

RESEARCH ARTICLE

Transient organic jams in Puerto Rican mountain streams after hurricanes

Ellen Wohl¹  | Sarah K. Hinshaw¹ | Julianne E. Scamardo¹ | Pablo E. Gutiérrez-Fonseca² 

¹Department of Geosciences, Colorado State University, Fort Collins, Colorado, USA

²Department of Environmental Sciences, University of Puerto Rico – Rio Piedras, San Juan, Puerto Rico

Correspondence

Ellen Wohl, Department of Geosciences, Colorado State University, Fort Collins, CO 80523-1482.

Email: ellen.wohl@colostate.edu

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Abstract

Extreme storms in forested environments commonly increase inputs of coarse particulate organic matter (CPOM) and large wood (LW) to streams. Protruding boulders and bedforms, mid-channel bars, and standing trees can trap CPOM and LW. These organic accumulations can become large enough to span the bankfull channel width, or the accumulations can be predominantly along the channel margins. We refer to both types of accumulations as transient organic jams (TOJs). TOJs can create diverse geomorphic and ecological effects in channel and floodplain environments. We use data collected from mountain streams of the Luquillo Mountains of north-eastern Puerto Rico following September 2017 Hurricanes Irma and Maria. We examine the location, characteristics, and geomorphic effects of TOJs in channel segments representing diverse drainage areas and channel gradients. We ask three questions: (a) Does the downstream spacing of TOJs correlate with variables such as drainage area or channel gradient? (b) What variables best predict the volume of organic matter within individual TOJs or within a channel segment? And (c) is there a threshold within a river network that separates channel segments with channel-spanning versus marginal TOJs? Datasets include multiple TOJs along each of 12 stream segments and presence/absence of channel-spanning TOJs along an additional six streams. Data analysis with multiple linear regressions indicates that downstream spacing, average volume, and total volume per channel length of TOJs correlate significantly with bankfull channel width. Using the akaike information criterion with correction (AICc) model selection method, Strahler stream order has the most influence on the probability of TOJs being marginal or spanning.

KEYWORDS

coarse particulate organic matter, hurricane, large wood, mountain stream, tropics

1 | INTRODUCTION

Extreme storms in forested environments commonly create increased inputs of coarse particulate organic matter (CPOM; >1 mm in diameter) and large wood (LW; >10-cm diameter and 1-m length) to streams (e.g., Kraft, Schneider, & Warren, 2002; Phillips & Park, 2009). Increased CPOM inputs during storms result from the combined effects of high winds or torrential rains that damage the forest canopy; overland run-off that mobilizes leaf litter; failure of hillslopes adjacent to channels; and mobilization of CPOM and LW stored within

the channel prior to the storm (Benson & Pearson, 1993; Covich, Crowl, Johnson, Varza, & Certain, 1991; Gomi, Sidle, & Richardson, 2002). Increased LW inputs result from individual tree topple, hillslope failure, and accelerated bank erosion associated with rainfall-run-off peak flows (Phillips & Park, 2009; Reeves, Burnett, & McGarry, 2003). The transport or deposition of this storm-generated CPOM and LW depends on factors such as the duration of the storm hydrograph and the depth of peak flow relative to features that protrude along the channel bed and banks and create at least temporary storage sites.

In mountain streams, features that can trap CPOM and LW include protruding boulders, mid-channel bars, standing trees on forested islands and along the channel banks, and bedforms such as steps (Small, Doyle, Fuller, & Manners, 2008; Wohl, 2017). Although protruding boulders and step-pool or pool-riffle bedforms can create flow separation and localized temporary storage of CPOM and LW, the trapping of CPOM and LW can enlarge the extent of flow separation. Essentially, CPOM and LW storage can initiate a self-enhancing feedback in which an enlarging backwater traps more organic material and, in some cases, bedload (Beckman & Wohl, 2014; Wohl & Scott, 2017). These organic accumulations can become so large that they span the bankfull channel width and create a temporary dam and associated backwater pool habitat. The persistence of a dam during and after the storm hydrograph presumably reflects the combined effects of the dimensions of the trapping feature (e.g., protruding boulder) relative to flow depth; the size and abundance of organic matter that is trapped and the associated porosity and permeability of the jam; the local changes in velocity and transport capacity created by trapping of organic matter; and the hydrograph during the storm (rate of rise and fall, magnitude, and duration) and during subsequent flows. We designate these accumulations of LW and CPOM, which may persist for less than a year, as transient organic jams (TOJs).

TOJs are of interest because of their potential geomorphic and ecological effects in channel and floodplain environments. An extensive literature documents the geomorphic effects of LW, which is an important component of the TOJs we describe in this paper. The effects of LW range from local in scale, such as focused erosion and deposition associated with altered flow velocity and shear stress, to reach-scale effects on channel planform and channel-floodplain connectivity. LW increases flow resistance via form roughness and flow obstruction (Curran & Wohl, 2003; Wilcox, Wohl, Comiti, & Mao, 2011). Enhanced pool volume results from bed scour and backwater effects associated with LW (Chen, Wei, Scherer, & Hogan, 2008; Richmond & Fausch, 1995). LW facilitates sediment deposition, increased sediment storage, and greater heterogeneity of channel substrate (Buffington & Montgomery, 1999; Massong & Montgomery, 2000; Wohl & Scott, 2017), as well as altering the type and magnitude of bedforms (Gomi, Sidle, Woodsmith, & Bryant, 2003; Keller & Tally, 1979). LW can increase bank erosion and channel avulsion (Abbe & Montgomery, 2003; O'Connor, Jones, & Haluska, 2003; Wohl, 2011), and LW can increase channel-floodplain (Jeffries, Darby, & Sear, 2003; Sear, Millington, Kitts, & Jeffries, 2010) and channel-hyporheic zone connectivity (Sawyer, Cardenas, & Buttle, 2012). Ecological effects of LW include storage of CPOM that supports the food web in forested streams (Beckman & Wohl, 2014; Bilby & Likens, 1980; Daniels, 2006); enhanced volume and diversity of aquatic habitat (Gurnell, Tockner, Edwards, & Petts, 2005); and enhanced floodplain habitat (Harmon et al., 1986; Steel, Richards, & Kelsey, 2003).

Stream ecologists focus on the dynamics of CPOM because of the importance of this material as an energy source in shaded streams (e.g., Webster et al., 1999), but geomorphologists have paid less attention to organic matter smaller than LW. However, CPOM trapped with LW can substantially influence the geomorphic and

hydraulic effectiveness of LW jams by plugging interstices between LW pieces and decreasing the porosity and permeability of the jam (Manners, Doyle, & Small, 2007). In small streams, an entire channel-spanning jam can also be composed of organic matter smaller than LW. The greater ratio of surface area to volume of CPOM relative to LW suggests that CPOM will decay and breakdown more rapidly than LW, but CPOM that persists through a single flood or for longer periods may create important geomorphic effects.

Smaller streams in high-relief environments typically have multiple characteristics that can result in channel-spanning accumulations of organic matter. Intense precipitation and flashier hydrographs (e.g., Patton & Baker, 1976; Saharia, Kirstetter, Vergara, Gourley, & Hong, 2017) can result in short-duration but high-magnitude pulses of CPOM into and along the channel (Turowski et al., 2013). A wide range of grain sizes that includes large, protruding boulders (Livers & Wohl, 2015; Montgomery & Buffington, 1997) creates obstacles and traps material in transport. Narrow channels can be completely spanned by individual pieces of LW (Gurnell, Piegay, Swanson, & Gregory, 2002). High-amplitude steps and pools can trap organic matter at the gradient inflection of step lips (Wohl & Merritt, 2008). Consequently, channel-spanning accumulations of organic matter might be expected to form in smaller streams. Larger, lower gradient mountain streams with at least limited floodplains and overbank flows might facilitate trapping of organic matter along channel margins, as CPOM and LW in transport leave the main channel and move into the hydraulically rougher floodplain, where the trunks of standing trees form effective traps for LW in transport.

These considerations lead us to propose that a threshold exists based on the combined effects of drainage area and channel gradient. This threshold separates streams in which organic matter accumulations formed during extreme storms span the channel from streams in which organic matter accumulations are localized and marginal rather than channel-spanning. Drainage area here is a proxy for discharge, and channel gradient is a proxy for channel and valley geometry and grain size: Steep gradients correspond to coarse-grained channels with step-pool bedforms, protruding boulders, and narrow valley bottoms (Livers & Wohl, 2015; Montgomery & Buffington, 1997).

We test this idea using data collected from mountain streams of the Luquillo Mountains of north-eastern Puerto Rico following Hurricanes Irma and Maria in September 2017. We examine the location, characteristics, and geomorphic effects of TOJs in channel segments representing a range of drainage areas and channel gradients. We ask three questions: (a) Does the downstream spacing of TOJs correlate with variables such as drainage area, stream power, or channel gradient? (b) What variables best predict the volume of organic matter within individual TOJs or within a channel segment? (c) Is there a threshold within a river network that separates channel segments in which TOJs are predominantly channel-spanning (Figure 1a) from channel segments in which TOJs are predominantly smaller than the bankfull channel width (Figure 1b)? And (d) how do spatial variations in underlying lithology and associated channel morphology affect CPOM and LW retention?



FIGURE 1 Examples of transient organic jams in the study area. (a) Example of a channel-spanning transient organic jam (TOJ) with upstream fine sediment accumulation, Quebrada Prieta. TOJ is approximately 1.2-m tall, and flow is towards the rear of the photo. (b) Example of marginal TOJs along the Rio Espiritu Santo [Colour figure can be viewed at wileyonlinelibrary.com]

2 | STUDY AREA

The study area is within the Rio Espiritu Santo (92 km²), Rio Blanco (72 km²), and Rio Mameyes (44 km²) drainages of the Luquillo Mountains in north-eastern Puerto Rico (Figure 2). The mountains rise from sea level to over 1,000 m in elevation over a distance of 15–20 km, resulting in relatively short, steep watersheds. Early Tertiary volcanism and uplift associated with island-arc subduction formed the Luquillo Mountains. Much of the study area is underlain by volcaniclastic rocks and lava units that are complexly faulted and steeply tilted (Briggs & Angular-Cortes, 1980; Seiders, 1971). The southern portion of the study area, within the Rio Blanco drainage, is underlain by a Tertiary granodiorite batholith that is eroding rapidly (Brown, Stallard, Larsen, Raisbeck, & Yiou, 1995; White et al., 1998). Erosionally resistant contact metamorphic rocks surrounding the granodiorite form steep cliffs and create local base levels for portions of the river network upstream from these units (Pike, Scatena, & Wohl, 2010), resulting in much lower stream gradients than occur at similar elevations underlain by the volcaniclastic units. These low-gradient stream reaches have sand

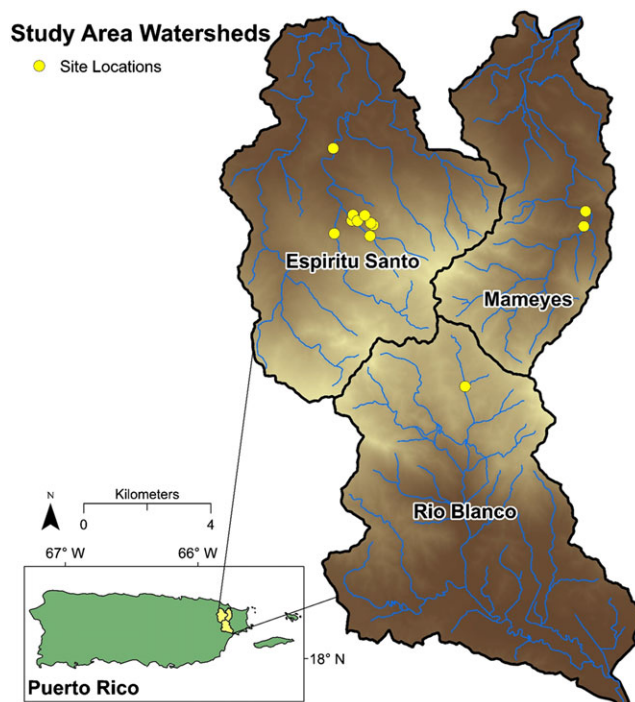


FIGURE 2 Location map of the study areas in north-eastern Puerto Rico. Major drainage basins in which study sites were located are labelled [Colour figure can be viewed at wileyonlinelibrary.com]

and fine gravel substrate, in contrast to the predominantly boulder substrate of the volcaniclastic streams.

The Luquillo Mountains have a humid subtropical maritime climate influenced by north-easterly trade winds and local orographic effects that create steep gradients in precipitation (Pike et al., 2010). Mean annual precipitation increases from 1,500 mm at the coast to >4,500 mm at elevations above 1,000 m (Garcia-Martino, Warner, Scatena, & Civco, 1996). Convective storms, easterly waves, cold fronts, and tropical storms affect precipitation and temperature (van der Molen, 2002), and high-intensity rainfall and floods can occur in any month. Hurricanes and tropical storms are common from August through October, with daily rainfalls typically in excess of 200 mm (Heartsill-Scalley, Scatena, Estrada, McDowell, & Lugo, 2007). The maximum recorded daily rainfall exceeds 600 mm (Scatena & Larsen, 1991).

Streams in the Luquillo Mountains are flood-dominated channels similar to those of montane environments in the Greater Antilles and regions along active tectonic zones in the humid tropics (Ahmad, Scatena, & Gupta, 1993; Gupta, 1988). Peak flood discharges can be 1,000 times greater than baseflow (Pike et al., 2010). Baseflow unit discharge is 0.02 m³ s⁻¹ km⁻², but the highest peak unit discharge recorded at a stream gage in the region is 19.7 m³ s⁻¹ km⁻² (Pike et al., 2010). Peak flows are very flashy, with a duration typically less than an hour, and streams return to baseflow within 24 hr of large flood peaks (Pike et al., 2010; Figure 3).

Our study areas are within the Luquillo Experimental Forest, a 113-km² protected forest reserve managed by the U.S. Department of Agriculture Forest Service. Watersheds drain protected primary forest in the upper elevations and mature secondary forest at mid-elevations. The Colorado forest, dominated by *Cyrilla racemiflora*,

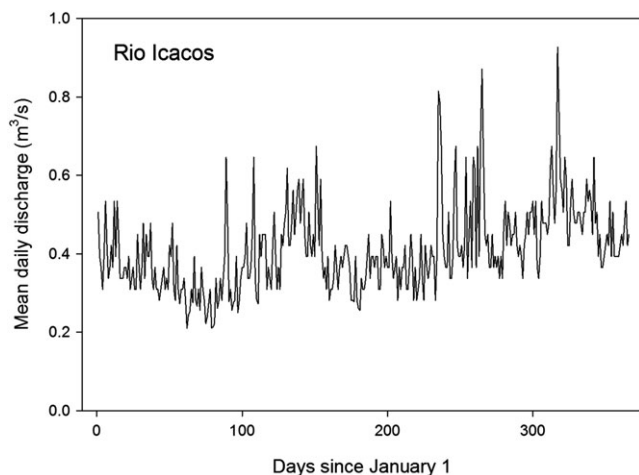


FIGURE 3 Mean daily discharge for U.S. Geological Survey gage 50075000 on the Rio Icacos near Naguabo (drainage area 3.3 km²) during the period 1944–2017

grows at mid-elevations (600–900 m), and areas underlain by granodiorite (Scatena, Doherty, Odum, & Kharecha, 2002). The palm forest, dominated by the native mountain palm *Prestoea montana*, typically grows on poorly drained sites. The tabonuco forest, dominated by *Dacryodes excelsa*, grows in lower elevation (100–600 m) sites.

Hillslopes exceed 30° in many headwater areas, and hillslopes and channels are strongly coupled (Scatena & Lugo, 1995). Landslides deliver much of the sediment that enters channels (Larsen, Torres-Sánchez, & Concepción, 1999; Simon & Guzman-Rios, 1990). Because of the high fluvial transport capacity, little fine sediment is present in channels, despite the deeply weathered bedrock, thick saprolite, and abundant clay present on the hillslopes (Frizano, Johnson, Vann, & Scatena, 2002; Schellekens et al., 2004). Landslides also deliver very large boulders to the channels (Larsen, 1997). First-order channels in the volcanoclastics include both small, ephemeral streams and perennial streams dominated by boulders (Scatena, 1989; Schellekens et al., 2004). Second- and third-order channels feature high gradients, exposed bedrock, matrices of large boulders with finer sediment in the interstices, and periodic waterfalls that can reach 30 m in height (Pike et al., 2010). Bedforms at the study sites are predominantly cascade or step-pool, with pool-riffle bedforms at a few sites. Pool-riffle sequences occur at lower elevations, larger drainage areas, and low-gradient stream reaches underlain by granodiorite. If hurricanes and associated landsliding have not occurred recently, the channels lack LW and coarse organic material (Covich et al., 1991; Pike et al., 2010).

Hurricanes pass over Puerto Rico every 21 years on average and pass over the Luquillo Experimental Forest every 50–60 years (Scatena & Lugo, 1995). The frequency of these events is among the highest in the North Atlantic Basin (Neumann, Jarvinen, & Pike, 1987). Boose, Serrano, and Foster (2004) used historical records to estimate average return intervals for hurricanes. F0 damage (loss of leaves and branches) and F1 damage (scattered blowdowns and small gaps) on the Fujita scale occur every 4 and 6 years, respectively. Average return intervals for F3 damage (forests levelled) in the Luquillo Experimental Forest are 50 to 150 years, but actual forest damage depends on land use history and the effects of recent hurricanes

(Boose et al., 2004). The most recent severe hurricane to affect the study area prior to 2017 was Hurricane Hugo in September 1989. Hugo caused F3-level damage in the study area. Post-hurricane studies recorded rapid regeneration of canopy cover but slower recovery of fine litterfall over the succeeding 5 years (e.g., Zimmerman, Willig, Walker, & Silver, 1996).

Covich et al. (1991) documented the formation of TOJs along Quebrada Prieta and inferred that the jams increased retention of food resources and limited washout of invertebrate consumers. These TOJs persisted for more than 8 months after Hugo. Leaves within the TOJs were slowly removed by streamflow, allowing microbially conditioned leaf detritus to move downstream relatively continuously, with pulses of leaf and woody material moving downstream during infrequent, low-intensity rains (Covich et al., 1991).

Pyron, Covich, and Black (1999) examined the effect of wood additions on shrimp populations in a small Luquillo stream. The numbers of shrimp increased with pool size, but wood additions had no effect on numbers of shrimp per pool area, presumably because the numerous crevices among large boulders supplied sufficient habitat structure for the shrimp. Wood may, however, be important during the brief window following a hurricane when crevice habitat is reduced by siltation.

Hurricane Irma did not directly hit the main island of Puerto Rico, but it did pass nearby, creating rainfall totals of 2,540 to 3,810 mm over high elevations in the central part of the island between September 5 and 7, 2017 (Cangialosi, Latta, & Berg, 2018). The highest recorded wind speed associated with Irma was 80.5 km hr⁻¹ at the San Juan airport on September 6, 2017 (Cangialosi et al., 2018). Hurricane Maria crossed Puerto Rico from south-east to north-west during the course of several hours on September 20, 2017, with winds of 175 to 250 km hr⁻¹ (Pasch & AB Penny, 2018). Both Irma and Maria caused extensive damage to the forest canopy, and Maria caused severe flooding in parts of Puerto Rico, although not in the study area. The occurrence of two hurricanes within a short timespan provided an opportunity to document the effect of these disturbances on CPOM and LW accumulations in the Luquillo streams.

3 | METHODS

3.1 | Field methods

Our study design focuses on channel reaches, defined here as a continuous length of channel with consistent gradient and bedform type. We surveyed 12 channel reaches in the field and noted the presence or absence of channel-spanning TOJs in the vicinity of a trail or road access point to the stream at an additional six sites. Global Positioning System (GPS) location was noted for all 18 sites.

The length of each channel reach that we surveyed was at least 10× bankfull width. Within each reach, we surveyed downstream channel length and gradient using a TruPulse 360B laser rangefinder (±0.1 m accuracy) between successive TOJs. At each TOJ, we surveyed bankfull channel width, valley-bottom width, bankfull depth, and angle of valley side slope. We recorded categories for bedforms (cascade, step-pool, riffle-run, and pool-riffle), substrate (gravel, cobble, boulder,

and bedrock), forest (palm or mixed palm-hardwood forest), and hurricane damage to the forest canopy (minimal <10%, moderate 10–50%, and extensive >50% canopy defoliation), as well as noting whether hillslope failures were present at or upstream from the TOJ. We mapped the location of each TOJ using a handheld GPS unit (typically ± 3 m horizontal accuracy) and photographed the TOJ. We measured the dimensions of LW pieces within the TOJ. For TOJs composed of CPOM, we measured the bounding dimensions (height, width, and length), visually estimated porosity to the nearest 10% (range 20–80%), and calculated the resulting volume. We also noted the presence of features associated with the TOJ: CPOM stored outside of the TOJ; bed aggradation; change in bed grain size; bank erosion; and formation of a backwater pool or vertical bed step.

Field-recorded GPS locations were used to calculate contributing drainage area at the downstream end of each channel segment. We used stream gage records from five U.S. Geological Survey sites that correspond to our field areas to evaluate the stream flows associated with the 2017 hurricanes, as well as longer term records of peak and base flows in the field area. We estimated bankfull discharge for each river segment using a relation from Pike et al. (2010):

$$Q = DA(0.0042E_{\text{avg}} + 0.406) \quad (1)$$

in which Q is the bankfull discharge ($\text{m}^3 \text{s}^{-1}$), DA is the drainage area (km^2), and E_{avg} is the average upstream elevation (m). This relation was developed for the watersheds in which we conducted field work.

Stream order was derived for each reach using a stream network created from digital elevation models (DEMs) of north-eastern Puerto Rico. DEMs were downloaded from the U.S. Geological Survey National Map at a 1/3 arc-second resolution (<https://nationalmap.gov/>). A stream network was created using a threshold drainage area of 0.5 km^2 and the *STREAMObj()* function in MATLAB TopoToolbox 2.2 (Schwanghart & Scherler, 2014). Threshold drainage area was chosen by trial and verified using known stream orders for the Prieta and the Sonadora from the literature (Covich et al., 1991; Pike et al., 2010). Stream order was then exported to a shapefile where reach coordinates could be used to determine reach order in ArcGIS 10.4.

3.2 | Statistical methods

We fit linear regression models to the data on TOJ spacing, TOJ average volume, and TOJ total volume per channel length to determine whether the occurrence and size of TOJs could be predicted by physical reach characteristics (Ott & Longnecker, 2016). Independent (predictor) variables considered in the model were drainage area, channel gradient, discharge, total stream power (product of bankfull discharge and reach-average channel gradient), bankfull width, cross-sectional area, and Strahler stream order. We modelled TOJ spacing, TOJ average volume, TOJ total volume per channel length, and reach predictor variables as reach averages. We checked the residuals of each model to verify that the model assumption of homoscedasticity was met. Variables that did not meet the model assumption of normality were natural log transformed: drainage area, discharge, stream power, and cross-sectional area. All response variables—TOJ spacing, average volume, and volume per channel

length—were also natural log transformed to meet model assumptions. Full models were created for the three response variables that included all predictor variables using the *lm()* function in R. The significance of each predictor variable in each model was tested at $\alpha = 0.05$ to determine which predictor variables have explanatory power.

The odds of having a channel-spanning TOJ were calculated using a logistic regression of all surveyed TOJs (Ott & Longnecker, 2016). Individual data points were used instead of reach averages in order to account for reaches that had both channel-spanning and marginal TOJs. The binomial event was defined as having a channel-spanning jam. Predictor variables used in the logistic regression include Strahler stream order, slope, and bankfull width. A full logistic regression model was created using the *glm()* function in R. The significance of each predictor variable in the model was tested at $\alpha = 0.05$.

4 | RESULTS

The dataset consists of 12 surveyed stream segments (Table 1) and an additional six sites at which we noted channel-spanning TOJ presence or absence. In total, we surveyed 97 TOJs.

4.1 | Predictors of TOJ characteristics

Bankfull width was the only significant predictor of TOJ average volume (Figure 4). Six out of seven predictor variables were significant in the TOJ spacing model, and two out of seven predictor variables were significant in the total TOJ volume per channel length model (Table 2). AICc was used for selection of model variables in the TOJ spacing and total TOJ volume models, where the model with the lowest AICc—which was also based on bankfull width—was chosen as the final model (Hurvich & Tsai, 1989). Model selection was performed using the *dredge()* function in the MuMIn R package, resulting in the following empirical equations for TOJ spacing, average volume, and total volume:

$$\log(TOJ_{\text{sp}}) = 0.099W_{\text{bf}} + 1.934, \quad (2)$$

$$\log(TOJ_{\text{vol}}) = 0.0825W_{\text{bf}} + 1.299, \quad (3)$$

$$\log(TOJ_{\text{totvol}}) = -0.58 \log(Q) + 0.14(W_{\text{bf}}) - 2.78, \quad (4)$$

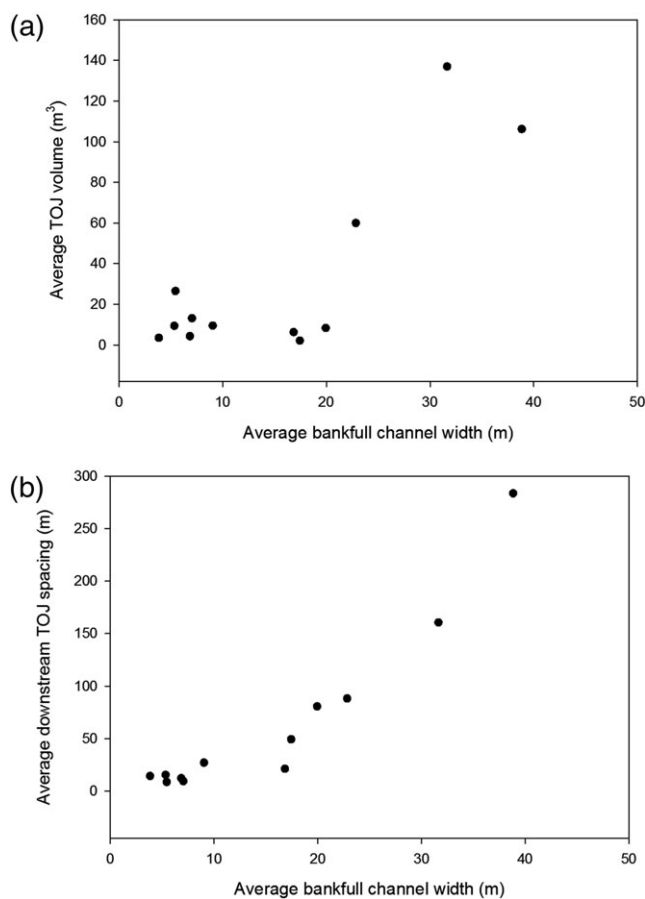
where TOJ_{sp} is the downstream spacing of TOJs, TOJ_{vol} is the average volume of TOJ, TOJ_{totvol} is the total volume per channel length, and W_{bf} is the bankfull channel width. The r^2 value for the spacing, average volume models, and total volume models were 0.89, 0.40, and 0.89, respectively. With respect to the first two research questions, all three response variables correlate significantly with channel bankfull width (Figure 4). TOJ total volume per channel length also correlates significantly with discharge, as does TOJ spacing (Table 2).

Using a logistic regression, Strahler stream order was the only significant predictor of whether a TOJ would be spanning or marginal (Table 3). In first-order streams, there is a 91.8 to 1 odds ratio that a TOJ is marginal versus channel spanning. In second-order streams,

TABLE 1 Summary characteristics of stream segments

Reach	A (km ²)	S (m m ⁻¹)	avg W_{bf} (m)	avg D_{bf} (m)	Total power (W m ⁻²)	Stream order	Reach L (m)	Avg TOJ spacing (m)	Spacing/bfw	Avg TOJ vol (m ³)	TOJ load (m ³ ha ⁻¹)	Channel spanning
Toronja	0.2	0.11	3.9	0.8	0.04	1	178	13.7	3.5	3.2	608	y
Prieta A	0.03	0.15	5.4	0.9	0.02	1	221	14.8	2.7	9.1	1,140	y
Prieta B	0.2	0.18	6.9	1.0	0.02	1	132	11.6	1.7	4.0	574	y
Prieta C	0.01	0.20	7.1	0.8	0.004	1	121	8.8	1.2	12.8	2,224	y
Prieta	0.3	0.18	9.1	1.2	0.13	2	451	26.4	2.9	9.2	361	Mixed
Sonadora 1	2.6	0.22	22.9	2.7	1.76	3	414	87.6	3.8	59.7	189	n
Sonadora 2	2.9	0.26	16.9	1.9	2.24	3	358	20.6	1.2	6.0	180	n
E. Santo 1	5.8	0.24	20.0	3.0	4.66	4	400	80.0	4.0	8.0	40	n
E. Santo 2	15.7	0.05	17.5	1.6	1.9	4	222	48.7	2.8	1.8	46	n
Icacos	3.3	0.02	5.5	1.0	0.21	3	320	80.0	14.5	26.2	597	y
Mameyes 1	18.9	0.03	31.7	2.0	1.46	5	320	160	5.0	136.7	263	n
Mameyes 2	18.7	0.02	38.9	2.0	0.96	5	393	283	7.3	105.9	385	n

Note. A is the drainage area; S is the bankfull channel gradient; avg W_{bf} is the average bankfull channel width; avg D_{bf} is the average bankfull channel depth; Reach L is the reach length; Spacing/bfw is the ratio of average TOJ downstream spacing to bankfull channel width; avg TOJ vol is the average volume of TOJs in reach; TOJ load is the m³ of material per hectare of channel surface; y indicates channel-spanning TOJs are present; and n indicates they are not. TOJ: transient organic jam.

**FIGURE 4** Relationship between bankfull channel width and (a) transient organic jam (TOJ) volume and (b) TOJ downstream spacing. Each point represents an average value for each of the study reaches

there is a 1 to 5.24 odds ratio that a TOJ is marginal. From these odds ratios, it is evident that TOJs are more likely to be channel spanning in first-order streams and marginal in higher order streams. Thus, with

TABLE 2 Reach-averaged predictor variables used in multiple linear regression of TOJ volume and TOJ spacing

	Spacing	Average volume	Total volume per channel length
	<i>p</i> value (F statistic)	<i>p</i> value (F statistic)	<i>p</i> value (F statistic)
Drainage area (km ²)	0.006122 (11.97)	0.2454 (1.523)	0.2974 (1.208)
Slope (m m ⁻¹)	0.422 (0.7005)	0.2827 (1.289)	0.7863 (0.077)
Discharge (cms)	0.005765 (12.22)	0.2 (1.883)	0.0000105 (43.75)
Stream power (W m ⁻²)	0.007796 (11)	0.4043 (0.7582)	0.271 (1.358)
Bankfull width (m)	0.000001679 (98.82)	0.01595 (8.386)	0.0000108 (43.75)
Cross-sectional area (m ²)	0.00005494 (44.63)	0.08633 (3.618)	0.7208 (0.135)
Stream order	0.0005887 (24.39)	0.06946 (4.133)	0.7427 (0.1139)

Note. Bolded values are significant at $\alpha = 0.05$.

TOJ: transient organic jam.

respect to the third research question, stream order appears to provide a threshold for differentiating portions of a river network with and without channel-spanning TOJs.

4.2 | Differences in TOJs in relation to channel morphology

Because we have only one study reach in a stream underlain by granodiorite (Icacos), we cannot statistically compare TOJ characteristics in relation to channel morphology as influenced by underlying lithology. Given the strong correlation between bankfull channel width and

TABLE 3 Summary of predictor variables for logistic regression for channel-spanning or marginal TOJs

	Channel-spanning response <i>p</i> value
Slope (m m^{-1})	0.05798
Bankfull width (m)	0.137717
Stream order	0.000118

Note. Bolded values are significant at $\alpha = 0.05$.

TOJ: transient organic jam.



FIGURE 5 Example of individual pieces of large wood partly buried in the bed of the Rio Icacos in the study reach. The pieces are oriented parallel to stream, and each is approximately 12 cm wide. Note the dispersed coarse particulate organic matter between the logs [Colour figure can be viewed at wileyonlinelibrary.com]



FIGURE 6 Example of backwater sedimentation upstream from a transient organic jam, now dissected, along Quebrada Prieta A. Channel here is approximately 4.5 m wide, and dissected channel fill is approximately 0.5 m thick. Flow is right to left [Colour figure can be viewed at wileyonlinelibrary.com]

TOJ characteristics for the entire dataset, we qualitatively compare the Prieta A and B sites (Table 1) to the Icacos site because of the similarity in bankfull width values among these sites. The Icacos has larger (26 vs. 9 and 4 m^3) but much more widely spaced (80 vs. 11.6 and 14.8 m) TOJs and a comparable TOJ load (597 vs. 1,140 and 574 $\text{m}^3 \text{ha}^{-1}$). The Icacos also has many more individual, dispersed LW pieces, many of which are at least partially buried in the streambed (Figure 5). Together, the volume of dispersed pieces and the TOJs equate to 659 $\text{m}^3 \text{ha}^{-1}$.

5 | DISCUSSION AND CONCLUSIONS

The strong correlation between bankfull channel width and the downstream spacing and volume of TOJs likely reflects the combined effects of transport capacity and trapping potential. Individual LW pieces are more likely to span narrower channels and be pinned against the upstream side of trees along the channel banks or against boulders that protrude farther into the relatively shallow flow of a small stream. Once trapped, LW pieces may facilitate the trapping of smaller, organic material and sediment. As channel width increases as a function of increasing drainage area and discharge, the greater flow depth and velocity likely limit formation of TOJs except along the channel margins, where flow entering the floodplain becomes shallower and encounters greater hydraulic roughness. The much larger ratio of TOJ spacing to bankfull width along the Rio Icacos (Table 1) may reflect the lack of protruding boulders or living upright trees within the bankfull channel. The absence of boulders and upright trees in this sand-bed channel likely reduces the number of potential trapping sites for TOJ formation.

The predominance of channel-spanning TOJs where bankfull channel width is ≤ 10 m on first-order streams (channel width tends to be greater in the tropics than in many temperate-latitude streams), as observed at the Luquillo sites, contrasts strongly with analogous patterns relative to stream order in mountain streams of the temperate zone. Studies from sites in North America suggest that channel-spanning jams and wood load per unit area reach a maximum in third- to fourth-order channels in which bankfull channel width is in the range of 5–20 m (Pfeiffer & Wohl, 2018; Wohl & Scott, 2017), although CPOM storage per unit area may be greatest in first-order channels (Pfeiffer & Wohl, 2018). In other words, the bankfull channel widths in which channel-spanning jams are most likely to form are comparable between tropical and temperate environments, although these widths occur at smaller drainage areas and lower stream orders in the tropics because of the greater discharge per unit drainage area.

The flashier hydrograph and faster rates of wood decay in tropical environments likely limit the persistence of channel-spanning jams through time. A survey of 30 stream reaches in Costa Rica (Cadot, Wohl, Goode, & Jaeger, 2009), for example, found only seven channel-spanning jams, most of which occurred in stream reaches with bankfull width ≤ 10 m. These jams either disappeared or changed substantially during 3 years of observation (Cadot & Wohl, 2011). Comparisons of sites in Panama and Costa Rica suggest that tropical streams with bankfull widths > 10 m are most likely to have

channel-spanning jams only in close proximity to a large landslide that abruptly introduces substantial quantities of LW to a channel, although these jams are transient on timescales of a few years (Wohl et al., 2012; Wohl, Ogden, & Goode, 2009). The lack of large landslides close to the stream reaches in the Luquillo study sites may help to explain the absence of channel-spanning TOJs on the larger streams.

Both marginal and channel-spanning TOJs create important geomorphic and ecological effects during a period of weeks to years following a hurricane in the Luquillo Mountains. As observed after Hurricane Hugo, channel-spanning TOJs can store fine sediment and thus attenuate the downstream fluxes of sediment derived from landslides and other upland sources (Gellis, 1993; Figure 6). The efficiency of CPOM incorporation into the food web of a stream segment is directly related to how long leaf litter remains in the segment and is available for consumption by microbes and detritivores (Bilby & Likens, 1980). Investigations in small, steep streams of the temperate zone suggest that LW can retain substantial quantities of CPOM (e.g., Beckman & Wohl, 2014; Small et al., 2008; Webster, Covich, Tank, & Crockett, 1994), although the CPOM may not be retained through successive floods, as it is in bank storage sites (Small et al., 2008). The lack of CPOM retention through successive floods in the Small et al. (2008) study likely reflects the fact that only single pieces of LW were included in the study. Investigations of channel-spanning LW jams with visually estimated porosity and permeability values similar to those of the Luquillo TOJs suggest that CPOM can be retained through a snowmelt flood peak that lasts for more than a week (e.g., Beckman & Wohl, 2014; Livers & Wohl, 2016) and that first-order streams can have the highest CPOM storage per unit area in a stream network (Pfeiffer & Wohl, 2018), although comparable data are not available for temperate-zone, rainfall-dominated streams. The continuing retention of CPOM in TOJs may be particularly important in the study area given the observed decreases in fine litterfall following a hurricane that damages the forest canopy (Zimmerman et al., 1996).

Marginal TOJs can create cover, substrate diversity, and nutrient sources in backwaters or pools and along the channel-floodplain boundary. Marginal TOJs emplaced high above the channel (Figure 1b), in particular, may be more likely to decay in place and provide nutrients to floodplain soils, rather than being remobilized. Examining soils underlying decaying wood in Puerto Rico, Zalamea, Gonzalez, Ping, and Michaelson (2007) and Zalamea, Gonzalez, and Lodge (2016) found less variable soil temperature, greater soil organic matter, more fulvic and humic acids, higher %C, and higher C : N ratios under decaying logs than in adjacent soils, although the stage of decay exerted an important influence on observed patterns.

Given the well-developed downstream hydraulic geometry relations in the study area (Pike et al., 2010), bankfull channel width can be predicted from drainage area. With an accurate DEM or topographic map, Strahler stream order is also easily determined. Consequently, the type (channel-spanning vs. marginal), downstream spacing, and volume of TOJs resulting from future hurricanes in the study area can likely be predicted with reasonable accuracy. This type of relationship is also likely to be present in other mountain streams with periodic disturbances (e.g., Fox & Bolton, 2007; Webster et al., 1994), particularly tropical streams subject to hurricanes.

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ORCID

Ellen Wohl  <https://orcid.org/0000-0001-7435-5013>

Pablo E. Gutiérrez-Fonseca  <https://orcid.org/0000-0003-0777-8889>

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