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Climate Change and Land Use Drivers of Fecal Bacteria in Tropical Hawaiian Rivers

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Abstract

Potential shifts in rainfall driven by climate change are anticipated to affect watershed processes (e.g., soil moisture, runoff, stream flow), yet few model systems exist in the tropics to test hypotheses about how these processes may respond to these shifts. We used a sequence of nine watersheds on Hawaii Island spanning 3000 mm (7500–4500 mm) of mean annual rainfall (MAR) to investigate the effects of short-term (24-h) and long-term (MAR) rainfall on three fecal indicator bacteria (FIB) (enterococci, total coliforms, and *Escherichia coli*). All sample sites were in native Ohia dominated forest above 600 m in elevation. Additional samples were collected just above sea level where the predominant land cover is pasture and agriculture, permitting the additional study of interactions between land use across the MAR gradient. We found that declines in MAR significantly amplified concentrations of all three FIB and that FIB yield increased more rapidly with 24-h rainfall in low-MAR watersheds than in high-MAR watersheds. Because storm frequency decreases with declining MAR, the rate of change in water potential affects microbial growth, whereas increased rainfall intensity dislodges more soil and bacteria as runoff compared with water-logged soils of high-MAR watersheds. As expected, declines in % forest cover and increased urbanization increased FIB. Taken together, shifts in rainfall may alter bacterial inputs to tropical streams, with land use change also affecting water quality in streams and near-shore environments.

Climate change is expected to alter precipitation, storm frequency, and storm intensity (Muller et al., 2011), with resultant shifts in the amount and timing of surface water runoff delivered to streams and near-shore regions (Milly et al., 2005). Despite substantial uncertainty associated with forecasting future weather patterns, a strong drying trend is anticipated for large areas of the tropics (IPCC, 2013), with reductions in total annual rainfall and increases in the number of dry days accompanied by an increase in the intensity of individual rainfall events leading to greater flow variability (Easterling et al., 2000). Such changes are likely to affect water quality in the tropics because runoff and sediment transport are important drivers of bacterial inputs to tropical rivers. Water quality in the tropics is threatened by rapidly growing demand for fresh water, expanding populations of non-native animals (e.g., pigs, goats, and cows), and changing land use that can also alter sediment and bacterial delivery to streams (Laws and Ferentinos, 2003; Viau et al., 2011b). Additionally, in Hawaii the use of cesspools/septic systems, the accumulation of livestock/wildlife feces, and erosion due to deforestation drive nonpoint source runoff, impairing water quality (Viau et al., 2011a). Wildlife have the potential to substantially alter the bacterial loads of surface waters (Strauch, 2011), especially feral pigs, whose behavior (e.g., rooting and wallowing) further increases sediment and bacterial inputs (Dunkell et al., 2011).

In the tropics, favorable soil conditions (e.g., temperature, moisture, and soil organic matter) permit the survival and reproduction of bacteria, resulting in a continual flushing of bacteria into surface water resources (Lopez-Torres et al., 1987; Fujioka et al., 1998). Many common pathogenic agents associated with contaminated water are of fecal origin, and fecal indicator bacteria (FIB) (e.g., *E. coli* and *Enterococcus*) can indicate substantial risk to recreational water users (Viau et al., 2011b). Although FIB have been shown to survive and reproduce in tropical environments (Fujioka et al., 1998), it is unclear how hydrologic processes linking soil and freshwater

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Abbreviations: FIB, fecal indicator bacteria; LULCC, land use/land cover change; MAR, mean annual rainfall.

microbial communities are affected by precipitation change (Belnap et al., 2005).

Quantifying the water quality response to sudden short-term changes in rainfall and gradual climate shifts in rainfall over long time scales is a pressing need (National Research Council, 2012). Across narrow, low-order watersheds of windward Hawaii Island, mean annual rainfall (MAR) decreases from its peak of 7500 mm to 3000 mm within a short (<30 km) distance, providing a novel space-for-time hydrological system to examine how climate affects watershed processes (Pickett, 1989). Previous research has identified how short-term changes in rainfall influence surface runoff and the export of particulates and bacteria (Muirhead et al., 2006). Soil bacteria exposed to constant physiological stress from drying and rewetting (such as in low-MAR watersheds) are better adapted to respond to future shifts in water stress (Fierer et al., 2003). However, in wet tropical forests, soils remain moist throughout the year, and the soil microbial response to changes in rainfall are difficult to predict (Collins et al., 2008). Thus, although declining MAR may reduce total surface runoff, FIB may increase in more ephemeral streams due to the increase in the size and concentration of pulse events (Tryland et al., 2011) or the accumulation of organic matter during low-flow periods (Larned, 2000). Additionally, land use/land cover change (LULCC) influences soil retention, bacterial production, and runoff (Hathaway et al., 2010), with the conversion of native forest to agriculture and urbanized landscapes having consequences for the capture, retention, and release of water (Foley et al., 2005; Takahashi et al., 2011).

On Hawaii Island, conservation efforts have protected native forest above 600 m in elevation. By sampling at this elevation and below lands converted to agriculture, we can examine the interactive effects of climate and land use history on water quality. Using this system, we tested the following hypotheses: (i) declines in MAR will result in an increase in FIB in rivers draining native tropical forests (H1); (ii) decreasing MAR will increase a watershed's FIB yield response to rainfall (H2); and (iii) reduced forest cover and increasing urbanization will increase FIB and FIB yield relative to intact forest systems, and MAR will magnify this effect (H3).

Materials and Methods

Field Site Location

Throughout most of the year, the northeast Pacific Ocean circulation pattern produces easterly trade winds that bring moisture-laden air to Hawaii Island. This air is forced up the slope of Mauna Kea (summit, 4205 m), a large shield cone volcano, until it reaches the temperature inversion at about 1500 m, which suppresses further vertical movement, resulting in the release of moisture (Erasmus, 1986). As air masses move around the island, less moisture is available and mean annual rainfall decreases, producing a steep rainfall gradient over a short distance (ranging from 7500 to 3000 mm annually on the east-facing slopes). Watersheds on this island are uncharacteristically similar with respect to watershed shape (short, narrow, single- or low-order streams, with moderately steep gradients typical of a young shield volcano), vegetation type (>85% stand basal area dominated by Ohi'a lehua [*Meterosideros polymorpha* Gaudich]), land cover (native forest >600 m and agriculture <500 m above sea level), and geology (13,000–64,000 yr Mauna Kea lava flows). Water samples were collected from nine rivers at sites located along this MAR gradient above the human-dominated landscape where no point-sources of wastewater are found (Table 1).

Table 1. Reach elevation, mean annual rainfall, catchment size, and land-cover characteristics for each study site based on Hawaii Fish Habitat Assessment.

River	Elevation	Mean annual rainfall†	Catchmen	Population density	Land cover			
					Urban	Pasture	Forest	Agriculture
	m	mm	km^2	people km^{-2}	%			
Wailuku		5620						
Piihonua	610		395.9	0.00	0.0	0.0	100.0	0.0
Boiling Pots	275		537.3	83.8	32.4	24.3	41.9	1.4
Wainaku Street	5		599.4	963.7	76.2	6.2	16.6	1.0
Honolii‡	475	7028	31.3	0.0	0.0	1.9	98.1	0.0
Pahoehoe‡	430	7170	1.3	0.0	0.5	5.7	93.8	0.0
Kapue‡	470	7238	20.7	0.0	0.0	6.7	93.3	0.0
Downstream	40		27.9	447.9	25.7	16.2	42.5	15.5
Kolekole‡	500	7479	17.2	0.0	0.0	0.0	100.0	0.0
Downstream	5		54.3	0.5	5.9	36.2	56.3	1.6
Umauma‡	490	6840	46.0	0.0	0.0	0.0	100.0	0.0
Makahiloa‡	460	5246	9.6	0.0	0.0	0.0	100.0	0.0
Pahale‡	515	4995	12.2	0.0	0.0	13.7	81.2	5.0
Downstream	80		10.1	54.9	2.4	18.0	51.7	27.9
Manowaiopae‡	475	5023	3.8	6.1	0.0	24.4	62.5	13.1
Downstream	110		4.4	52.7	13.4	59.6	21.9	5.1
Kaawalii‡	490	4440	33.1	1.0	0.2	18.2	62.4	19.3

† Values based on Giambelluca et al. (2013).

‡ Long-term study sites.

Stream Flow

Sample sites were continuously monitored at 15-min intervals for stream flow. Flow was available at Honolii from the U.S. Geological Survey (USGS) (gaging station number 16707000). Stage in Kaawalii, Kapue, Kolekole, Makahiloa, Pahale, and Pahoehoe was measured using HOBO U20 depth sensors (Onset), and stage in Umauma and Manowaiopae streams was measured by WaterLOG Model H-312 (Design Analysis Associates, Inc.) depth sensors. Flow was then calculated by developing a rating curve for each river as described in Gore (2007). Base flow was calculated as Q_{90}, the flow that occurs 90% of the time, and median flow was calculated as Q_{50}. The base flow stability index (Q_{90}:Q_{50}) was used as an indicator of flow stability (e.g., higher values represent more stable base flows) based on Caissie and Robichaud (2009) for water year 2012 (the duration of the sampling period). A linear regression was used to examine the relationship between MAR and Q_{90}:Q_{50}.

For the Wailuku River, flow was available at Piihonua from the USGS stream gage (station number 16704000), and flow was estimated at the Wainaku Street site (W) based on a linear relationship generated between the Piihonua gage (P) and a discontinued gage (station number 16713000) located adjacent to Wainaku Street. The relationship was determined using 10 d of stream flow measurements ($n = 315$) spanning a 6-mo period selected to capture the widest range of stream flow measurements available. Based on flow maxima and minima, there was a 1-h delay between the Piihonua gage and the Wainaku gage, and all Wainaku Street readings were adjusted accordingly. A line of best fit using a least-squares regression ($R^2 = 0.97$) was used to generate a linear relationship: $W = 1.878P + 195.76$ (RMSE = 174.94). No data were available for the Boiling Pots site, so discharge was assumed to be equivalent to the Wainaku Street site 30 min before the reading (this site lies approximately halfway between Piihonua and Wainaku Street), although we recognize there will be errors associated with this assumption.

Rainfall

Rainfall data were gathered at 15-min intervals using three HOBO RG3 data logging rain gages (Onset Computer Corp.) and two Campbell Scientific weather stations (Fig. 1). Storm events were determined as any event that produced at least 6.4 mm (0.25 inches) of rainfall in a 24-h period. Storm recurrence interval for each rainfall gage was calculated as the mean (± SE) number of days between storm events with less than 6.4 mm (0.25 inches). Rainfall intensity was calculated as the maximum single day rainfall event divided by the median single day rainfall event. To calculate rainfall in the 24 h before sampling for each watershed, we used weighted average values based on linear distances to the nearest gages. The MAR for each watershed was determined using Giambelluca et al. (2013) using a 30-yr base period from 1978 to 2007. Relationships between 24-h rainfall and stream flow were examined with Spearman rank correlations for each watershed.

Data Collection

Sample collections occurred approximately monthly between October 2011 and October 2012 on nine rivers, spanning a range of climatic (e.g., wet vs. dry) and stream flow conditions. Additional samples were taken on four of the nine rivers (Kapue, Kolekole, Pahale, Manowaiopae) between May and October 2012 at downstream sites in the agricultural zone, also selected to represent a wide variation in MAR (Supplemental Fig. S1). These sites only represented the conversion of native forest to agriculture; therefore, to examine the interactions between urbanization, stream flow, and FIB, samples were collected across a wide range of flows during the month of March 2012 from three sites on the Wailuku River: a native forest site within the Hilo Forest Reserve (Piihonua,), a midpoint location at the beginning of urbanization (Boiling Pots), and an urbanized

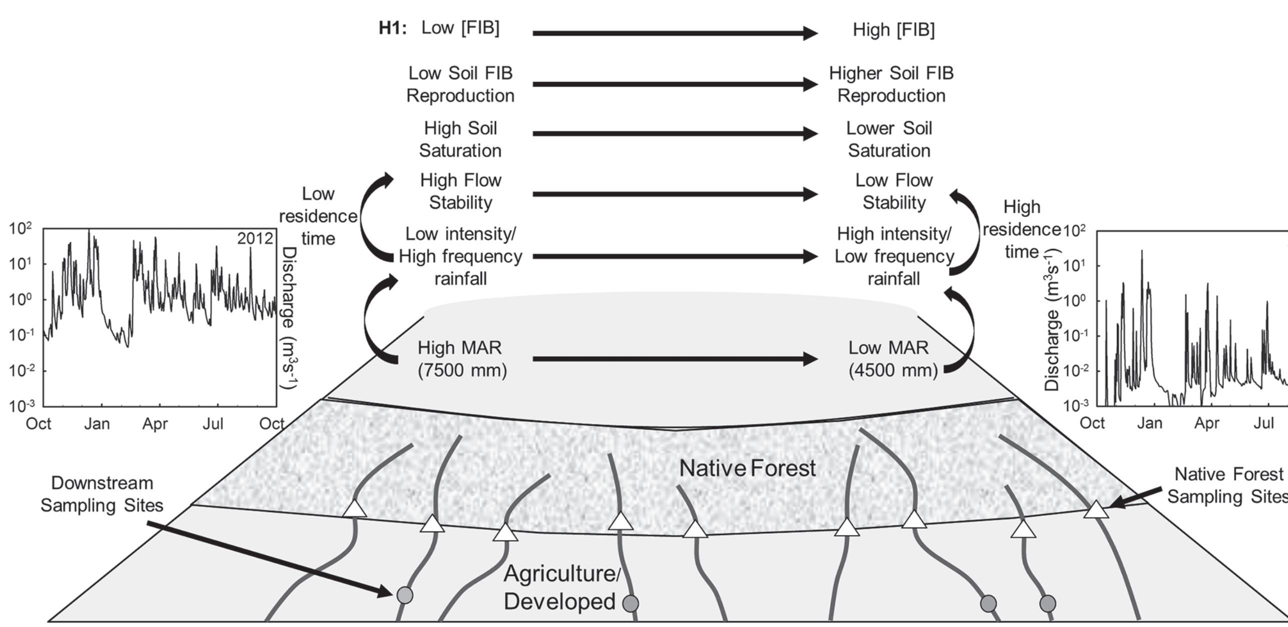

Fig. 1. Schematic of Windward Hawaii Island, with rivers, sample sites, land-cover, mean annual rainfall, and projected influences on stream bacteria. FIB, fecal indicator bacteria; MAR, mean annual rainfall.

location (Wainaku Street). During all collections, five replicate water samples were taken from the thalweg of each river, with the mean value of these samples was used in subsequent analyses. However, samples could only be safely collected from the sides of rivers during high flow events. All samples were collected using 100-mL sterile Whirl-Pak (Nasco) bags. Samples were stored on ice under dark conditions in the field and returned to the laboratory as quickly as possible (within <6 h).

Fecal Indicator Bacteria Analysis of Water Samples

Water samples were processed for *Enterococcus* spp., total coliforms, and *E. coli* using standard USEPA-approved (U.S. Environmental Protection Agency, 2007) IDEXX defined-substrate technology (IDEXX). Aliquots (10 mL) of each sample were dispensed using sterile pipets into Whirl-Pak bags, and the final volume was brought to 100 mL. Dilutions where then mixed with Entrolert (enterococci) or Colilert (for total coliforms and *E. coli*) for 1 min, allowed to rest for 1 min, and incubated in Quanti-Tray 2000 (IDEXX) for 24 h at 35°C (total coliforms and *E. coli*) and 41°C (enterococci). Colored wells were enumerated for bacteria under ambient (total coliforms) and ultraviolet (356 nm) light (enterococci and *E. coli*), and the most probable numbers (MPNs) were calculated based on a MPN table (IDEXX). Mean enterococci, total coliform, and *E. coli* values were calculated for each collection for subsequent use.

Land Cover Assessment

Watershed delineation and land cover summarization were completed and made available by the Hawaii Fish Habitat Partnership and National Fish Habitat Partnership; data are described in Esselman et al. (in review; http://ecosystems.usgs.gov/fishhabitat/). A watershed refers to the entire upstream land area draining into an individual stream reach. Individual land cover types present within the study area from the National Land Cover Database (NLCD) 2001 (Homer et al., 2004) were quantified within the catchment area above each study reach using the following four coarse land cover types as depicted in Supplemental Fig. S1: % forest (evergreen, scrub, mixed scrub), % pasture/grassland (grassland, pasture/hay, open, bare land), % urbanized (high, medium, and low density), and % agriculture (cultivated crops). Population density (persons per km^2) based on NLCD data for each catchment was also quantified. Values for % forest and % pasture ($R = -0.701$) and for % developed and population density ($R = 0.835$) were highly correlated; therefore, % pasture and population density were removed from all subsequent analyses.

Statistical Analysis

To test the hypothesis that FIB differed between watersheds, the mean FIB of each collection was compared using a two-way ANOVA that accounted for repeated-measures using PROC MIXED from SAS 9.3 (SAS Institute) with $\alpha = 0.05$. Fixed effects of the model included site (watershed) and date (time) along with their interaction. The covariance structures for all repeated measures were autoregressive of order (i.e., measurements on the same river in June were potentially more correlated with July than August). Post hoc comparisons using Tukey's HSD with adjusted P values were used to compare individual watersheds. Based on significant ($P < 0.05$) post hoc differences, watersheds were grouped into low-MAR (<5400 mm) (Kaawalii, Manowaiopae, Pahale, Makahiloa) and high-MAR (>6800 mm) (Umauma, Kolekole, Kapue, Pahoehoe, Honolii). To test the independent and interactive effects of short-term climate (24-h rainfall) and MAR on log-transformed FIB yield, we used a multiple linear regression model JMP 10.0.2 (SAS Institute).

To test the hypothesis that land cover and MAR interact, associations between log-transformed FIB and land cover were first examined using a multiple linear regression analysis for the wettest month (March 2011) and driest month (September 2012) of sampling. Following a strongly significant relationship for % forest cover, we used a multiple linear regression analysis to examine the effect of MAR, % forest cover, and their interaction on FIB. Finally, we used a general linear model to test the independent and interactive effects of short-term climate (24-h rainfall) on log-transformed FIB yield (FIB × discharge) at three levels of urbanization (intact forest, partial urbanization, and majority urbanized) on the Wailuku River. Differences in y-intercepts and slopes in the linear regression were compared using an analysis of covariance following the homogeneity of regression assumption.

Results

Rainfall and Stream Flow

Mean (± SE) monthly rainfall was greatest in the highest-MAR watershed (Kolekole: 528 ± 103 mm) and least in the lowest-MAR watershed (Manowaiopae: 243 ± 63 mm) (Supplemental Fig. S2). As expected, mean storm recurrence interval, measured as the mean (± SE) number of days between runoff producing rainfall events (>6 mm in 24 h), in Kolekole (0.61 ± 0.11 d) and Honolii (0.53 ± 0.10 d) was less than in Manowaiope (1.98 ± 0.44 d) or Kaawalii (2.58 ± 0.85 d). Rainfall intensity increased from 24.81 at Kolekole and 26.9 at Honolii to 142.9 at Manowaiopae and 171.63 at Kaawalii. There was generally a correlation between stream flow and 24-h rainfall (Supplemental Table S1). Base flow stability (Q_{90}:Q_{50}) ranged between 0.173 and 0.255 for the four highest-MAR watersheds and between 0.001 and 0.097 for the four lowest-MAR watersheds, increasing linearly [$y = (8.016 \times 10^{-5}) \times \text{MAR} - 0.3768$] with MAR ($R^2 = 0.82$; Supplemental Table S1).

Fecal Indicator Bacteria and Fecal Indicator Bacteria Yield across a Mean Annual Rainfall Gradient

Fecal indicator bacteria increased with decreasing MAR in most sampling months (Fig. 2), supporting the first hypothesis (H1). We found significant time and watershed effects on [enterococci], [total coliforms], and [*E. coli*] (Table 2). Post hoc analysis resulted in low-MAR (4440–5400 mm) watersheds that were significantly different ($P < 0.05$) from high-MAR (6800–7400 mm) watersheds. Fecal indicator bacteria yield was greatest in low-MAR watersheds, although only after rainfall events with >30 mm for enterococci and total coliforms. Using multiple linear regression, we found significant effects of rainfall, MAR, and rainfall × MAR interaction effects on FIB yield (Table 3), which explained some of the variability in enterococci (R^2 = 0.40), total coliforms (R^2 = 0.47), and *E. coli* (R^2 = 0.20), suggesting that both short-term (24 h rainfall) and long-term (MAR) climate patterns influence FIB yield in tropical rivers. The significant negative interaction effects indicate that the effect of rainfall differs across the MAR gradient for enterococci and total coliforms (H2).

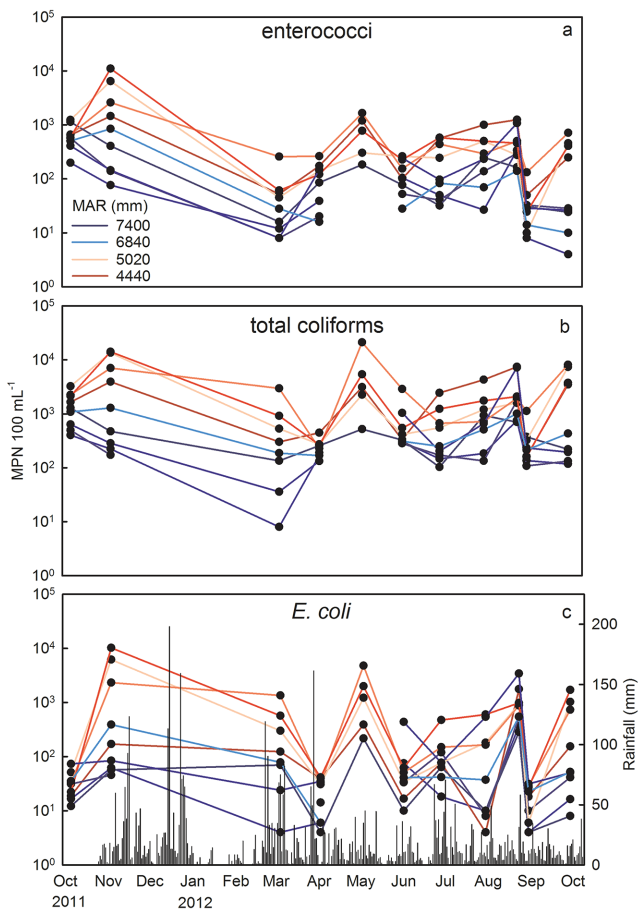

Fig. 2. Mean concentration (most probable number [MPN] 100 mL^{-1}) of (a) enterococci, (b) total coliforms, and (c) *Escherichia coli* from nine river reaches draining predominantly native-forested watersheds along windward Hawaii Island. Red lines indicate low mean annual rainfall (MAR) watersheds; blue lines indicate high MAR watersheds. (c) Total daily rainfall (mm) at Honolii rainfall gage.

Land Use/Land Cover Change and Fecal Indicator Bacteria

Fecal indicator bacteria were consistently greater in urbanized (Fig. 3) and deforested (Supplemental Fig. S3) sites compared with native forest sites (H3). Land cover explained more of the variability in samples from the driest month (September) (enterococci, R^2 = 0.75; total coliforms, R^2 = 0.74; *E. coli*, R^2 = 0.69) than in the wettest month (March) (enterococci, R^2 = 0.63; total coliforms, R^2 = 0.58; *E. coli*, R^2 = 0.64), whereas % forest cover had the greatest effect on March [enterococci], [total coliforms], and [*E. coli*] and September [enterococci] and [total coliforms]. Interestingly, % agriculture had little effect on FIB. There were significant negative linear regressions between % forest cover and log [enterococci] [R^2 = 0.47; $F(1,13)$ = 13.4; $P < 0.01$], log [total coliforms] [R^2 = 0.49; $F(1,13)$ = 14.6; $P < 0.01$], and log [*E. coli*] [R^2 = 0.48; $F(1,13)$ = 14.0; $P < 0.01$] in March 2012 and even stronger relationships between % forest cover and log [enterococci] [R^2

Table 2. *F*-statistic (degrees of freedom) results from a repeated-measures analysis of variance examining $\log_{10}(x + 1)$–transformed enterococci, total coliforms, and *Escherichia coli* concentration (most probable number 100 mL^{-1}) over time in nine watersheds along windward Hawaii Island.

	Enterococci	Total coliforms	*E. coli*
Time	F(1,396) = 62.17***	F(1,396) = 7.68**	F(1,396) = 8.17**
Watershed	F(8,396) = 3.20**	F(8,396) = 4.87***	F(8,396) = 4.80***
Time × watershed	F(8,396) = 0.87	F(8,396) = 0.87	F(8,396) = 0.70

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

Table 3. Whole model and individual effect sum of squares and *F*-statistic from a multiple linear regression model examining the effect of 24-h rainfall and mean annual rainfall (MAR) on log-transformed enterococci, total coliforms, and *Escherichia coli* yield from monthly (n = 10) samples of nine rivers spanning a mean annual rainfall gradient along windward, Hawaii Island.

Fecal indicator bacteria	Effect	Estimate†	Sum of squares	*F*
Enterococci	whole model		74.16	21.0***
	24-h rainfall, mm	32.52	43.60	37.2***
	MAR‡	0.36	15.61	13.3***
	24-h rainfall × MAR	−0.014	10.99	9.35**
Total coliforms	whole model		87.32	28.6***
	24-h rainfall, mm	37.98	59.45	58.4***
	MAR	0.32	11.95	11.7***
	24-h rainfall × MAR	−0.017	16.53	16.2***
E. coli yield, MPN s^{-1} km^{-2}‡	whole model		48.63	8.61***
	24-h rainfall, mm	16.97	11.88	6.31*
	MAR	−0.062	44.43	23.6***
	24-h rainfall × MAR	−0.007	2.74	1.45

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† In thousandths.

‡ MPN, most probable number.

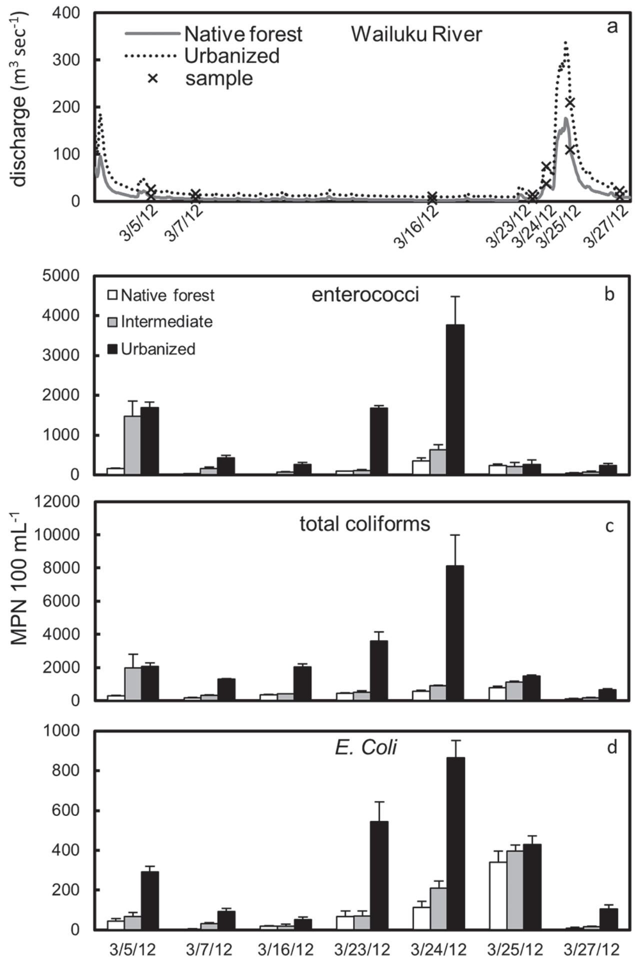

Fig. 3. (a) Discharge (m^3 s^{-1}) and sample collections on the Wailuku River during the month of March, 2012. Mean (± SE) concentrations (*n* = 5) of (b) enterococci, (c) total coliforms, and (d) *Escherichia coli* for seven collections on the Wailuku River, Hilo, Hawaii at flows indicated in (a). MPN, most probable number.

= 0.80; $F(1,11) = 47.7$; $P < 0.001$], log [total coliforms] [$R^2 = 0.66$; $F(1,11) = 24.2$; $P < 0.001$], and log [*E. coli*] [$R^2 = 0.44$; $F(1,11) = 10.6$; $P < 0.01$] in September 2012.

On the basis of these results, we examined the independent and interactive effects of MAR and % forest cover on FIB in streams with a multiple linear regression model and found that the model explained much of the variability in the data (enterococci, $R^2 = 0.53$; total coliforms, $R^2 = 0.63$; *E. coli*, $R^2 = 0.62$), although the individual effects of % forest cover or MAR were not consistently significant (Table 4). Mean annual rainfall had a significant effect on [total coliforms] and [*E. coli*], but % forest cover by itself did not have any significant effects. The significant positive interaction between forest cover and MAR for [total coliforms] suggests that climate change and land cover could have interactive effects on FIB.

Similarly, FIB increased in the Wailuku River with increasing urbanization (Fig. 4). Positive correlations between FIB load and rainfall were the strongest at the most urbanized site (H3). The slopes of the regression lines between in FIB yield and 24-h rainfall were significantly different among the three levels of urbanization for enterococci [$F(2,2) = 5.15$; $P < 0.01$] and almost significant for total coliforms [$F(2,2) = 2.56$; $P = 0.08$] and *E. coli* [$F(2,2) = 2.41$; $P = 0.09$]. We also found significant differences in the intercept of the regression models for enterococci [$F(2,2) = 28.5$; $P < 0.001$], total coliforms [$F(2,2) = 14.6$; $P < 0.001$], and *E. coli* [$F(2,2) = 9.63$; $P < 0.001$], with larger values at increasingly urbanized sites.

Discussion

Using a space-for-time model system to examine the consequences of forecasted shifts in climate (decreasing MAR, increasing number of dry days) in Hawaii, we found that stream FIB increased with decreasing MAR (H1); FIB yield increased more rapidly with 24-h rainfall in lower-MAR watersheds (H2); and reducing % forest cover or increasing urbanization resulted in increased levels of bacteria (H3). In native tropical soils, wildlife feces augments naturally occurring bacteria, contributing to the contamination of surface waters via runoff (Dunkell et al., 2011; Fujioka et al., 1998), and it remains unclear how this influences FIB in tropical rivers or the potential for climate change to alter

Table 4. Whole model and individual effect sum of squares and *F*-statistic from a multiple linear regression analysis examining the effect of % forest, mean annual rainfall (MAR), and their interaction on log transformed enterococci, total coliform, and *Escherichia coli* from forested and deforested sites in March 2012 spanning a mean annual rainfall gradient along the windward coast, Hawaii Island.

Fecal indicator bacteria	Effect	Estimate†	Sum of squares	*F*
Enterococci ($R^2 = 0.53$)	whole model		3.010	6.21**
	% forest	1.73	0.005	0.03
	MAR	−0.35	1.378	3.17
	% forest × MAR	0.04	0.089	0.55
Total coliforms ($R^2 = 0.63$)	whole model		3.005	8.81**
	% forest	6.98	0.076	0.67
	MAR	−0.39	0.662	5.82*
	% forest × MAR	0.01	0.607	5.34*
Escherichia coli ($R^2 = 0.62$)	whole model		4.884	8.63**
	% forest	6.31	0.062	0.33
	MAR	−0.51	1.127	5.98*
	% forest × MAR	0.006	0.218	1.16

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† In thousandths.

bacteria loading. Whereas in temperate climates drainage from septic tanks and cesspools, pasturelands, and urban runoff contribute to the bacterial loading of surface waters in deforested and urbanized watersheds (Crowther et al., 2002; Hathaway et al., 2010), few studies have quantified such impacts in the tropics or whether climate change and LULCC interact to increase contamination relative to their independent effects. Results demonstrate that the individual and synergistic effects of LULCC and rainfall in tropical watersheds impair surface water quality.

Precipitation Drives Fecal Indicator Bacteria Yield in Streams

Tropical island climates are characterized by intense, short-duration storms producing runoff that carries large quantities of sediment into streams (Augustijn et al., 2011). High variability in the quantity, distribution, and intensity of rainfall creates spatially and temporally heterogeneous pulses of soil microbial activity (Belnap et al., 2005; Davidson et al., 2000), resulting in highly variable water quality. For example, in soils along Florida riverbanks, flushing during storm events was the primary contributor of FIB to rivers (Solo-Gabriele et al., 2000), and increases in stream *E. coli* in Puerto Rico were dependent on fluctuations in rainfall (Lopez-Torres et al., 1987). In this study, increasing 24-h rainfall resulted in greater enterococci and total coliform yield, with the rate of increase greatest in low-MAR watersheds. Such changes in surface water quality can represent a significant epidemiological risk to recreational water users (Viau et al., 2011b).

Differences in long-term rainfall patterns between watersheds influence soil moisture and affect the survival and reproduction of soil bacteria (Solo-Gabriele et al., 2000; Tryland et al., 2011). In high-MAR watersheds, soils are often fully saturated and anaerobic, but in low-MAR watersheds, a longer storm recurrence interval resulted in periods without rainfall leading to reductions in soil water potential. When soils are drier, small increases in soil moisture result in large increases in microbial respiration (Fierer et al., 2003). Thus, the infrequent rewetting of drier soils produces greater concentrations of FIB in runoff compared with the frequent wetting of already wet soils. This is supported by Kieft et al. (1987), who found that the magnitude of soil microbial activity (e.g., soil C release, soil respiration) was proportional to the increase in water potential; by Carter et al. (1987), who reported that *Campylobacter* sp. decreased during seasonally wetter periods of the year; and by Hathaway et al. (2010), who concluded that reductions in FIB concentration with increases in rainfall indicated “wash-off dynamics” in the watershed. Although microbial activity increases with added soil moisture, soil saturation in high-MAR watersheds likely limits physiological activity (Davidson et al., 2000). We did not test for the survival of bacteria in soil or stream systems, but differential decay rates of bacteria from different sources could also affect FIB (Anderson and Stone, 1994).

Additional factors that may have influenced FIB in streams include rainfall intensity, which can dislodge soil particles that transport FIB (Tryland et al., 2011), and stream flow stability, which influences the movement of sediment loads and the resuspension of organic matter that magnifies bacterial growth within streams (Grant et al., 2011). In some cases, storm loading of FIB can be as much as 30 to 37 times greater than base flow (Stumpf et al., 2010) because watersheds that exhibit “flashy” hydrographs (e.g., stream flow dominated by runoff) are more likely to have high concentrations of suspended sediment, leading to large fluctuations in bacteria (Bai and Wu-Seng, 2005). However, dilution effects from large rainfall events in watersheds with saturated soils (high-MAR watersheds) may also influence FIB in surface water (Santiago-Rodriguez et al., 2012). Reduced flows in lower-MAR watersheds may also have increased residence time for bacteria and sediment, leading to increased FIB reproduction (Bai and Wu-Seng, 2005) and to increased accumulation of organic debris that accentuates bacterial growth (Larned, 2000). Significant interactions between short-term (24-h rainfall) and long-term (MAR) climate patterns due to expected increases in the intensity and reductions in the frequency of rainfall events will lead to greater FIB yields.

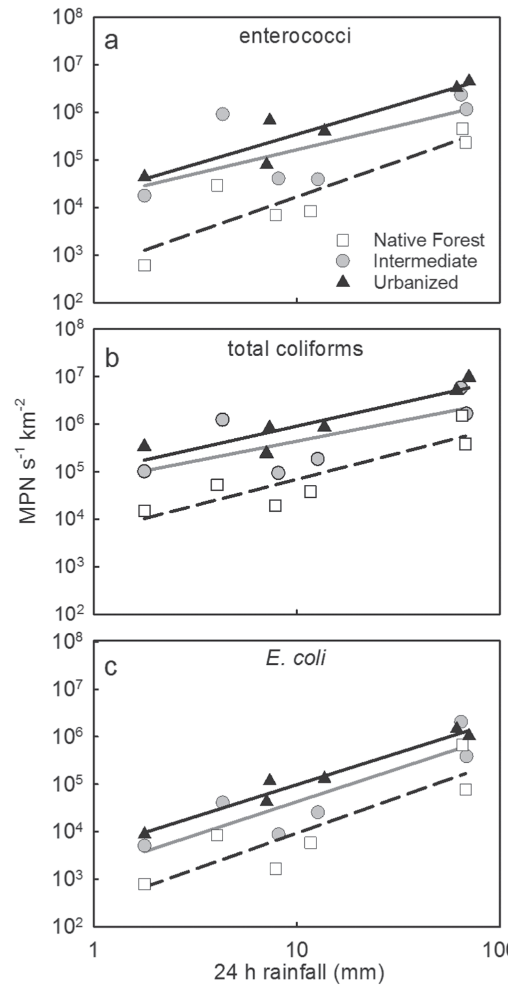

Fig. 4. Fecal indicator bacteria yield (MPN s^{-1} km^{-2}) vs. 24-h rainfall (mm) at three sites of increasing urbanization along the Wailuku River, Hawaii Island. MPN, most probable number.

Influence of Land Use/Land Cover Change on Fecal Indicator Bacteria

We found that as % forest cover increased and urbanization decreased, there was a decline in FIB. More importantly, significant interaction effects suggest potential interactive consequences between rainfall change and LULCC (H3). The conversion of native-dominated forests to pasture, agriculture, and urbanized development has been shown to be a major contributor to stormwater nutrient pollution in streams and coastal waters. With increasing deforestation, Phan et al. (2011) found that forecasted climate change will result in increasing threats to sedimentation, with expected consequences for bacterial contamination. Urbanization influences microbial pollution because impervious surfaces, poorly constructed septic systems, legacy cesspools (e.g., drywells), and reductions in riparian vegetation affect bacteria in runoff and groundwater (Hathaway et al., 2010; Kelsey et al., 2004). The prohibitive cost of installing municipal sewer or septic systems in lava-dominated substrates limits the development of proper waste disposal systems and results in the rapid degradation of groundwater, surface flows, and near-shore environments, especially after storm events (Izuka, 2011). Consequently, in the face of changing climate patterns, the management of storm water in urbanized settings is a global challenge that is made more difficult on young islands in the tropics.

Conclusions

Clean freshwater is an essential resource for sustaining humans and their communities, including the economic, agricultural, recreational, and aesthetic value of landscapes. Rivers support habitat for unique assemblages of flora and fauna, and the transport of nutrients to near-shore ecosystems supports coastal marine communities. Climate change is expected to alter the amount and distribution of rainfall, with consequences for watershed processes; however, few systems exist to examine such processes in real time. Using a space-for-time substitution, we demonstrate that in tropical island rivers, reductions in MAR increase a watershed's bacterial yield as well as the rate of change in yield with rainfall and that land cover change (e.g., deforestation and urbanization) may have additive or interactive consequences that exacerbate climate-driven effects on surface water quality. The increase in bacteria load in freshwater and near-shore environments is likely to pose an increased risk to human health as tropical communities expand and as the growth of tourism magnifies the potential population at risk for water-related diseases.

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