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Forest cover lessens the impact of drought on streamflow in Puerto Rico

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Abstract

Tropical regions are experiencing high rates of forest cover loss coupled with changes in the volume and timing of rainfall. These shifts can compromise streamflow and water provision, highlighting the need to identify how forest cover influences streamflow generation under variable rainfall conditions. Although rainfall is the key driver of streamflow regimes, the role of forests is less clear, particularly in tropical regions where forest loss is an ongoing risk. Forest cover loss alters evapotranspiration, rainfall infiltration and storage, and may increase stream ecosystem vulnerability to rainfall extremes. Puerto Rico, an island with spatially heterogenous forest cover and a marked geographic rainfall gradient, is projected to experience more frequent droughts and flash flooding. Using 15-min streamflow data collected between 2005 and 2016 from 20 US Geological Survey stream gages and 3-hourly Multi-Source Weighted-Ensemble Precipitation rainfall estimates, we utilized flow-duration curves and linear mixed regression models to examine the role of forest cover in regulating the timing and volume of streamflow. The mixed model approach helps to account for differences in watershed characteristics. We determined the effects of rainfall and forest cover on low and peak flows in Puerto Rican streams, then evaluated changes in these relationships under dry and wet antecedent rainfall conditions. Watersheds with high forest cover had consistently greater low and peak streamflow than deforested ones under all rainfall conditions, although the effect was more marked during wet antecedent conditions, suggesting that peak flow is largely the result of saturation excess overland flow. During dry antecedent rainfall conditions, highly forested watersheds had higher streamflow than deforested ones, suggesting greater hillslope storage and release may also be at play. Our results demonstrate that forest cover generated a net increase in hillslope infiltration and storage and may lessen drought impacts on streamflow in Puerto Rico. Resilience to prolonged drought may be limited by finite water storage potential in this steep, mountainous setting, highlighting maintenance of forest cover as an important water management strategy to increase infiltration.

KEYWORDS
flow duration curves, forest cover, infiltration-evapotranspiration trade-offs, linear mixed models, streamflow, tropical forest hydrology

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1 | INTRODUCTION

Deforestation in the tropics, interacting with climate change influencing the amount and intensity of rainfall, has the potential to affect water availability for humans and ecosystems. Climate change is expected to change the timing, magnitude, and duration of precipitation in many regions (Dai, 2012; Feng et al., 2013; Greve et al., 2014; Mora et al., 2013; Neelin et al., 2006), with some of the fastest changes occurring in the tropics (Anderson, 2011; Christensen et al., 2007; Hoegh-Guldberg et al., 2018; Mora et al., 2013). In the Caribbean, projected higher maximum temperatures and aridity (Reyer et al., 2017) lead to an overall drying trend (Diaz, 1996; Taylor et al., 2018) and increased drought risk (Lehner et al., 2017), with longer moderate to extreme drought conditions (Taylor et al., 2018). Anthropogenic warming is also expected to increase atmospheric moisture content and extreme rainfall rates associated with tropical cyclones, which are common in the Caribbean (Gutmann et al., 2018; Knutson et al., 2013, 2015; Kossin, 2018).

Precipitation determines the magnitude and timing of ecosystem water inputs and is the primary driver of most streamflow patterns. Streamflow and water provision will be affected by projected changes in climate (Pachauri and Meyer, 2014), however, in forested watersheds, other controls on streamflow include interactions between climate, forest cover and the physical characteristics of the system (Bruijnzeel, 2004; Tallis & Polasky, 2009; Wei et al., 2018; Wu, 2013). Ultimately, these interactions determine the volume, timing, and quality of water supply. As a result, ongoing large-scale losses of forest cover in tropical regions coupled with changes in rainfall patterns (Vörösmarty et al., 2000) are likely to alter water provision and human well-being.

Although forests play an important role in regulating the movement of water in watersheds, the effect of forest cover on streamflow is variable (Bonell et al., 2010; Bosch & Hewlett, 1982; Filoso et al., 2017; Ghimire et al., 2014; Krishnaswamy et al., 2018; Qazi et al., 2017). Some studies have found a negligible or negative effect of forest cover on streamflow (Beck et al., 2013; Birkel et al., 2012; Simonit & Perrings, 2013; Uriarte et al., 2011), while others have found positive influences on low flow or dry season flow and reduced maximum storm flows (Addor et al., 2018; Krishnaswamy et al., 2018; Ogden et al., 2013).

These complex and contrasting outcomes led to the "infiltration-evapotranspiration trade-off" hypothesis, which posits that the direction and magnitude of the effect of forest cover on streamflow relative to other land covers are the net result of heightened demand from transpiration, decreased inputs from canopy interception, and increases in water supply through greater infiltration and soil water storage (Bruijnzeel, 1989). Transpiration rates in forests tend to be higher than in other land cover classes, leading to lower streamflow in forested watersheds (Bosch & Hewlett, 1982; Brown et al., 2013; Calder, 2002; Farley et al., 2005; Timbe et al., 2017), although forest clearing may increase surface temperatures and lead to higher soil evaporation rates (Hashimoto et al., 2004). Tree roots and litter inputs also develop soil structure that in turn, decreases overland flow and increases soil water storage, infiltration capacity, and groundwater recharge (Bargués Tobella et al., 2014; Bonell et al., 2010; Bruijnzeel, 2004; Ilstedt et al., 2007).

In tropical forests, after the initial quick flow discharge, infiltrated storm rainfall remaining after evapotranspiration may discharge as delayed flow from hillslope groundwater, which may have residence times ranging from weeks to years (Muñoz-Villers et al., 2016; Post & Jones, 2001; Shanley et al., 2011). Forest cover increases soil macro-porosity and rainfall infiltration, which may act to keep soil water storage at capacity (Bonell et al., 2010; Muñoz-Villers & McDonnell, 2012; Zimmermann et al., 2006). This leads to increased groundwater to supply streams (i.e., baseflow) during dry conditions (Hamilton & King, 1983; Ilstedt et al., 2016; Ogden et al., 2013; Peña-Arancibia et al., 2019; Scott et al., 2005). Additionally, the surface roughness of forest land cover can lower peak streamflow during intense rainfall events (Bradshaw et al., 2007).

The complexity of factors that determine rainfall partitioning to infiltration, runoff and forest water demand has made distilling generalizations about the impacts of forests on stream processes difficult. Forest cover effects on streamflow depend on a variety of local and regional factors, including geology, topography and soil water storage characteristics of watersheds (Malmer et al., 2010; Zhou et al., 2015), the scale of analyses (Ellison et al., 2012), climate (Addor et al., 2018; Zhou et al., 2015), and forest age and history of degradation (Bruijnzeel, 2004) The paucity of studies on driving factors and streamflow response in meso-scale tropical watersheds supports the need for more research to examine how geophysical and climatic factors influence the relationship between forest cover and streamflow.

The variety of responses observed in determining the impacts of forest cover on streamflow may also reflect the chosen temporal scale of analysis. Many studies examining the impact of forest cover on streamflow have focused on annual flow metrics (Bentley & Coomes, 2020; Bosch & Hewlett, 1982; Brown et al., 2005; Farley et al., 2005; Filoso et al., 2017). However, in many tropical areas, precipitation is highly variable at inter-annual and intra-annual scales, exhibits high seasonality, and includes frequent intense rainfall events (Biasutti et al., 2012). Water delivery systems often include widely distributed local withdrawals and reservoirs, and total annual stream output may matter less for consistent water supply than the timing of delivery. In these regions, hydrologic signatures such as peak rainfall event-related streamflow and low inter-event streamflow may be more relevant for water provision and flood mitigation than measures of total annual streamflow (Ellison et al., 2017; Larsen, 2016).

Here, we examine how forest cover and rainfall individually and jointly influence several streamflow metrics in 20 watersheds in Puerto Rico between 2005 and 2016. The island is an ideal location for this study because it has a high number of gaged streams with similar geology and slopes, and variation in forest cover (50%–99%) that span a large rainfall range, providing a robust data set to examine these relationships for a tropical environment. Surface streamflow contributes 84% of total water used for human consumption in the island (Molina-Rivera, 2014) and same-day rainfall (causing overland or near surface flow) accounts for much of the variation in streamflow, even during extreme drought (Clark et al., 2017; Post & Jones, 2001; Schellekens et al., 2004). Droughts have led to multiple periods of water rationing (Larsen, 2000), and projected changes to the rainfall regime have led to calls for re-evaluating Puerto Rican water management systems (Murry et al., 2019). This situation highlights the need for studying the effects of forest cover and interactions between rainfall and forest cover on streamflow extremes, groundwater baseflow, and total streamflow in Puerto Rico. Additionally, results from this set of observations across a climate gradient in Puerto Rico can inform driving factors and streamflow response in other meso-scale humid-tropical watersheds. Understanding these relationships will contribute towards improving water and forest management in other tropical regions with similar climatic and physical characteristics.

Our study examines the impacts of forest cover on two streamflow metrics in Puerto Rico, low flow (minimum streamflow during rainless periods) and peak flow (maximum streamflow during rainfall events). We used these data to answer the following questions:

1. What is the effect of forest cover on peak and low streamflow? If forest cover increases infiltration and groundwater subsurface storage enough to offset evapotranspiration under average climate conditions, higher low flows are expected in watersheds with high forest cover compared with less forested watersheds. If forest cover mitigates potential effects of high-intensity rainfall, decreasing overland flow and increasing time to infiltration, we hypothesize that peak flows in highly forested watersheds will be lower than in less forested watersheds. Higher peak flows in highly forested watersheds would indicate a greater rate of overland or shallow-subsurface flow in these areas compared to less forested watersheds. This could mean either that forest cover does little to mitigate intense rainfall (infiltration excess overland flow) or that soils are more persistently saturated in highly forested areas (saturation excess overland flow).
2. How do the relationships between forest cover and streamflow change under wet and dry antecedent rainfall conditions? We hypothesize that under wet antecedent rainfall conditions (a) the hydrological properties of highly forested watersheds (i.e., high rainfall interception, infiltration, storage, and land surface roughness) will reduce overland and shallow-subsurface flow volume during rainfall events, leading to lower peak streamflow than in less forested areas that may experience quicker saturation and less flow resistance during wet periods. If we find that heavily forested areas have higher or unchanged peak flows with high antecedent moisture, this will suggest that forest cover does not have significantly different hydrological properties than other land cover types. During drier antecedent conditions (b), if forest water demand outweighs the increased infiltration and water storage provided by forest relative to other land cover types, we can expect low flows in heavily forested areas to be lower than less forested areas.

2 | DATA AND METHODS

2.1 | Study site

Puerto Rico (~9000 km^2, 18°N and 66°W in the tropics) is a heavily forested Caribbean island (Figure 1) with complex topography (0–1331 m asl) (Carswell, 2016; Kennaway & Helmer, 2007). Forest cover is the dominant land cover class in Puerto Rico, comprising

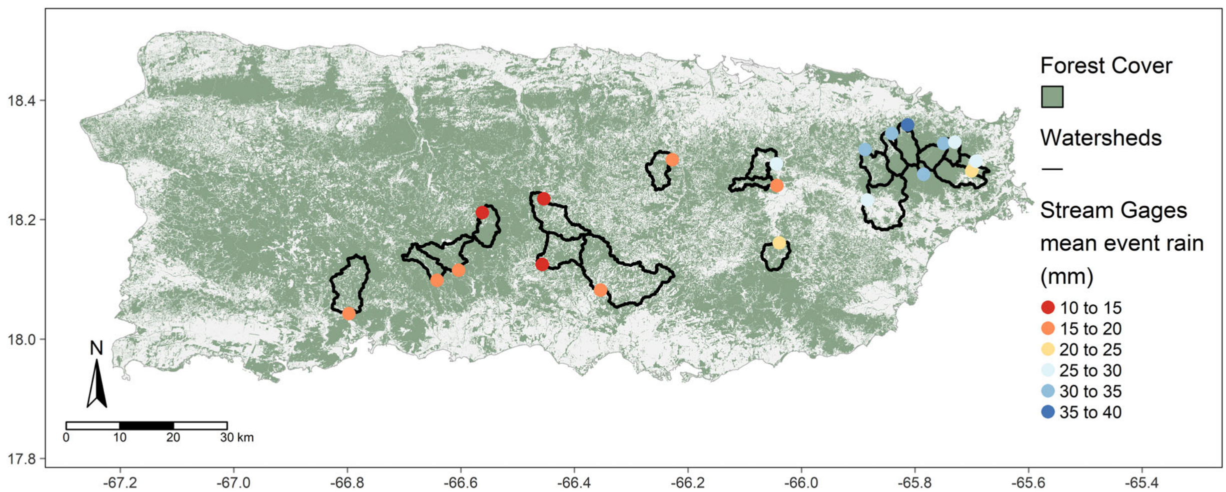

FIGURE 1 Monitoring stations (i.e., stream gages) and watershed locations in Puerto Rico. Forest cover was taken from 2010 NOAA CCAP data (NOAA, 2010). Stream gage locations were obtained using the DataRetrieval R package (De Cicco et al., 2018), and watersheds were delineated using the "streamstats" package (Hagemann, 2021). Points represent the unique USGS gage locations and point colours represent the gage-specific mean rainfall event depth (mm) after separating rainfall into discrete events of at least 12-h duration throughout the study period. Watersheds are shown in black and forest cover across the island is shown in green. This map was generated using the "stars" (Pebesma, 2021b) and "tmap" (Tennekes, 2018) packages

approximately 45.7% of total land area, followed by pasture (34.7%) and urban (15.4%) (Kennaway & Helmer, 2007). Puerto Rico has volcanic, granitic, and sedimentary geology types that weather to produce soil types with distinctive hydrologic properties (Bawiec, 1998; McDowell et al., 2013; Murphy & Stallard, 2012a; Reed & Bush, 2005). Infiltration rates vary from 0 to 106 mm/h in El Yunque National Forest (EYNF) in the northeast (Harden & Scruggs, 2003), and island-wide eighth hour infiltration rates vary from <1 to 292 mm/h (López et al., 1968).

The topographic relief and prevailing trade winds generate large variation in rainfall across the island; mean annual rainfall (1963–1995) ranges from 700 mm/year on the south coast to >4600 mm/year at high elevation in the northeast (Daly et al., 2003; Murphy et al., 2017). The island experiences a bimodal wet season common to the Caribbean region, with an early wet season from May to July and a late wet season from August to October (Murphy and Stallard 2012). In 2010, annual evapotranspiration ranged from 9 to 2262 mm/year across the island (Senay et al., 2020), and was approximately 940 ± 593 mm/year in the EYNF (Zhang et al., 2018), between 1963 and 1995. High elevation (>200 m a.s.l.) forested watersheds lose up to 36% of storm rainfall from overland and shallow subsurface flow within hours rather than days (Schellekens et al., 2004; Scholl et al., 2015), even during periods of intense drought (Clark et al., 2017). These characteristics have implications for water availability for human use: the lack of adequate water distribution and storage infrastructure paired with shallow reservoir depths and high sedimentation rates means that much of the water from rainfall is lost as reservoir evaporation or as surface flow to the ocean before it can be used (Larsen, 2000; Molina-Rivera, 2014).

Puerto Rico has experienced five major droughts since 1899, with many more moderate droughts (Murphy and Stallard 2012). The most recent major drought was in 2015, the worst in 20 years, where more than two thirds of the island was under moderate to extreme drought conditions for months (Clark et al., 2017; USDM, 2019) (Figure 2). Because of the steep mountainous terrain paired with a climate that produces long-duration intense rainfall events, the island also has the greatest flash-flooding threat of any US state or territory (Murphy & Stallard, 2012b).

2.2 | Data

2.2.1 | Streamflow

We selected 20 US Geological Survey monitoring stations (Figure 1) with unmodified perennial flows (see Supporting Information S1) of the 89 stations with data available for the study period 2005–2016 (USGS, 2020). This period includes a severe drought in 2015–2016, numerous dry periods (Figure 2), and normal and wet years for precipitation extremes. To ensure that dry periods were captured for each stream gage, we excluded gages for which the period of record did not include the major 2015 drought period and those that did not have measured values for at least 5 years (e.g., the period of record

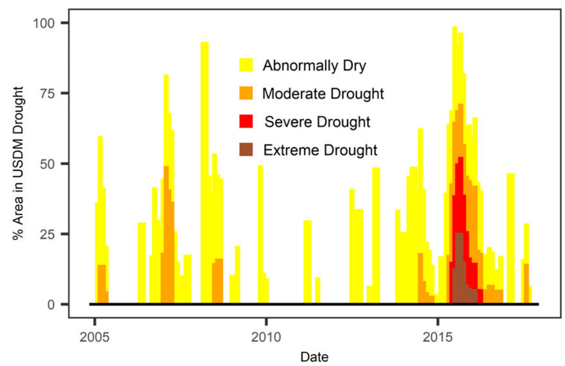

FIGURE 2 US drought monitor (USDM) averaged values of weekly cumulative percent area within each drought category for the entire island of Puerto Rico during the study period (2005–2017). As values for each drought category are cumulative, values for each D category are the sum of the percent of Puerto Rico in that category as well as the percent of Puerto Rico in more severe categories (e.g., D0 a value of 100 and a D1 value of 80 at the same time would mean that all of Puerto Rico was experiencing at least abnormally dry conditions, but 80% of Puerto Rico was experiencing moderate drought conditions or drier). Data were accessed from https://droughtmonitor.unl.edu on December 9, 2019

began after January 1, 2011 or ended before January 1, 2016), using gage attributes extracted using the dataRetrieval package (De Cicco et al., 2018). We delineated contributing watershed areas for each stream gage and various watershed characteristics using the "delineateWatershed" function in the "streamstats" package (Hagemann, 2021). To control for geological influence on streamflow, stream gage sites were limited to those with watershed contributing areas containing 50% or more of the most common near-surface lithology on the island (volcaniclastic) (Bawiec, 1998; Reed & Bush, 2005). Watersheds containing pipelines, lakes over 10 ha in area, or dams anywhere in the watershed area were located by flow modification features flagged in the National Hydrography Dataset (USGS, 2020) and excluded from analysis. We also used the HU12 Hydrologic Unit Modification (HUMOD) codes to filter out watersheds affected by karst topography and to exclude sites with recorded flow regulations and diversions in the USGS water year records (see Supporting Information S1).

Instantaneous streamflow from 2005 to 2016 calendar years at selected USGS gages collected at approximately 15-min intervals was obtained using the "DataRetrieval" package (De Cicco et al., 2018). We restricted streamflow values to those marked as "approved for publication". We also determined the instantaneous peak and low streamflow for each 3-hourly rainfall observation period (Section 2.2.2), and approximated missing values up to 12 h using the "na.approx" function in the "zoo" package (Zeileis et al., 2015).

To account for variation in drainage area and facilitate cross-watershed comparisons, all streamflow was converted to specific discharge in millimetres per unit time by dividing by the contributing watershed area for each gage; the term "streamflow" in this document refers to specific discharge.

TABLE 1 Watershed characteristics for selected streamflow monitoring stations

USGS site identification number (site_no)	Contributing drainage area (ha)	Forest cover fraction of drainage area (%)	Fraction of drainage area above 700 m asl (%)	Slope (degrees)	Mean rainfall event amount (mm)	Mean rainless period duration (hours)
50025155	2296	93	83	24	14	44
50034000	4333	69	69	22	15	50
50044810	2100	65	0	18	16	52
50053025	1887	75	2	19	20	51
50055380	1249	71	0	14	20	63
50055750	5724	50	6	12	27	63
50058350	1955	69	0	13	25	68
50061800	2646	81	9	15	31	56
50063800	2243	94	26	14	36	54
50064200	1887	85	27	14	32	60
50065500	1755	99	18	21	31	54
50067000	1006	96	0	18	29	58
50070900	2839	79	8	17	21	58
50071000	3861	78	6	17	27	60
50075000	321	99	44	15	32	55
50106100	11 283	65	8	18	16	56
50110900	3725	72	23	20	14	48
50113800	3073	89	38	23	17	50
50114900	1907	84	32	22	16	52
50124200	4876	79	17	21	16	57

2.2.2 | Rainfall events and rainless periods

Although Puerto Rico has a relatively large number of rain gages, the steep topography causes heterogeneity in rainfall patterns. Few of the 20 selected stream gages had collocated or nearby hourly or better rain gage data during our study period. Therefore we obtained global rasters of Multi-Source Weighted-Ensemble Precipitation (MSWEP) 3-h rainfall (0.1-degree spatial resolution) from 2004 to 2016 (Beck et al., 2019) and extracted the spatially-weighted average rainfall values for each watershed contributing area. We identified discrete rainfall events and rainless periods using the "IETD" package in R (Duque, 2020). This package uses a rainless period length threshold from a rainfall time series to partition the data into individual rainfall "events". Rainfall events were separated using a 6-h rainless threshold (2 consecutive zero-rainfall values from MSWEP) as streams in Puerto Rico often respond to rainfall within 1–2 h (Schellekens et al., 2004; Scholl et al., 2015). The rainless periods were determined as the time in hours to the next rainfall event so the entire time series was classified as either rainfall event or rainless period. Watershed contributing areas in the study ranged from 321 to 11 283 ha (Table 1) and often small rainfall events did not affect streamflow. All rainfall events and rainless periods with durations below 12 h were omitted from the analysis, as MSWEP has a 1.5-h gage inference rounding error rate. 12-h events contain at least two samples (6 h) with values independent of potential error. This created a set of rainfall events ranging in size from 0.60 mm to 571.69 mm and comprised 81% of total rainfall during the study period. This events time series was used primarily to determine periods that contained peak and low streamflow values, as the 3-h resolution of the MSWEP data exceeded the actual duration of many rain events (Scholl & Murphy, 2014; their Table 3).

To examine the effect of wet and dry antecedent rainfall conditions on streamflow, we calculated the average 33% and 66% MSWEP rainfall quantiles for 30-day (33% = 95.26 mm, 66% = 177.04 mm) antecedent conditions across all watersheds throughout the study period. We classified antecedent rainfall conditions as dry (<33rd), or wet (>66th) if 30-day antecedent rainfall amounts fell within the respective thresholds.

2.2.3 | Watershed characteristics

Watershed-level forest cover proportion was determined using the 2010 Puerto Rico C-CAP Land Cover dataset (NOAA, 2010). Estimates of forest cover loss derived using the Global Forest Watch data viewer (Hansen et al., 2013) showed that between 2005 and 2016 Puerto Rico lost less than 1% of the primary forest cover present in 2000, so we concluded that there were no significant changes to forest cover during the study period. We also considered the proportion of the watershed above 700 m asl, calculated from the Puerto Rico Coast Digital Elevation Model (DEM) (NOAA, 2006), to account for

TABLE 2 Streamflow metrics used for each type of analysis

			Watershed characteristics		Rainfall variables			Interactions
Analysis type	**Flow type**	**Dependent variable**	**% Forest**	**% >700 m**	**Lag 6-h Total**	**Duration rainless period**	**30-day antecedent**	**Ant. Rain * % Forest**
Flow duration curves	Low	Q95n	X				X	X
	Peak	Q5n	X				X	X
Linear mixed models	Low	Minimum rainless period flow	X	X		X	X	X
	Peak	Maximum rain event flow	X	X	X		X	X

the relationships between increased elevation and moisture that may not be represented by the rainfall data. Cloud condensation begins at approximately 700 m in Puerto Rico (Bassiouni et al., 2017; Scholl et al., 2021; Van Beusekom et al., 2017) and cloud immersion causes actual evapotranspiration rates to be lower above this elevation; in addition, MSWEP rainfall for high elevation wet sites may be underestimated (Beck et al., 2019). Using the DEM, we also calculated watershed slope steepness in the study area (mean watershed slopes of 11–23 degrees), however, slope displayed high collinearity with forest cover and could not be included in our analysis. We used the R packages "raster" (Hijmans et al., 2011), "sf" (Pebesma, 2021a), and "sp" (Pebesma et al., 2013), to extract these watershed characteristics for each watershed contributing area (see Supporting Information S1).

2.3 | Statistical analyses

To identify the relationship between forest cover and streamflow regimes under different rainfall conditions, we used two complementary methods: flow duration curves (FDCs) (Brown et al., 2013; Alice Elizabeth Brown et al., 2006; Lane et al., 2005) and statistical models (Lewis, 2006; Uriarte et al., 2011; van Dijk et al., 2009). FDCs are cumulative frequency curves derived from streamflow time series to determine the percentage of time a given value of streamflow was met or exceeded during a study period (see Section 2.3.1). The magnitude of watershed-level streamflow extremes can then be regressed against watershed characteristics, while statistical models (see Section 2.3.2) determine the single and interactive effects of covariates (e.g., forest cover and rainfall) across watersheds.

2.3.1 | FDC quantiles and linear regression models

FDCs were derived for each stream gage using all 15-min instantaneous streamflow for the study period (2005–2016) and were calculated separately for wet and dry 30-day antecedent rainfall conditions. Most watersheds in Puerto Rico displayed substantial subdaily changes to streamflow. Examination of hydrographs indicated streamflow was back to pre-rainfall levels within hours in the smallest watershed (gage station 50075000, Table 1), and within no more than a few days in the largest watershed (gage station 50106100, Table 1). To ensure that we preserved the flow peak magnitudes that would be lowered by averaging streamflow to hourly or daily estimates, we chose to use instantaneous streamflow at 15-min intervals to create FDCs. By using FDC-derived probability of exceedance values (Q) for specific quantiles (*n*) of 15-min instantaneous streamflow data for each watershed, we evaluated the relationships between streamflow extremes and forest cover using simple linear regressions (Table 2).

To evaluate streamflow extremes (Question 1), we calculated and normalized (see next paragraph) the FDC-derived specific discharge for streamflow that met or exceeded for 5% (peak streamflow, Q5) and 95% (low streamflow, Q95) of the study period. To examine how the effects of forest cover on low runoff varied during dry and wet periods (Question 2), we separated the streamflow data into wet and dry 30-day antecedent conditions based on the >66th and <33rd percentiles of rainfall, respectively. Wet and dry antecedent FDCs were then generated for each watershed and Q5 and Q95 determined for all 15-min runoff values during periods with wet and dry 30-day antecedent rainfall conditions. We regressed these summary values against watershed forest cover to evaluate whether watersheds with high forest cover display less extreme streamflow regimes.

To account for potential differences in total rainfall inputs to individual watersheds, the streamflow quantiles (Q5 and Q95) for the 20 watersheds in the study were normalized (Q_n) by a mean rainfall event scaling factor for each individual watershed using the following equation: $Q_n = Q \times R_{max}/R$; where Q is the station-specific streamflow probability of exceedance quantile for an individual watershed, n is the probability exceedance quantile, R is the study-period individual watershed mean rainfall event amount (Table 1), and Rmax is the maximum study-period mean rainfall event amount (R) observed from the set of watersheds.

To account for potential heteroskedasticity and uncertainty in extremely high streamflow records (Peña-Arancibia et al., 2015; Petersen-Øverleir, 2004), we also repeated the FDC analysis for Q10 and Q15 values (see Supplementary Information S1). Similar relationships between forest cover and the additional peak streamflow metrics indicates that we have appropriately characterized relationships between forest cover and peak streamflow.

2.3.2 | Mixed linear regression models

Linear mixed effects regression models (LMEs) are also valuable tools for cross-watershed comparison as they can account for the hierarchical and non-independent structure of watershed-scale streamflow data (Lewis, 2006). LMEs (Bates et al., 2015; Zurr et al., 2009) can simultaneously incorporate fixed effects (e.g., rainfall) as well as random effects that capture the hierarchical nature of the data (i.e., grouping variables such as watershed) (Lewis, 2006). They have been used to explain potential drivers of water quality (Uriarte et al., 2011), to predict runoff in un-gaged basins (Müller & Thompson, 2015), and to evaluate trends in streamflow over time (Vervoort et al., 2021).

LMEs are linear regressions between the dependent variable (i.e., streamflow) and independent predictors of interest (fixed effects, e.g., rainfall and forest cover) that incorporate random (group) effects (Bolker et al., 2009). Random effects (intercepts) for the relationship of rainfall to streamflow capture differences in baseline streamflow across individual stream gages, or watersheds. By accounting for dependent variable variation among groups (i.e., watersheds), and interactive relationships between fixed effects, we can make broad inferences about the relationships between the fixed effects and dependent variables across all watersheds.

Here we used LMEs to determine the magnitude and direction of the effects of rainfall and forest cover on low and peak streamflow during the study period. Maximum instantaneous streamflow for each gage during each rainfall event and minimum instantaneous streamflow for each gage during rainless periods between rainfall events were chosen to represent peak and low streamflow (mm/s), respectively. The LMEs were used to evaluate the relationships between streamflow extremes and covariates (fixed effects), namely rainfall events and rainless periods, and forest cover (Question 1). Because most hydrographs peak within hours after rainfall begins, peak flow during rainfall events was regressed against the sum of the rainfall values for 6 h before peak streamflow occurred (i.e., for the same 3 hourly increment when peak flow occurred and the previous). Low streamflow during rainless periods was regressed against the duration of the rainless period (i.e., the time in hours since the last rainfall event) (Table 2). Both models included an event-based rainfall metric (6-h rainfall to predict peak flow, and rainless period duration to predict low flow), proportion of forest cover, and proportion above 700 m in elevation (Table 2). Models also included an interaction effect between forest cover and the chosen rainfall metric. LMEs of instantaneous peak and low runoff were calculated separately and compared for dry and wet 30-day antecedent rainfall conditions (Question 2).

To account for potential non-independence of streamflow data during rainfall events or rainless periods, we visually interpreted the partial autocorrelation of events for each watershed and response using the "stats" package (Figures S1–S4) and found little temporal autocorrelation past 1 lagged event. Nevertheless, we included an AR2 (i.e., second order autocorrelation structure) temporal autocorrelation term in the model to account for potential autocorrelation in the streamflow event data.

LMEs were fit using the "nlme" package (Pinheiro et al., 2020). We tested model assumptions and goodness of fit using the "performance" package in R (Lüdecke et al., 2019). LMEs assume that response variables and model residuals are normally distributed, relationships between the response and covariates are linear, and collinearity between predictors is low. Streamflow and rainfall metrics were log transformed to meet these assumptions and all covariates were scaled by centring each predictor and dividing the centred values by the standard deviation (Becker et al., 1988). Scaling covariates enables direct comparison of model coefficients and facilitates model convergence.

3 | RESULTS

3.1 | Question 1: What is the effect of forest cover on instantaneous peak and low streamflow?

We hypothesized that high watershed forest cover, via increased soil infiltration and recharge, has a negative effect on peak flow (Q5) and a positive effect on low flow (Q95). We calculated FDCs for each of the 20 watersheds to examine the effect of forest cover on streamflow. Normalized Q5 (Q5n) and Q95 (Q95n) FDC quantiles derived for each watershed for the study period, were both higher in watersheds with high forest cover than in those with low cover ($R^2 = 0.61$ and $R^2 = 0.65$, $p < 0.01$ for Q5n and Q95n, respectively) (Figure 3). We also found positive relationships between forest cover and both Q10 and Q15 FDC quantiles (see Supplementary Information S1), suggesting that our results are not driven by uncertainty in rating curves. This suggests that increasing forest cover has a positive effect on low streamflow but does not prevent peak flow extremes.

We also examined results from the LMEs to establish how rainfall and forest cover influence low and peak streamflow. Fixed effects accounted for 30%–45% of the observed variance in streamflow metrics (marginal R^2), while considering both fixed and random effects (conditional R^2) increased these values to 44%–64% (Table 3). Goodness of fit values attributed to fixed effects were higher for peak flow (0.45 and 0.40 for wet and dry conditions, respectively) than for low streamflow observations (0.31 and 0.31 for wet and dry conditions, respectively), the opposite pattern that we observed for analysis of FDCs (Table 3).

Not surprisingly, the amount of rainfall in the 6 h before peak streamflow was recorded had a positive effect on peak streamflow (dry conditions: estimate $= 0.93$, $SE = 0.02$, wet conditions: estimate $= 0.94$, $SE = 0.01$) (Figure 4a) while duration of rainless periods had a negative effect on low streamflow (dry conditions: estimate $= -0.08$, $SE > 0.01$, wet conditions: estimate $= -0.14$, $SE = 0.01$) (Figure 4b). We had hypothesized that forest cover would buffer intense rainfall, slow down overland flow, and increase infiltration and subsurface storage enough to offset evapotranspiration, leading to higher low flow and lower peak flow in watersheds with high forest cover. Results from LMEs demonstrate that watersheds with high forest cover had greater low streamflow (dry conditions:

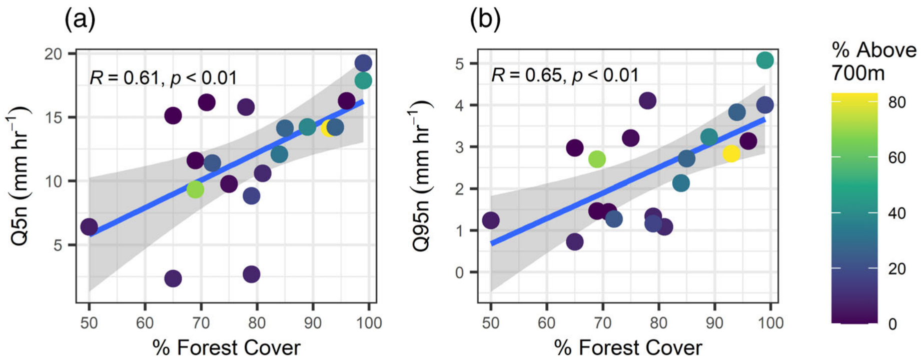

FIGURE 3 Regressions between watershed-level forest cover and (a) 5th (i.e., Q5n, peak flow), and (b) 95th (i.e., Q95n, low flow) normalized quantiles derived from flow duration curves. Streamflow at 5% and 95% exceedance probabilities were determined for each monitoring station using 15-min streamflow. All streamflow values have been normalized by rainfall event volume averages. Each point represents one of 20 stream monitoring stations, and the colour of the points indicates the watershed percent above 700 m in elevation. Blue lines depict significant ($p \leq 0.05$) linear regressions and grey area indicates 95% confidence intervals. Instantaneous streamflow values have been converted to mm/h from mm/s to enable visualization

TABLE 3 Goodness of fit values from linear mixed models of streamflow, including marginal and conditional R^2 (i.e., proportion of the variance explained from fixed effects alone and the combination of fixed and random effects, respectively), and root mean square error (RMSE)

Hydrologic signature	Conditions	# sample points	Marginal, R^2	Conditional, R^2	RMSE
Peak Streamflow	Wet	6230	0.45	0.58	1.06
Peak Streamflow	Dry	5636	0.40	0.60	1.02
Low Streamflow	Wet	4746	0.31	0.44	0.60
Low Streamflow	Dry	4435	0.30	0.64	0.46

Note: Goodness of fit values were estimated using the "performance" package (Lüdecke et al., 2019). The sample sizes in each model are also shown.

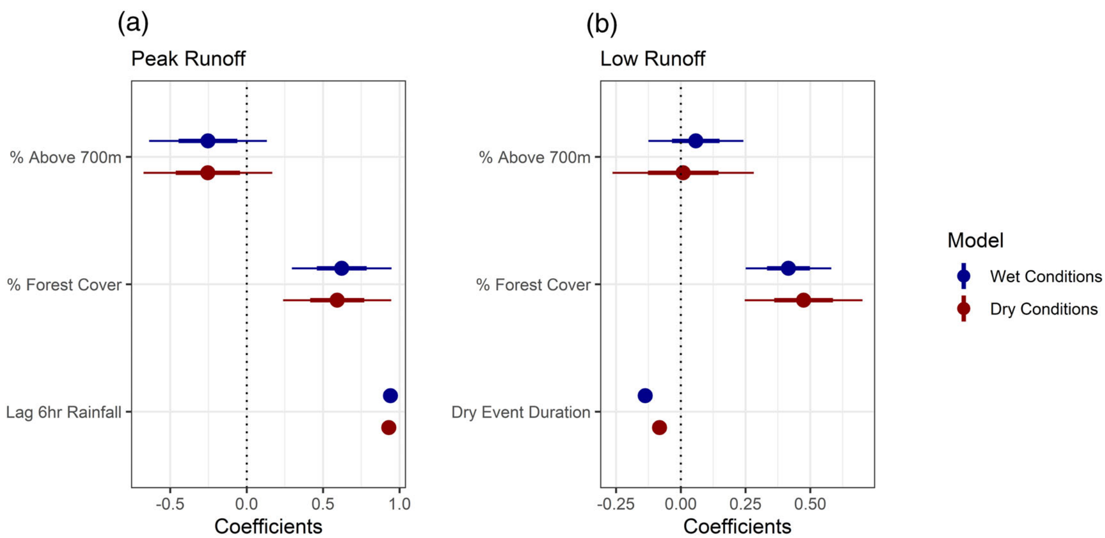

FIGURE 4 Standardized parameter estimates for covariates included in linear mixed models of peak (a) and low (b) streamflow data. Horizontal lines represent 95% confidence intervals for the estimates. Coefficients with lines intersecting the dotted zero-effect line are not significant

estimate = 0.47, *SE* = 0.11, wet conditions: estimate = 0.42, *SE* = 0.08) (Figure 4b), indicating increased infiltration and subsurface storage, and possibly evapotranspiration suppression above 700 m, in heavily forested watersheds compared to less forested watersheds. However, the same was true for peak flow, contradicting our expectation (dry conditions: estimate = 0.59, *SE* = 0.17, wet conditions: estimate = 0.62, *SE* = 0.15) (Figure 4a). It is possible that the greater flows with high forest cover reflects occult orographic precipitation at high elevations that is not captured by the MSWEP rainfall product, but the proportion of watershed area above 700 m in elevation did not show an effect on low or peak streamflow. If rainfall is underestimated in high elevation watersheds that tend to be highly

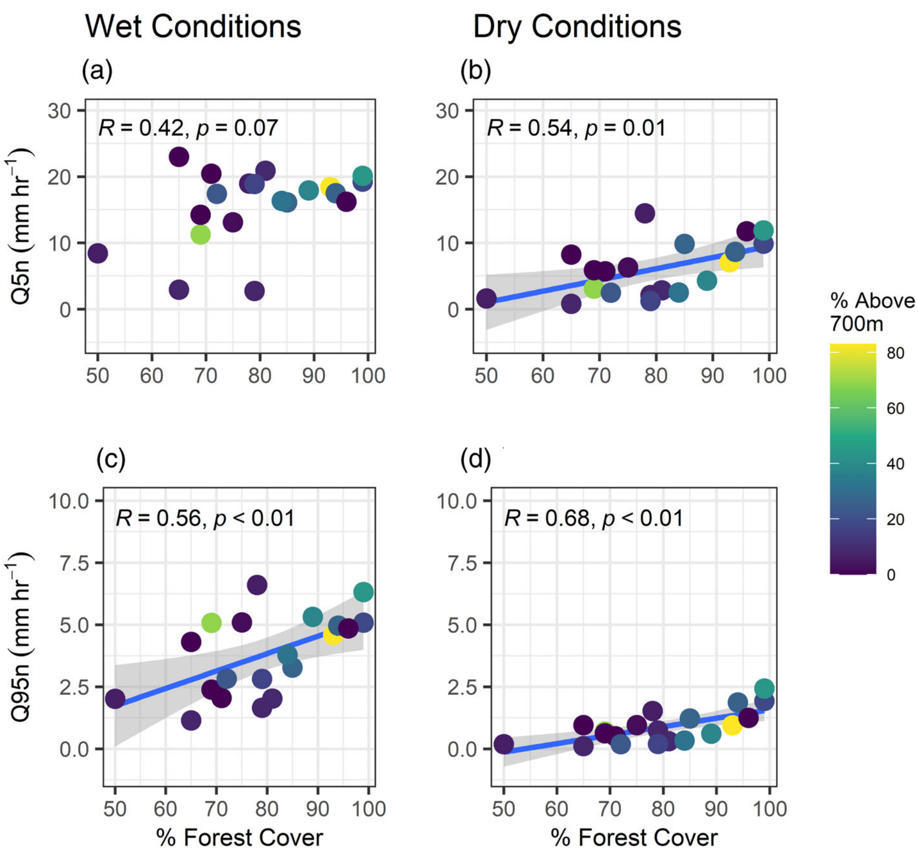

FIGURE 5 Flow duration curve results for Q5 (a,b) and Q95 (c,d) streamflow quantiles for wet (left) and dry (right) antecedent rainfall conditions. Quantiles are visualized in a regression with watershed-level forest cover. Streamflow at 5% and 95% exceedance probabilities were determined for each monitoring station, and all streamflow values have been normalized by rainfall event averages. Points represent stream monitoring stations and point colours represent the watershed percent above 700 m. blue lines depict significant or marginally significant ($p \leq 0.10$) linear regressions and grey area indicates 95% confidence intervals. Instantaneous streamflow values have been converted to mm/h from mm/s to enable visualization

forested, there will be higher peak flow values for every millimetre of estimated rainfall in highly forested watersheds than in less forested watersheds. If this is the case, then after accounting for rainfall, our models would find a positive relationship between forest cover and peak flow.

3.2 | Question 2: How do the relationships between forest cover and streamflow change under 30-day wet and dry antecedent rainfall conditions?

We expected that under wet 30-day antecedent rainfall conditions, high canopy rainfall interception and hydraulic roughness in watersheds with high forest cover would lead to lower peak streamflow than in less forested watersheds. However, strong relationships between rainfall amount and peak flow were evident during both wet (estimate = 0.94) and dry (estimate = 0.93) 30-day antecedent rainfall conditions, suggesting that peak flow is largely driven by short term rainfall regardless of antecedent rainfall conditions (Figure 4a). FDC quantiles demonstrate that the relationship between forest cover and peak flow is less variable under dry 30-day antecedent rainfall conditions ($R^2 = 0.54$, $p < 0.05$), and forest cover has little effect on peak flow during wet antecedent conditions ($R^2 = 0.42$, $p = 0.07$) (Figure 5a,b). Positive relationships between FDC-derived peak flows and forest cover were consistent when examining Q10 and Q15 to account for heteroskedasticity in rating curves (see Supplementary Information S1).

We also expected that greater evapotranspiration in heavily forested areas would reduce low streamflow relative to less forested watersheds, particularly under dry antecedent rainfall conditions. However, low flow values were greater in watersheds with high forest cover during both wet and dry 30-day antecedent rainfall conditions, using either FDC quantiles (wet conditions: $R^2 = 0.56$, $p < 0.05$, dry conditions: $R^2 = 0.68$, $p < 0.05$) (Figure 5c,d) or LMEs (wet conditions = 0.42, dry conditions = 0.47) (Figure 4b). All watersheds displayed decreased low flow under dry antecedent conditions (Figure 5c,d), nevertheless, the positive relationship between FDC low flows and forest cover during dry antecedent rainfall conditions remained.

4 | DISCUSSION

4.1 | Effect of forest cover on instantaneous low streamflow

A positive relationship between forest cover and low streamflow under dry antecedent rainfall conditions (Figure 5d) suggests that infiltration and recharge in highly forested areas in Puerto Rico are greater than those in less forested areas, as suggested by Bruijnzeel (1989). After accounting for rainfall effects, our analysis indicated watersheds with high forest cover displayed increased dry-period low streamflow compared to less forested watersheds. When comparing the relative contributions of climatic and biophysical catchment characteristics for predicting low flows (Q5) in US catchments, Addor et al. (2018) found that the frequency of high rainfall events was negatively correlated with low flows, while the proportion of forest cover (the next most important predictor) was positively correlated with low flows. With steep watershed slopes in the study area, slowing overland flow and limiting erosion during intense rainfall events (Birkel et al., 2012; Bruijnzeel, 2004; Uriarte et al., 2011) may be a primary forest-cover function that contributes to observed results in our study. These effects likely offset the higher evapotranspiration rates of forest compared to other land cover types (Wu et al., 2006, 2007).

Previous studies have concluded that deep soil profiles in Puerto Rico may drive annual and interannual streamflow variability through storage and steady release to streams (Post & Jones, 2001). The absence of a negative effect of forest cover on low streamflow at any time during the study period may reflect relatively high levels of water storage in the deeper weathering profile (Buss et al., 2013; Krishnaswamy et al., 2018). Although upper soil layers quickly weather to less-permeable clays, they transition to saprolite and extend over 50 m to bedrock in some areas in watersheds with volcanic geology in Puerto Rico (Buss et al., 2013).

The positive relationship between forest cover and low streamflow (Figure 3, Figure 5) may also be the result of the association between rooting depth and soil profile depth in Puerto Rico. Greater forest rooting depth implies that infiltrating rainfall is available for vegetation uptake over a greater depth interval, leading to higher transpiration (Seyfried & Wilcox, 2006). Although rooting depth is difficult to determine and is highly variable globally and locally (Fan et al., 2017), root distribution in the first meter of the soil profile can act as a proxy for maximum rooting depth. Puerto Rico has a shallower rooting depth than other studied tropical forests, with approximately 80% of root biomass in the first 20 cm of soil depth (Yaffar & Norby, 2020). In a study of tree uprooting by hurricane winds in Puerto Rico, Lenart et al., 2010 reported 0.33 m as the mean depth of highest root density in the soil profile; also in Puerto Rico, Evaristo et al., 2016 noted most roots are found within the top 0.4 m where permeability is highest. Shallow rooting depth paired with deep soil profiles having higher storage capacity may explain the net positive effect of forest cover on low streamflow in Puerto Rico, consistent with the results from previous studies in tropical regions with deep soil profiles (Cheng et al., 2020; Krishnaswamy et al., 2018; Ogden et al., 2013). However, further studies are required to determine whether this is generalizable to other wet tropical regions or whether this increased storage and gradual release to streams can be sustained under prolonged drought conditions. The longest rainless period in this study was 43 days, thus longer or more frequent droughts would test the current balance of net recharge over forest evapotranspiration.

4.2 | Effect of forest cover on instantaneous peak streamflow

In our study, we found positive relationships between high percentage of forest cover and peak streamflow (Figure 3), particularly under dry antecedent conditions (Figure 5). Rainfall intensities during periods of high rainfall likely surpass infiltration rates in Puerto Rico, even in highly forested areas (Clark et al., 2017; Larsen & Simon, 1993). Drought may also alter infiltration rates through changes to soil pores, and can make surface soils water repellent (Gimbel et al., 2016). This increases the proportion of rainfall going immediately to the streams rather than infiltrating and being retained in the soils and may explain why we found a larger effect under dry antecedent conditions. Although forest cover decreases flood risk globally (Bradshaw et al., 2007), our results are consistent with those of previous studies conducted in Puerto Rico (Beck et al., 2013; Clark et al., 2017; Ramírez et al., 2009) that characterized peak flow as a rapid response to rainfall regardless of forest cover or drought conditions. High rainfall intensity paired with steep topography and poorly-transmissive upper soil layers (Harden & Scruggs, 2003; López et al., 1968) could explain why peak streamflow was not significantly reduced by increased forest cover. We addressed this possibility by scaling probability exceedance quantiles to watershed rainfall event characteristics in the FDC analyses, and by using both watershed regression intercept and evaluating dry and wet 30-day antecedent rainfall conditions separately in the statistical models. All the watersheds included in this study had at least 50% forest cover with limited (<15%) impervious surface related to urban development (NOAA, 2010). Because peak flows are highly influenced by impervious surface in a watershed (van Dijk et al., 2009), flood risk may increase dramatically in watersheds with less forest cover and more impervious surface.

4.3 | Limitations, uncertainties and other potential contributing factors

The use of MSWEP (a gridded product combining radar and gauge rainfall data) results in uncertainty in rainfall-streamflow relationships that may have affected our results. Rainfall in Puerto Rico is spatially variable, increasing with elevation and decreasing across a windward-leeward gradient (Murphy & Stallard, 2012b), and has been difficult to properly characterize (Murphy et al., 2017). In Puerto Rico and elsewhere, forests are often concentrated in topographically complex areas which are not well suited for development. Because rainfall at high elevation in tropical forests is difficult to measure due to high rainfall rates, wind, under-catch of small droplets and radar-to-precipitation conversion error (Beck et al., 2019; Murphy et al., 2017), the MSWEP data may underestimate high elevation watershed rainfall. The easterly trade winds also deliver additional small-droplet precipitation to high elevation windward watersheds in Puerto Rico that current rainfall data sets are unable to account for. (Scholl et al., 2021). These increase uncertainty in rainfall-streamflow relationships as well as the relationship between forest cover and streamflow in the analysis. However, linear mixed models should partially account for errors in rainfall estimates by including watershed-level random intercepts. The FDC analysis also examined streamflow quantiles normalized by rainfall event amount estimates to partially account for watershed differences in rainfall event amount. Further, we found similar relationships using Q10 and Q15 to represent peak flow in lieu of Q5, which indicates that we are appropriately characterizing peak flows. Our linear mixed models used the duration of rainless periods to predict low streamflow rather than rainfall amount, as MSWEP is more adept at detecting rainfall than estimating specific rainfall amounts (Beck et al., 2019). In contrast, potential underestimation of rainfall amount, particularly in highly forested watersheds, means that our estimates of the impact of forest cover on peak flow are more uncertain and using precipitation data sets with lower uncertainty, when these become available, would be a good direction for further study.

Factors not included in this study, such as soil infiltration capacity and land surface slope, could have an effect on streamflow values. Linear mixed models offer an advantage in streamflow modelling by accounting for hierarchical data structures and among-group variation, but the inability to include collinear fixed effects prevents the inclusion of other important predictors in the model. Topographic slope and watershed proportion of impervious surface are important predictors of the streamflow regime, but due to the high collinearity scores when these variables were included, they had to be excluded from the analysis (Zurr et al., 2009). The spatial pattern of impervious surface distribution within a watershed could play an important role in constraining surface streamflow to the stream channel (Gorokhovich, 2000; Gorokhovich et al., 2000), however, all watersheds studied were on steep, mountainous terrain with less than 15% impervious surface and mean watershed slope values of at least 11 degrees (Table 1). As all watersheds were relatively steep and largely undeveloped, the landscape component with the most variability across watersheds was forest cover proportion. To some extent, the recharge-enhancing functionality of forest cover may cut across these other factors.

Hydrologic soil group is also closely related to infiltration and runoff rates (USDA, 2009). Strong collinearity between watershed fraction of forest cover and watershed fraction of soil group B, BD and D prevented the inclusion of hydrologic soil group. However, interesting patterns between forest cover and infiltration rates can be inferred. We found a positive correlation between forest cover and groups B (moderate infiltration rate when wet, $r = 0.45$) and BD (moderate infiltration rate when wet if drained, very low infiltration rate when wet if not drained, $r = 0.61$) paired with negative correlation between forest cover D (very low infiltration rate when wet, $r = -0.76$). This indicates either that forests prefer soils with better infiltration, or they create them.

Catchment area and geology may also influence our results (Buss et al., 2013; McDowell et al., 2013; Xiao et al., 2019). Larger catchments with longer surface flow paths and higher subsurface storage may buffer the effects of rainfall on streamflow, particularly the effects of extremely high rainfall on peak flow. While there is moderate correlation between watershed forest cover and catchment area ($r = -0.55$), larger catchments do not appear to result in directional deviations from the regressions of FDC-derived summary values and forest cover based on visual interpretations (see Supplementary Information S1). We have also implicitly considered catchment area in the linear mixed models. By converting streamflow to specific discharge and including watershed-level random intercepts, we enable comparisons between watersheds of different sizes when evaluating the relationships between flow and forest cover. Agreement between the FDC and linear mixed model results indicates that this approach has captured important relationships between forest cover and streamflow extremes. However, 16 of the 20 watersheds selected for this analysis were underlain by volcanic geology, and the remaining 4 watersheds partially contained granitic rock, did not appear to be outliers within the regressions (see Supplementary Information S1). This suggests that selecting watersheds with a majority volcanic geology was enough to enable comparison of watershed forest cover while minimizing the potential effects of geology.

4.4 | Comparisons with previous findings in Puerto Rico

Previous studies examining the role of forest cover on streamflow in Puerto Rico found no clear relationships (Beck et al., 2013; Uriarte et al., 2011), or a negative relationship with total annual streamflow (Wu et al., 2007). In contrast, our results show forest cover correlated with several streamflow metrics. One possible explanation for the discrepancy with previous work is our chosen period of study. Beck et al. (2013) used a rainfall–runoff model approach and focused on streamflow from 1951 to 2000, while much of the forest cover in Puerto Rico was regenerating from early 20th century deforestation. By 2000, nearly all of the newly forested areas in Puerto Rico were at least 10 years old (Kennaway & Helmer, 2007). Further, cyclonic storms are a part of the normal rainfall regime in Puerto Rico and can cause substantial forest damage. Our study controlled for the potential effects of forest damage and regrowth on streamflow, as the last severe storm to make a direct landfall in Puerto Rico before our study period was Hurricane Georges in 1998. Although there is evidence that afforestation decreases streamflow (Bosch & Hewlett, 1982; Brown et al., 2013; Farley et al., 2005; Timbe et al., 2017) for up to five decades after forest establishment (Bentley & Coomes, 2020), mature forests tend to display more conservative water use strategies than regenerating forests (Giambelluca, 2002). Although Beck et al. (2013) did not find a consistent relationship between forest cover and total annual flows across all watersheds, 8 of the 12 watersheds in their study displayed decreases in low streamflow after forest regeneration. It is possible that our chosen period of study captured the stabilized rainfall-streamflow relationships after the bulk of forest regeneration (Filoso et al., 2017). Our results suggest that, with time and under specific climatic and geophysical conditions, recovering forests can increase infiltration and water storage enough to provide a buffer against drought conditions.

The contrasting results between this study and previous studies in Puerto Rico could also be due to the temporal scale of analysis. Our study used 15-min streamflow with 3-h rainfall and peak and low streamflow rather than mean daily data, the metric used by Uriarte et al. (2011), Beck et al. (2013), and Wu et al. (2007). This resulted in more accurate pairing of peak or low flow timing with preceding moisture conditions and more directly related watershed response to individual rain events. We conclude that in this rapidly responding wet-tropical system, mean daily streamflow estimates may be too low-resolution to characterize watershed behaviour.

Although global studies have shown increased forest cover generally decreases water yield, the distinct rainfall regimes in the tropics may result in different forest functions in tropical catchment hydrology than in temperate areas. A recent meta-analysis of studies examining the relationships of forest cover and annual water yield found that studies conducted in Central America have the highest regional rate of positive effects, followed by Asia and Africa (the Caribbean was not included as a region in that study) (Filoso et al., 2017). Similarly, other studies conducted in Central America on larger and heavily forested watersheds have also found positive relationships between low streamflow and forest cover (Krishnaswamy et al., 2018; Ogden et al., 2013). Central America has a humid tropical climate, with high annual rainfall and a reduction in rainfall seasonality over the last century (Feng et al., 2013), similar to Puerto Rico. The positive relationships between forest cover and streamflow in the watersheds we studied in Puerto Rico may be due to high rainfall inputs throughout the year and several factors; enhanced recharge through forest soils, high storage in the deep saprolite above bedrock (Kolb & Ryan, 2021), and steep topography. This is likely representative of other areas with similar topographic, climatic, and geological characteristics in this latitude range in the humid tropics.

5 | CONCLUSIONS

The goal of this study was to determine the effects of forest cover, rainfall, and their interactions on streamflow characteristics in Puerto Rico. To do so, we examined the effect of forest cover and rainfall over a period that included multiple high-intensity (as much as 19.5 mm per 3 h) and long (was as much as 571.7 mm over nearly 31 days) rainfall events, rainless periods from 12 h to 43 days, including a severe drought. Under both dry and wet antecedent rainfall conditions, we found that low streamflow was greater in watersheds with high forest cover than in less forested watersheds, indicating that forest cover moderated the impacts of drought on streamflow in Puerto Rico. Our results are consistent with those from a number of recent tropical studies (Bonell et al., 2010; Krishnaswamy et al., 2018; Ogden et al., 2013; Peña-Arancibia et al., 2019; Qazi et al., 2017) supporting the infiltration-evapotranspiration trade-off hypothesis (Bruijnzeel, 1989). Our findings suggest that on balance, tropical forests in these watersheds increase infiltration and groundwater recharge enough to "bank" water to offset evapotranspiration during dry periods, increasing resilience to a major drought during our study period. However, future rainfall deficits under expected increases in drought frequency across the Caribbean may test this relationship. We also found that forest cover had a positive effect on peak flows under both wet and dry 30-day antecedent rainfall conditions. This finding may be due to underestimation of rainfall for highly forested watersheds at high elevations, or slopes steep enough, and rainfall intense enough, that peak flow (Q5 or event-based peaks) was not affected by forest cover.

Our findings support the notion that forest cover in Puerto Rico regulates water provision and increases resilience to drought conditions by enhancing infiltration and storage of rainfall. However, this resilience may change under climate projections of increasing aridity and drought—the geology and subsurface structure is relatively invariant but the forest, which appears to be a fundamental part of routing water to storage, will be affected by drought. The drought threshold beyond which groundwater reserves become depleted is unknown. If future droughts are prolonged and the Caribbean experiences an overall drying trend, any advantages that forest cover provides may not persist and the relationship between increased forest cover and low flow values may eventually become negative. Future research to quantify climatic thresholds beyond which tropical forests would no longer provide a positive influence on streamflow would be very informative for water management decisions.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study were derived from the following resources available in the public domain: USGS streamflow, https://github.com/USGS-R/dataRetrieval; USGS NHD, https://www.usgs.gov/core-science-systems/ngp/national-hydrography; USGS geology, https://mrdata.usgs.gov/geology/pr/; and NOAA Puerto Rico Coastal Digital Elevation Model, https://www.ncei.noaa.gov. MSWEP rainfall data are available on request from GloH2O at http://www.gloh2o.org.

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SUPPORTING INFORMATION

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