace KA, Raikes JA, Whittaker RJ. The biogeochemistry of phosphorus after the first century of forest development on Rakata Island, Krakatau, Indonesia. Biogeochemistry. 1998; 40:37–55.

Silva L, Williams DD. Buffer zone versus whole catchment approaches to studying land use impact on river water quality. Water Res. 2001; 35:3462–3472. [PubMed: 11547869]

Spiegelhalter, DJ.; Best, NG.; Carlin, BR.; van der Linde, A. Bayesian measures of model complexity and fit. Black-well; London: 2002. p. 583-616.

Stauffer JC, Goldstein RM, Newman RM. Relationship of wooded riparian zones and runoff potential to fish community composition in agricultural streams. Can J Fish Aquat Sci. 2000; 57:307–316.

Turner BL II, Kasperson RE, Matson PA. A framework for vulnerability analysis in sustainability science. Proc Natl Acad Sci USA. 2003; 100:8074–8079. [PubMed: 12792023]

United Nations Population Division. World urbanization prospects: the 2005 revision. United Nations; New York: 2006.

Santiago, M.; Ramos, O.; Torres, H. U.S. Geological Survey. [Hydrologic units—Puerto Rico] [GIS map]. 1:20,000. U.S. Geological Survey and U.S. Department of Agriculture, Natural Resources Conservation Service; San Juan, Puerto Rico: 2002.

Walker LR, Syers JK. The fate of phosphorus during pedogenesis. Geoderma. 1976; 15:1–19.

Weisskoff, R. Factories and food stamps: the Puerto Rico model of development. John Hopkins University Press; Baltimore: 1985.

Weller DE, Jordan TE, Correll DL. Heuristic models for material discharge from landscapes with riparian buffers. Ecol Appl. 1998; 8:1156–1169.

Wiens JA. Spatial scaling in ecology. Funct Ecol. 1989; 3:385–397.

Wu W, Hall CAS, Scatena FN. Modelling the impact of recent land cover change on the stream flows in northeastern Puerto Rico. Hydrol Process. 2007; 21:2944–2956.

Zarin DJ, Johnson AH. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. Soil Sci Soc Am J. 1995; 59:1444–1452.

Zimmerman JK, Wright SJ, Calderon O, Pagan MA, Paton S. Flowering and fruiting phenologies of seasonal and a seasonal neotropical forests: the role of annual changes in irradiance. J Trop Ecol. 2007; 23:231–251.
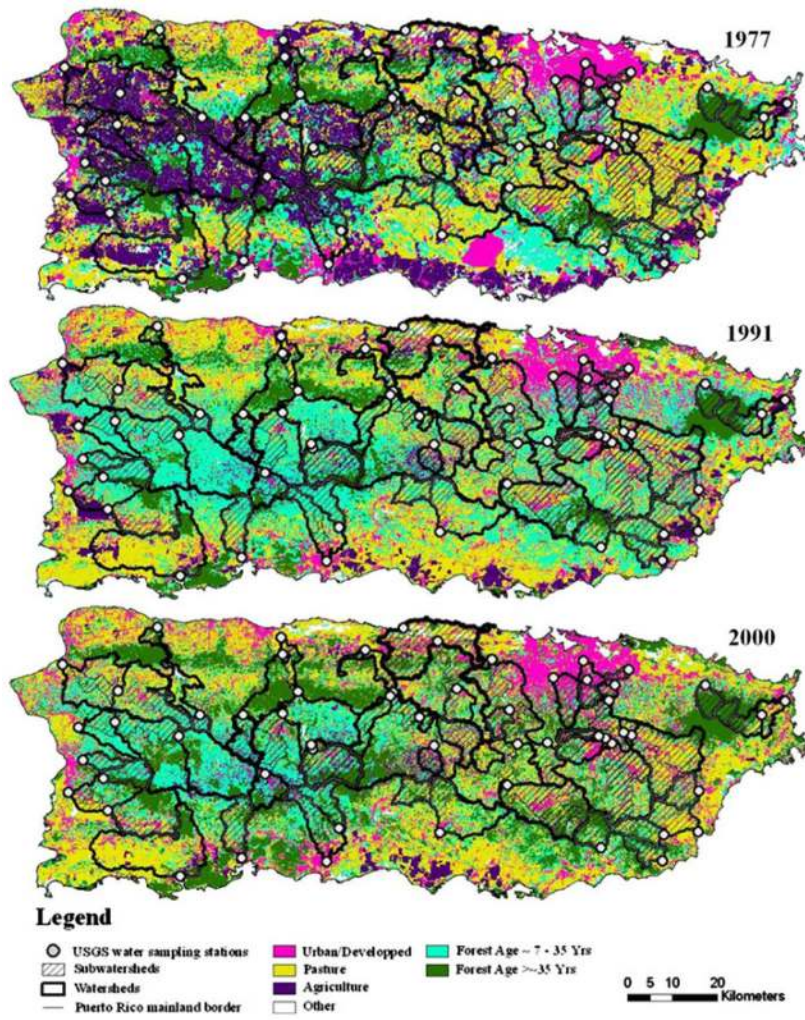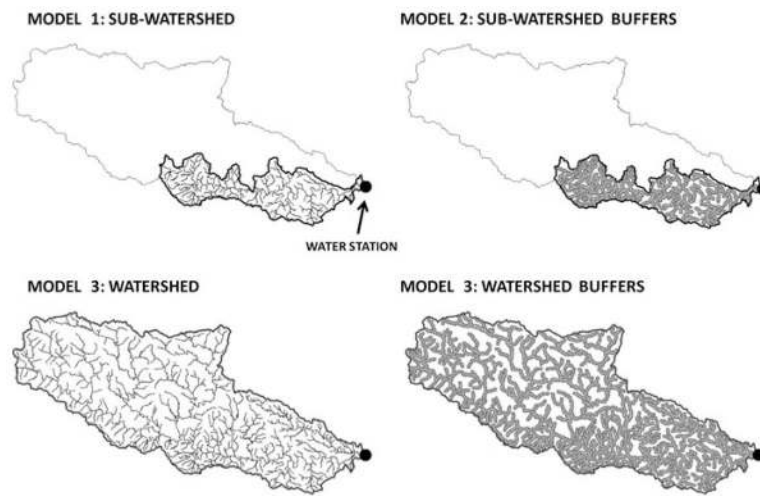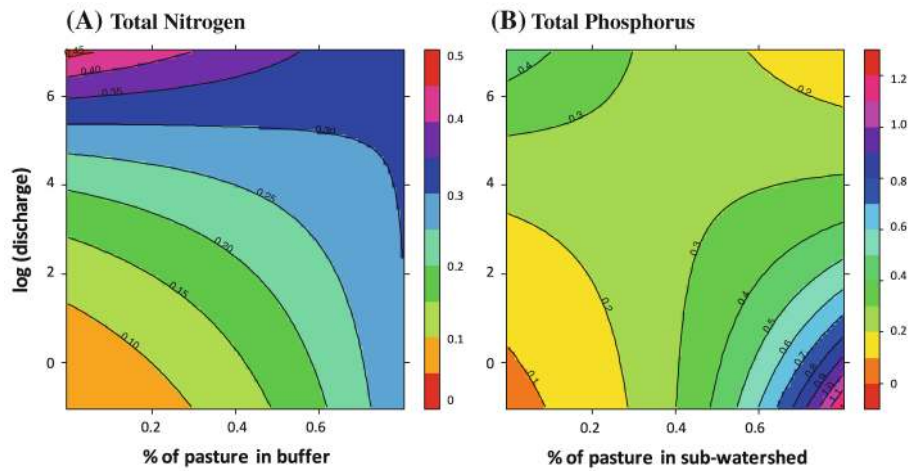
Fig. 1.
Distribution of LUC classes used in the analyses shown over the study watersheds
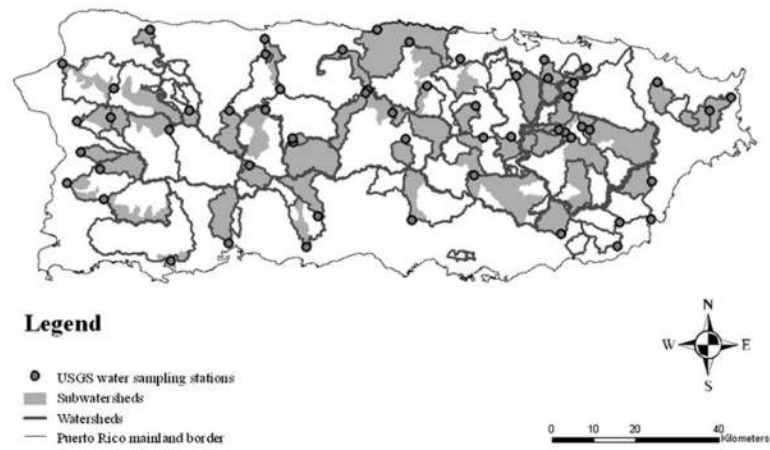
Fig. 2.
Distribution of USGS water sampling stations (*gray dots*), and delineation of watersheds and sub-watersheds used in these analyses

Fig. 3.
Schematic illustrating the four spatial scales over which land cover effects on water quality were calculated (Models 1–4 in Table 1)

Fig. 4.
Predicted interactive effects of the percent of land in pasture within a 60 m stream buffer in large watersheds and log(discharge) on stream concentration (mg/l) of **a** total nitrogen; **b** phosphorus. Data shown are predicted values for total N and P values obtained using the model, at a range of discharge values and land cover percentages representative of observed data. Temperature and pH were included at their mean observed values

Table 1

Model comparison results for water quality metrics

Water quality measure (units)	Probability distribution	No. stations	No. obs.	Other covariates	Model 1	Model 2	Model 3	Model 4	Model 5
Instantaneous discharge (ft³/s)	Lognormal	55	4,776	Precipitation Drainage area	14,935	14,942	14,928	14,937	**14,895**
DO (mg/l)	Gamma	57	6,015	log(Discharge)	22,636	22,656	**22,583**	22,589	22,810
Turbidity (nephelometric turbidity units)	Lognormal	56	5,338	log(Discharge)	18,413	18,423	**18,374**	18,392	18,407
Phosphorus (mg/l)	Gamma	56	5,841	log(Discharge)	**−8,767**	−8,702	−8,766	−8,711	−8,603
Total nitrogen (mg/l)	Lognormal	56	4,508	log(Discharge), temperature, pH	6,720	6,731	6,712	**6,704**	6,752
FC/FS	Lognormal	56	3,526	NA	**12,259**	12,263	12,268	12,269	12,233

Models 1 (subwatershed) and 3 (watershed) included the percent of land area in each land use/cover in the whole watersheds and in the sub-watersheds respectively. Models 2 (subwatershed) and 4 (watershed) included these same land cover categories but only within a 60 m buffer in watersheds and sub-watersheds. Model 5 did not include any land cover predictors. The number of stations and observations used to fit the model and other covariates included in the models are also provided. Model comparisons metrics are BIC (log-normal data) and DIC (gamma data). Most parsimonious models are highlighted in bold

Table 2

Parameter estimates for the most parsimonious model after backward stepwise variable selection at the spatial scale which had the best fit to the data (Table 1)

Water quality metric (units)	BIC/DIC	Sample R^2	Site R^2	Int.	log (Disch.)	pH	Temp.	Agric.	Past	Urban	Young forest	Agric. × log(dis)	Past × log(dis)	Urban × log(dis)	Young × log(dis)
DO (mg/l)	22,561	0.41	0.26	1.72 (0.05)	0.06 (0.01)			0.57 (0.0)		−1.3 (0.2)	0.46 (0.06)	−0.10 (0.02)		0.12 (0.03)	−0.09 (0.02)
Turbidity (NTUs)	18,353	0.32	−0.03	−1.5 (0.2)	0.84 (0.03)				2.5 (0.4)	3.1 (0.5)			−0.7 (0.1)		
Total nitrogen (mg/l)	6,668	0.56	0.12	0.8 (0.2)	0.27 (0.02)	−0.01 (0.00)	−0.13 (0.02)		1.8 (0.2)	1.8 (0.4)	−0.5 (0.5)		−0.33 (0.04)	−0.41 (0.08)	−0.27 (0.02)
Phosphorus (mg/l)	−8,773	0.58	0.15	−2.38 (0.2)	0.23 (0.05)			1.53 (0.2)	2.88 (0.34)	1.04 (0.43)	1.07 (0.27)	−0.27 (0.06)	−0.62 (0.07)		−0.23 (0.06)
FC/FS	12,217	0.17	0.3	−1.6 (0.4)				2.1 (0.5)	2.6 (0.6)	3.5 (0.6)	1.6 (0.4)				

Mature, older forest is used as the intercept. Estimates are provided for LUC categories that were significantly different from those of older, mature forests. Standard errors are provided in parentheses. BIC/DIC values after stepwise variable elimination and sample-level and site-level goodness of fit are also provided