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Comparison of discharge pulses in temperate and tropical rainforest headwater stream networks

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ABSTRACT

We use sub-daily gage records from montane headwater channels in the Luquillo Experimental Forest of Puerto Rico (tropical rainforest) and the HJ Andrews Experimental Forest of Oregon (temperate rainforest) to characterize differences in discharge pulses (rapid, high-magnitude discharge fluctuations) and determine whether the characteristics of discharge pulses differ with respect to drainage area between these two regions. The study sites have different precipitation regimes and runoff generation mechanisms, and we quantify differences in discharge pulses between sites. The assessment of discharge pulses, which are defined as flows that are higher than one standard deviation above the historical mean flow at each site, represents a novel approach to characterizing flashy discharge events in headwater streams using high temporal resolution datasets. Our analyses indicate a clear difference between regions, with discharge in the Luquillo streams pulsing more frequently, for shorter periods of time, and at higher magnitudes than discharge in the Andrews streams. We also quantify how discharge pulses change with increasing drainage area at each of the sites. Differences in discharge pulse metrics with respect to drainage area include an increase in the number of pulses, an increase in the normalized magnitude of pulses, an increase in the standard deviation in normalized magnitude, and a decrease in kurtosis with increasing drainage area at the Luquillo site. These results indicate that there is no attenuation of discharge pulses with increasing drainage area at Luquillo. In contrast, there is a decrease in the normalized magnitude with increasing drainage area at the Andrews site, indicating some attenuation of discharge pulses with increasing drainage area. The characteristics of these pulsed events have implications for ecological processes by transporting sediment, biota, and organic matter, likely altering stream substrates, biotic communities, and organic matter retention times.

1. Introduction

Rapid, high-magnitude discharge fluctuations in forested headwater streams influence the transport of sediment and instream wood, as well as long-term riverine ecosystem processes (e.g, Bilby and Likens, 1979; Bonniwell et al., 1999; Cadol and Wohl, 2010; Merriam et al., 2002; Wohl and Cenderelli, 2000; Wohl and Jaeger, 2009). However, the hydrological characteristics of such short-term fluctuations in small headwater streams across different climates have received little attention. The use of metrics to analyze differences in fluctuations with sub-daily measurements has mostly only been assessed in systems with hydropeaking due to dams or in urban catchments (e.g., Alonso et al., 2017; ten Veldhuis and Schleiss, 2017), and not in headwater streams with short discharge pulses. Here, we quantify the differences in discharge fluctuations along montane headwaters between two regions: temperate rainforest in Oregon and tropical rainforest in Puerto Rico. We also determine whether the relationship between drainage area and discharge pulse characteristics is different between these regions. We draw on the hydrologic analyses to discuss the ecological implications of the characteristics of discharge pulses at these sites with respect to retention of stream organic matter as well as the export of nutrients and sediment using previously published literature.

In many headwater streams, limited subsurface storage, rapid surface and subsurface transmission of snowmelt and rainfall from

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adjacent uplands, and limited attenuation within the short channel network and confined valley bottoms all produce fast changes in discharge in response to changes in precipitation compared to lowland, higher-order streams and rivers (Niedzialek and Ogden, 2005; Schellekens et al., 2004; Wohl, 2010; Zhang et al., 2018). Fast changes in discharge promotes the rapid transfer of materials and organisms (Swanson et al., 1998). Headwater portions of stream networks, defined here as including streams that drain less than 100 km^2 and are 3rd order or lower, are emphasized as being disproportionally important for the transfer of material and organisms from uplands to lowlands (Adams and Spotila, 2005; Benda et al., 2003; Clarke et al., 2008; Haigh et al., 1998; Meyer et al., 1997; Swanson et al., 1998; Wipfli et al., 2007; Wohl, 2017). Rapidly fluctuating discharges help to promote transport of bedload (Green et al., 2015), suspended sediment (Bonniwell et al., 1999; Wohl and Cenderelli, 2000), large wood (LW) (Cadol and Wohl, 2010; Wohl et al., 2019b), and smaller particulate organic matter (POM) such as leaf detritus (Bilby and Likens, 1979; Merriam et al., 2002).

Because the increased transport capacity during discharge fluctuations can exert an important limit on stream retention of sediment and nutrients, we quantify and compare hydrologic characteristics of *discharge pulses* (rapid, high-magnitude discharge fluctuations) in headwater streams of tropic and temperate rainforests, where pulses are numerous and driven by intense rainfall. Our use of the term 'pulse' reflects the commonly accepted definition of a transient variation or disturbance from background conditions. Junk et al. (1989) and Benke et al. (2000) used the term *flood pulse* to describe overbank long duration floods in large tropical and subtropical systems, while Puckridge et al. (1998) and Tockner et al. (2000) used the term *flow pulse* to acknowledge the ecological importance of fluctuations in discharge relative to some level, regardless of whether the flow exceeds or is below bankfull. Specifically, Puckridge et al. (1998) "define a 'flow pulse' not in terms of a threshold, but as a rise and fall in discharge (or stage) at scales of space and time appropriate to the observer's frame of reference" (pg. 55). In headwater streams, which may have limited floodplain development due to confined valley bottoms, the term flood pulse is a less useful concept, since it implies only overbank flows and has been developed and emphasized in larger, tropical and subtropical river systems (Junk et al., 1989; Puckridge et al., 1998; Tockner et al., 2000). Because the original definition in the literature of *flow pulse* is not attached to a threshold, we use the term *discharge pulse* to distinguish a type of flow pulse, which we define here as a flow reaching one standard deviation above the historical mean in a headwater stream. Thus, our term *discharge pulse* can be seen as fitting within the concept of flow pulses, but attached to a specific threshold that is found through investigating the variability in flows in a given headwater stream.

Although studies of headwater streams in a variety of environments indicate the rapid discharge response of these systems to changes in precipitation (Schellekens et al., 2004; Wohl, 2010), less is known regarding the range of variability of short-duration high flows within headwater basins and between climatic zones. One of the reasons for few studies of short-duration variability within smaller drainages is the rarity of stream gaging networks with sufficient spatial density to capture differences across networks that cover less than a hundred square kilometers. Suitable gages also need to record flow characteristics over short time intervals in headwater networks, where a geomorphically and ecologically significant fluctuation in discharge can last less than an hour. Analyses of sub-daily flow measurements can provide insights into flow patterns that would be missed if only daily or seasonal data are available (Alonso et al., 2017; Bevelhimer et al., 2015; Spurgeon et al., 2016). This potential loss of information due to coarse temporal frequency is particularly true for headwater streams in which discharge pulses are of very short duration. In addition, metrics that characterize one portion of continuous discharge records (e.g., averages, variability metrics) may not fully describe the continuous nature of discharge pulses. Analyzing hydrographs as curves (i.e., functional data) in addition to using metrics allows for incorporating more information on discharge pulses and flood flows (Chebana et al., 2013; Stewart-Koster et al., 2014).

As drainage area increases, the processes that delay and dampen stream flow responses to precipitation (e.g., increased hillslope and valley bottom storage of surface and subsurface water) become more effective, resulting in greater attenuation of fluctuating flows (Dunne and Leopold, 1978; Woltemade and Potter, 1994). However, the changes in the characteristics of short-duration high flows with increasing drainage area has not been compared between climates in small headwater streams, and differences in precipitation regime and runoff characteristics among sites could potentially result in different changes in discharge pulses with increasing drainage area.

We use gauging records for the H.J. Andrews Experimental Forest (AEF) in Oregon, United States and Luquillo Experimental Forest (LEF) in Puerto Rico to examine differences in hydrograph characteristics of discharge pulses in a mountainous temperate rainforest compared to a mountainous tropical rainforest. We use statistical analyses to assess differences in characteristics for discharge pulses between these two regions. Metrics used for comparison include frequency of pulses, relative magnitude (expressed as a percentage above the historical average discharge), duration, and metrics indicating shape of individual discharge pulses (e.g., skew and kurtosis). We also determine differences in discharge pulse characteristics between the regions in relation to increasing drainage area, asking whether the relationship between pulse metrics and drainage area differs between regions. We use functional data analysis, which analyzes the entire pulse as a curve as opposed to calculating a metric from discharge pulses (Chebana et al., 2013), to determine representative curves for each climate zone to gain additional information on discharge pulse shape. We then discuss the ecological implications of differences in discharge pulses at the two sites.

Knowledge of these two sites based on previous studies are summarized in Table 1. The precipitation regimes differ between AEF and LEF, with more frequent rainstorms distributed throughout the year at LEF. In addition, at AEF, infiltration rates generally exceed precipitation rates, resulting in very little overland flow (Jones, 2000). There is substantial macropore flow and saturation overland flow at LEF, resulting in rapid delivery of frequent precipitation to the stream channels (Schellekens et al., 2004).

Because of the differences in precipitation regime, precipitation intensity, and runoff processes (Table 1), we expect that discharge pulses will be more frequent, of shorter duration, and of higher relative magnitude in non-seasonal, wet tropical rain forest streams (LEF) compared to temperate rain forest streams (AEF). We also expect that pulses in LEF will have a steeper falling limb due to the runoff processes at LEF, which include extensive macropore flow and saturation overland flow (Schellekens et al., 2004). Related to drainage area and pulse characteristics, we expect that different relationships between pulse characteristics and increasing drainage exist when assessing LEF compared to AEF as a result of differences in precipitation regimes relative to runoff processes. We anticipate that rapid transfer of precipitation to streams due to overland and macropore flow in the LEF (Schellekens et al., 2004) likely results in increasing relative magnitude of pulses with increasing drainage area compared to the AEF, which experiences greater infiltration rates relative to precipitation rates and more subsurface contribution to stream flow. In addition, we expect that the duration of pulses increases with increasing drainage area in the AEF due to the greater infiltration rates relative to precipitation rates delaying the delivery of precipitation to streams and the attenuation of pulses with increasing drainage area. Thus, the influence of drainage area increases on delaying and dampening delivery of precipitation to streams may be stronger in the AEF compared to the LEF.

Our detailed analyses are able to test and quantify the magnitude of these expected differences that exist between regions with long-term data and multiple metrics rather than assuming their general validity.

Table 1
Description of physical characteristics of the two study regions and expected differences in pulsing discharge characteristics.

	Andrews Experimental Forest (AEF)	Luquillo Experimental Forest (LEF)
Location	Oregon, USA	Puerto Rico, USA
Region	temperate wet forest	tropical wet forest
Mean annual precipitation	~2,200 to ~ 2,500 mm across elevation gradient (Post and Jones, 2001)	~2,000 to ~ 4,500 mm, variable across LEF (Murphy et al., 2017)
Precipitation regime	longer duration, seasonal rain events from broad low pressure fronts, 80% of annual precipitation occurs during winter months (Post and Jones, 2001); rain on snow events create the largest run-off events (Jones, 2000); seasonal snowpack present at high elevations; rainfall intensities have been observed as 1.5–2.6 mm/hr (Dutton et al., 2005)	short duration, orographic rain events throughout the year; rainfall evenly distributed throughout the year (Post and Jones, 2001); numerous rainfall events throughout the year (Brown et al., 1983); rainfall intensities observed have a mean value of 3.0 mm/hr and a median value of 1.9 mm/hr (Schellekens et al., 1999)
Run-off processes	infiltration rate generally exceeds precipitation rate (Jones, 2000); macropores at shallow depths, but highly porous, well-aggregated, and fine-textured soils release water over longer timescales after precipitation events (Post and Jones, 2001); no overland flow observed (Harr, 1977)	rapid transfer of rain water to streams through macropores and overland flow (Post and Jones, 2001); macropores in the top 20 cm, large events resulted in saturation overland flow due to rapidly reduced hydraulic conductivity with depth and development of perched water tables (Schellekens et al., 2004)
Expected discharge pulse characteristics	less frequent, longer duration, and lower magnitude pulses with a more gradual falling limb	more frequent, shorter duration, and higher magnitude pulses with a steeper falling limb
Expected influence of drainage area on discharge pulse characteristics	decreasing relative magnitude of pulses with increasing drainage area, duration of pulses increase with increasing drainage area	increasing relative magnitude of pulses with increasing drainage area

Assessing pulses as functional data, which looks at the curves of all individual pulses, to determine differences in pulses among regions has also not been investigated. These quantitative comparisons provide a numerical basis for understanding differences in headwater streams.

2. Study areas

The H.J. Andrews (AEF) and Luquillo (LEF) sites occur within temperate and tropical rainforests, respectively. The AEF sites represent drainage areas of 0.1 to 62.4 km^2 and the LEF sites represent drainage areas between 0.3 and 38.8 km^2. We chose to use streams within the AEF and LEF for a detailed analysis of discharge pulses because they met our criteria of (i) several gages on adjacent streams that drain less than 100 km^2 (7 seven at AEF and nine at LEF), (ii) 15-minute recording intervals for stream flow over several years for all but one gaging station at AEF, and (iii) extensive published research that characterizes stream ecosystems and biotic response. Streams at the two sites share a wet climate relative to other environments on Earth, but represent diverse conditions in terms of seasonality and intensity of precipitation (Post and Jones, 2001), as well as inputs, processing, and retention of coarse particulate organic matter. In the LEF tropical streams, the presence of short duration, frequent rainstorms throughout the year and the rapid delivery of water through macropores creates a flashy hydrograph characterized by rapid rise and recession and large differences between base flow and flood peaks (Schellekens et al., 2004) (Fig. 1a) (Table 1). Although streams at AEF have a flashier hydrograph compared to streams solely dominated by snowmelt runoff, high infiltration rates that exceed precipitation rates (Jones, 2000) and the presence of broad low-pressure fronts during winter that produce more prolonged precipitation can create more sustained flows with less difference between base flow and flood peaks than at LEF (Fig. 1b) (Table 1).

2.1. Andrews experimental forest streams

The AEF is located in the Cascade Mountains of western Oregon (Fig. 2a). The AEF covers a total of 64 km^2, from 1630 m elevation down to 412 m elevation. The hydrothermally altered volcaniclastic rocks of the Little Butte Formation (Swanson and James, 1975) are deeply dissected by glacial, fluvial, and hillslope processes, and covered by conifer forests dominated by Douglas fir (*Psuedotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Post and Jones, 2001).

The region has a maritime climate with wet winters and dry summers; annual precipitation normally exceeds 2540 mm, and deep snowpacks are common above 1000 m. A continuous flow of upper level moisture originating from the tropics can produce particularly strong winter storms. Convective storms during summer can also produce more localized, intense rainfall (Post and Jones, 2001). Overland flow occurs rarely because soil infiltration rates exceed 20 cm/h, which in turn exceeds most precipitation rates (Jones, 2000). Macropores are present at shallow depths, and soils are fine-textured, highly porous, and well-aggregated, resulting in the high infiltration rates that can accommodate precipitation inputs (Harr, 1977; Post and Jones, 2001). Streams carry flood flows during autumn and winter (Harr, 1981), and floods result from rainfall and rain-on-snow (Jones, 2000), with the highest stream flow normally resulting from warm rain-on-snow events during November to February when broad, low pressure systems move inland from the Pacific Ocean. Baseflow averages about 40% of mean annual streamflow (Post and Jones, 2001).

The seven stream sites analyzed here are all within the Lookout Creek watershed, which drains to the McKenzie River (Fig. 2a). Streams are steep and lined with boulders, and have either step-pool or pool-riffle morphology (Montgomery and Buffington, 1997). First- and second-order streams receive abundant wood and litter from adjacent slopes and riparian corridors via debris flows, windthrow, and tree fall (Nakamura and Swanson, 1993) (Fig. 2b). Mack Creek, a third-order stream in the drainage, stores an average of 812 m^3 of wood per ha of channel (Gurnell et al., 2002), and this large wood creates steps that account for nearly 30% of the total channel fall (Faustini and Jones, 2003). Less than 1% of the logs in Mack Creek move in most years and most movements probably occur during floods with a return interval greater than 25 years (Gurnell et al., 2002). Larger streams with wider channels have increasing instream photosynthesis, but microbially processed litter transported from upstream remains an important part of the energy base (Vannote et al., 1980). Loading and retention of wood in streams decreases progressively downstream (Minshall et al., 1983; Naiman and Sedell, 1979), but channels throughout the network have very high bed roughness (Grant et al., 1990) and enhanced hyporheic exchange along channel segments with closely spaced breaks in bed slope and concave water surfaces (Anderson et al., 2005).

2.2. Luquillo experimental forest streams

The LEF in northeastern Puerto Rico covers 113 km^2 of high relief terrain formed over mixed lithologies characteristic of island arc systems (Fig. 3a) (Larsen and Torres-Sánchez, 1998; Scatena and Lugo, 1995). Total monthly rainfall is distributed relatively evenly throughout the year as a result of Puerto Rico's location with respect to the maritime trade winds (Scatena, 1995). Precipitation typically

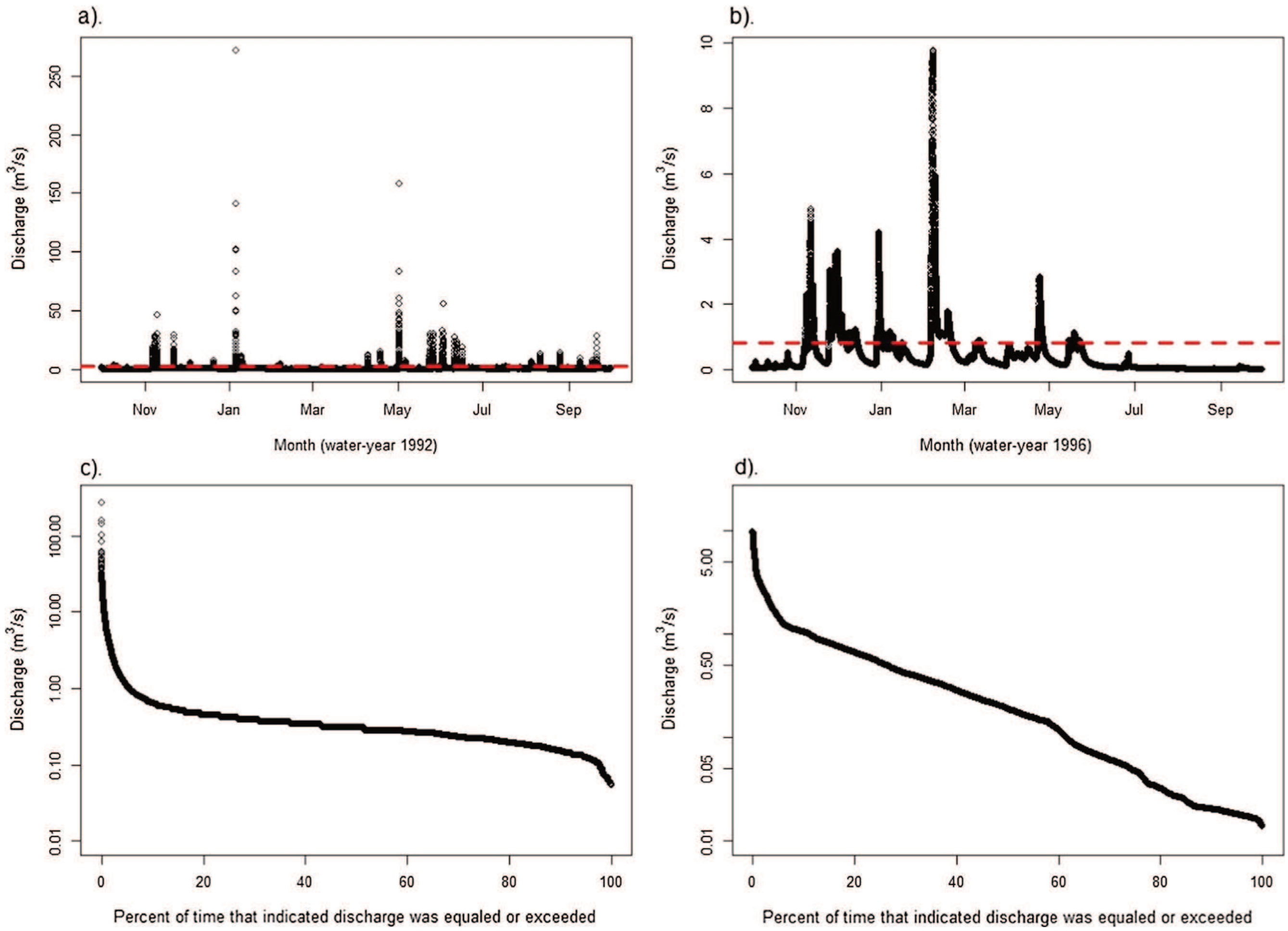

Fig. 1. Representative annual hydrograph from LEF (Rio Sabana discharge in water year 1992, which is October 1, 1991 through September 31, 1992), illustrating the extremely short duration of higher flows (a), and representative annual hydrograph from AEF (Mack Creek discharge in water year 1996) (b). Note that periods during which discharge exceeds base flow at AEF are of longer duration than at LEF. Horizontal line indicates one standard deviation for the historical mean of the record and demonstrates that any pulse above this value was identified as a discharge pulse. The flow duration curve for the period of record for Rio Sabana at LEF (c), and the flow duration curve for the period of record for Mack Creek at AEF (d).

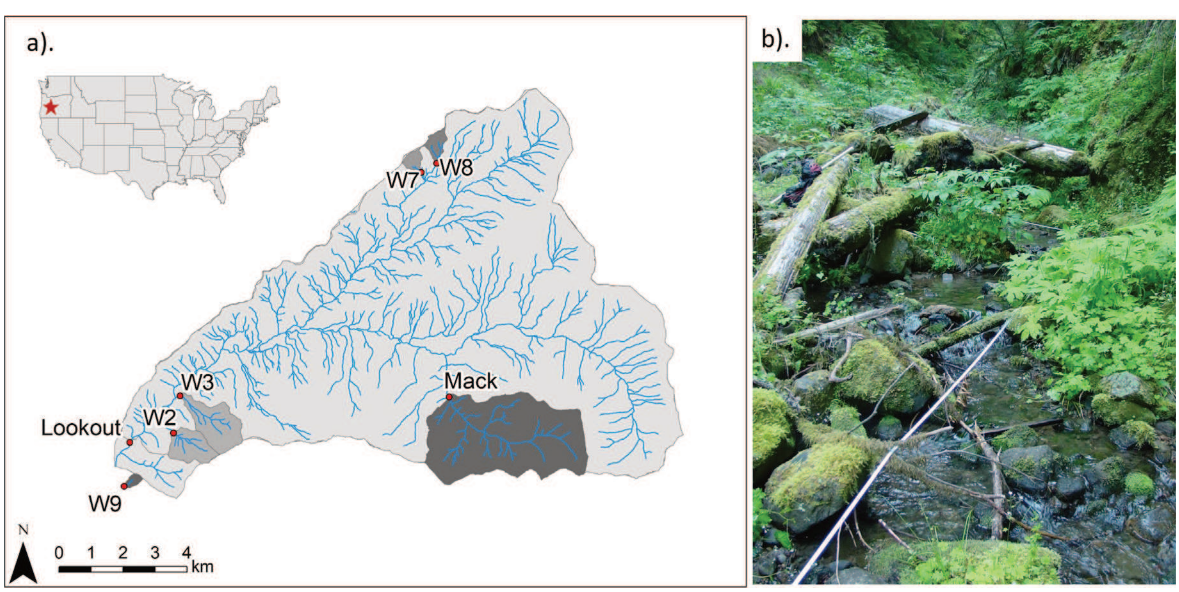

Fig. 2. Location map of study watersheds in the Andrews Experimental Forest of western Oregon (a), and View upstream at watershed 3 (photo by Ellen Wohl) (b). This site was chosen as being representative of the coarse-grained, steep channel beds of streams in Andrews. Note the abundance of wood in the channel.

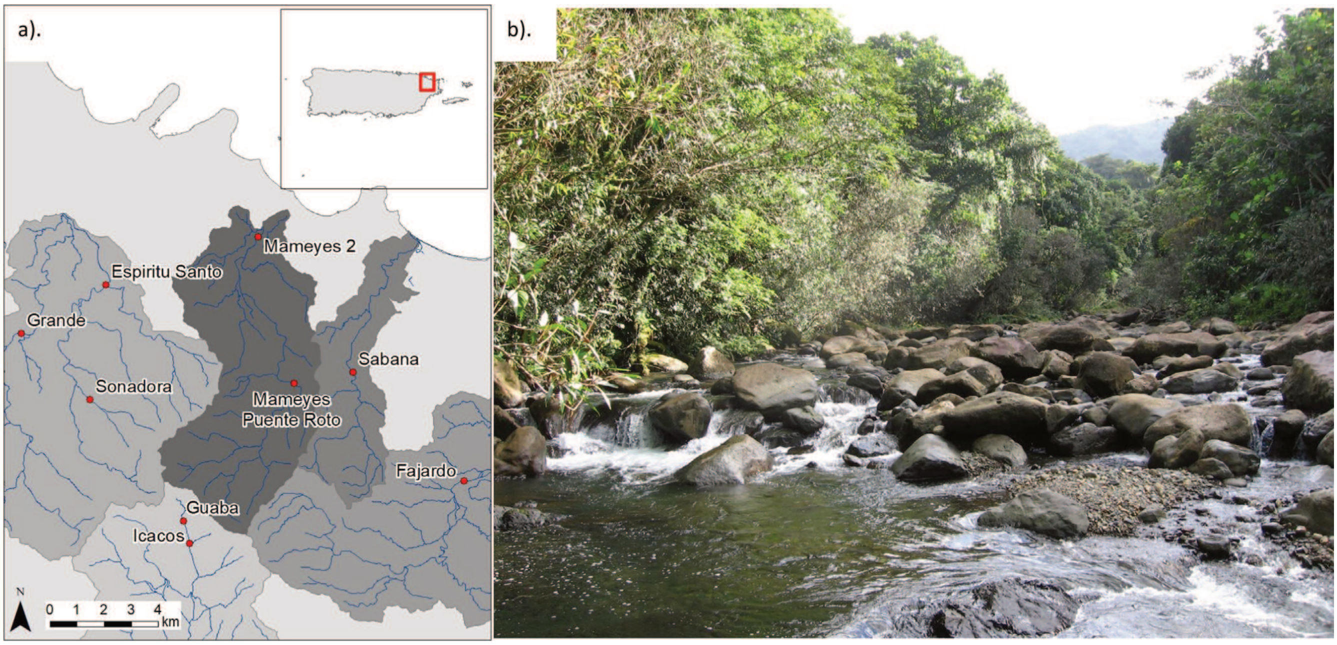

Fig. 3. Location map of study watersheds and gage sites in the Luquillo Experimental Forest of Puerto Rico (a), and view upstream at site Rio Mameyes (photo by Ellen Wohl) (b). This site was chosen as being representative of the coarse-grained, steep channel beds of streams in Luquillo. Note also the absence of wood in the channel despite the continuous riparian forest.

results from short-duration, frequent rainstorms, or from longer duration frontal systems or tropical hurricanes (Comarazamy and González, 2011; Murphy et al., 2017; Post and Jones, 2001). The short-duration storms can account for up to 80% of the total annual rainfall (Scatena, 1995), but the longer duration and frequent storms are more likely to produce landslides (Larsen and Simon, 1993; Scatena and Larsen, 1991) that introduce substantial sediment and organic matter to streams. Mean annual rainfall varies from approximately 4400 mm at the highest elevations (above 1000 m) down to 2300–2600 mm at elevations of 100 m or lower (Garcia-Martino et al., 1996; Ramseyer and Mote, 2018). Vegetation within the LEF is classified by elevation into elfin forest on the uppermost peaks, colorado forest dominated by *Cyrilla racemiflora* at 900–600 m elevations, palm forest dominated by sierra palm (*Prestoea montana*) and tabonuco forest dominated by *Dacryodes excelsa* at 600–100 m elevations (Scatena et al., 2002).

The LEF drainage network is composed of numerous small tributaries that merge to form nine major rivers (McDowell et al., 2012). The nine gaged stream sites within the LEF used in this analysis lie within five watersheds that drain to the coast in northeastern Puerto Rico (Fig. 3a). Headwater streams are steep and lined with large boulders, with occasional small pools of varying depth (Fig. 3b) (Pike et al., 2010). Peak flows occur during May through December, with discharge closely related to rainfall (Garcia-Martino et al., 1996). Rapid decreases in soil hydraulic conductivity with depth promote saturation overland flow and return flow that, together with abundant macropores in the top 20 cm of the soil profile, can reduce stream flow response to precipitation to less than 10 min in catchments of less than a few square kilometers (Schellekens et al., 2004). Frequent floods ranging from a few hours to a few days alter stream habitat availability (Scatena and Johnson, 2001) and nutrient fluxes (Heartsill-Scalley et al., 2012, 2007). Droughts and hurricanes occur infrequently (Covich et al., 2003; Scatena, 1989), but when they occur they affect the stream biota (Covich et al., 2006). Baseflow averages between 40 and 45% of mean annual streamflow (Post and Jones, 2001).

River corridors have similar vegetation communities comprising secondary, broad-leaf evergreen tropical forest and have similar geological and land-use histories. Secondary forests with closed riparian canopies provide a continuous input of leaf-litter for detritivores, although leaf fall peaks in April-June and reaches a minimum in December-March (Weigert, 1970; Zalamea and González, 2008). Primary production is low in small streams because of light limitation, and rapid decomposition results in a low standing crop of coarse organic matter (Webster et al., 2003). Undisturbed headwater streams in the LEF contain much less wood than undisturbed forested headwater streams in temperate regions (Pike et al., 2010).

3. Methods

3.1. Datasets used

Data available from the early 1950 s to 2013 were used for AEF stations in the analyses, and data available from the late 1980′s to 2005 were used for each LEF station (Table 2). Data were organized by water year, which begins on October 1 and ends on September 30 and is named for the year in which the water year ends. Water years where missing data were sufficient to impact calculations were left out of the analysis. Water years that were left out include LEF basins Espiritu Santu from 1993 to 1994 and Sonadora 1998, and AEF basin W7 from 1988 to 1993. At the Guaba station, a landslide that delivered large amounts of sand to the stream, potentially impacting the reliability of measurements in water-years 2004 and 2005. However, the 2004 and 2005 water-year metrics were not outside of the range of variability in the data prior to 2004, and thus we chose to leave those water-years in the analysis. Measurement increments for all stations are 15 min, except for the Lookout station at AEF, which has longer measurement intervals earlier in the record (60-minute increments from 1950 to 1986, 30-minute increments from 1986 to 2009). We maintained the high temporal resolution of the data (15-minute) for all stations except for Lookout station because it provides unique information at all stations and only one station deviated from the 15-minute interval. Table 2 summarizes the drainage areas, water years analyzed, and the mean flow over the record for each basin. Although the lengths of record differ for the LEF and AEF, with longer records from AEF station, we do not believe the difference in record length impacted the analyses because the number of discharge pulses identified was large overall (n = 12,779 total; AEF pulses = 4,148; LEF pulses = 8,631). We

Table 2
Drainage areas, water years (October 1 through September 30) used for analyses, and the threshold discharge used to identify discharge pulses (1 standard deviation above the mean flow for the period of record used).

Location	Site	Station ID number	Drainage Area (km^2)	No. of years used	Discharge pulse threshold (m^3s^{-1})	Years used	Latitude/Longitude (decimal degrees)
LEF	Guaba	50,074,950	0.3	12	0.079	1994–2005	18.2839, −65.7888
LEF	Sonadora	50,063,440	2.6	15	0.830	1988–1997, 1999, 2002–2005	18.3232, −65.8175
LEF	Icacos	50,075,000	3.3	12	1.345	1994–2005	18.2772, −65.7858
LEF	Sabana	50,067,000	10.3	12	3.026	1988–1995, 2002–2005	18.3309, −65.7313
LEF	Mameyes 1 (MameyesPuente Roto)	50,065,500	17.8	6	5.414	1995, 1999–2003	18.3288, −65.7508
LEF	Grande	50,064,200	19	14	5.134	1992–2005	18.3454, −65.8419
LEF	Espiritu Santo	50,063,800	22.4	17	7.828	1987–1992, 1995–2005	18.3599, −65.8139
LEF	Mameyes 2	50,066,000	34.7	7	10.165	1999–2005	18.3742, −65.7638
LEF	Fajardo	50,071,000	38.8	18	9.144	1988–2005	18.2989, −65.6938
AEF	W9	GSWS09	0.08	45	0.001	1969–2013	
AEF	W8	GSWS08	0.21	50	0.022	1964–2013	44.2663, −122.1708
AEF	W7	GSWS07	0.15	44	0.0134	1964–1987, 1994–2013	44.2645, −122.1752
AEF	W2	GSWS02	0.6	61	0.071	1953–2013	44.2125, −122.2445
AEF	W3	GSWS03	1.01	61	0.112	1953–2013	44.2195, −122.2429
AEF	Mack	GSWSMA	5.81	34	0.823	1980–2013	44.2193, −122.1673
AEF	Lookout	GSLOOK	62.42	64	8.675	1950–2013	44.2101, −122.2572

investigated the data for trends in the records, and no substantial trend was found in AEF data. Thus, inclusion of the entire dataset was deemed appropriate.

Discharge pulses were extracted by defining a discharge pulse to be when flow rate is faster than one standard deviation above that station's historical mean. Historical mean was calculated using the entire discharge record under analyses. We used one standard deviation as a threshold because after visual inspection, it consistently and adequately separated the rising and falling limbs of discharge pulses from baseflow fluctuations (see Fig. 1). Flow magnitude had to drop below the threshold for the next high flow to be counted as a separate pulse. We considered using two standard deviations for the threshold to limit the number of double peaks counted as a single pulse, but the number of peaks extracted were not appreciably different from using one standard deviation. In addition, using two standard deviations would have overly shortened pulse duration because a large portion of the rising and falling limbs were below the two standard deviation threshold.

A variety of metrics have been used to characterize stream flow at different time scales, particularly for observations made at daily intervals (e.g., Olden and Poff, 2003). In order to characterize the frequency, magnitude, and shape of short duration, potentially sub-daily discharge pulses for the LEF and AEF sites, for each station we computed nine summary statistics of discharge pulses by water year (day 1 = Oct 1): the average and standard deviation of peak magnitude of pulses as percent above historical mean (Qmax and sd(Qmax)), the number of pulses (n), the average and standard deviation of pulse duration in hours (D and sd(D)), the average and standard deviation of skew (S and sd(S)), and the average and standard deviation of the kurtosis (K and sd (K)). Percent above historical flow mean rather than absolute peak magnitudes were used to facilitate comparison across stations and to normalize the peak magnitude to mean discharge at each station. Duration was measured as the length of time flow was above the historical mean threshold for each individual pulse. Skew and kurtosis were measured to provide information about the shape of pulses, namely how asymmetric and how heavy tailed a pulse is, respectively. We then analyzed these summary characteristics graphically and statistically to portray differences between pulses in the AEF and LEF and the influence of increasing drainage area between each location.

3.2. Discharge pulses in relation to previous characterizations of flashiness

A discharge pulse is a flashy sequence of flow within a stream. The flashiness of a given stream system is usually described as the rate of change in flow (Poff et al., 1997). It has been characterized in different ways, including through the use of the ratio between a high percentile flow to a low percentile flow taken from a flow duration curve, the standard deviation standardized by the mean flow or the spread between the 75th and 25th percentile flow standardized by the median flow, other variations on the coefficient of variation (typically the standard deviation divided by the mean flow), and through creating a normalized index using the sum of the change in day-to-day flows (Baker et al., 2004; Richards, 1990). Our discharge pulse definition and extraction relates to flashiness, but in the sense that the discharge pulses are the flashy portions of the hydrograph. The usefulness of extracting discharge pulses based on a threshold defined by one standard deviation above the mean lies in the ability to analyze solely the pulse characteristics and patterns across headwater streams using high temporal resolution data.

3.3. Statistical analyses using discharge pulses metrics

In order to make cross-comparisons between basins in the two regions, we scaled each metric to be centered at 0 with standard deviation of 1 by subtracting the mean of each variable from all rivers and years for the entire dataset (including both regions) and then dividing this difference by the standard deviation of that variable from all rivers and all years. We used logistic regression and linear discriminant analyses in R version 3.1.1 (R Core Team, 2018) to investigate the hydrologic features of pulses that most distinguish AEF pulses from LEF pulses. Logistic regression was conducted using the scaled nine covariates to predict the categorical response temperate (AEF) or tropical (LEF). Linear discriminant analysis (LDA) was used on the scaled nine covariates to quantify how each contributes towards the prediction of temperate or tropical. To do this analysis, a coefficient was generated for each covariate. The magnitude of the coefficient reflects how much an increase in a covariate is associated with the chances the river is temperate or tropical if all other covariates are held constant. An LDA score was calculated for each station for each year by multiplying scaled covariates (X_i,…X_n) by their respective LDA coefficient (C_i*X_i), and then summing them ($\sum_{i=1}^{n=9} C_i X_i$). The results of LDA can be viewed graphically by constructing a density plot of LDA scores, which indicates how likely a combination of covariates will be exhibited by a AEF or LEF stream.

Multiple regression was used to investigate if drainage area has a different association with the characteristics of the discharge pulses for AEF or LEF regions. Separate regression models were completed using each of the nine covariates as response variables against the predictor variables of drainage area, region (AEF or LEF) and an interaction term between the two. The form of each model was:

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$$

where μ = the mean of the response hydrograph characteristic as a function of the covariates, x_1 = drainage area, x_2 = categorical variable AEF ($x_2 = 0$) or LEF (x_2=1).

The null hypothesis of interest is whether or not β_3, the coefficient for the interaction term, is zero. β_3 adjusts the slope of the regression corresponding to the tropical rivers, and thus a non-zero β_3 means that the association between drainage area and the response hydrograph metric (e.g., the number of pulses) is different for AEF rivers versus LEF. Alternatively, a zero coefficient for an interaction term would mean that the association between drainage area and the response hydrograph characteristic is the same regardless of region. If coefficients are small, it implies that drainage area has little effect on the response hydrograph characteristic. In order to satisfy the usual regression assumptions for normality, a Box-Cox power transformation was applied to the response in most of the models. To achieve a family-wise error rate of $\alpha = 0.05$, a Bonferroni correction was made and each interaction term was tested at level $\alpha/9 = 0.0055556$.

We also used functional data analysis (FDA) techniques to further characterize the shape of discharge pulses between the AEF and LEF using the R fda statistical package (Ramsay et al., 2018). The entire rise and fall of each discharge pulse is a functional observation. This method has been used in applications such as investigating flood frequency (Chebana et al., 2012) and flow-ecology relationships (Stewart-Koster et al., 2014). We extracted each discharge pulse that had at least 3 measurements over their duration, which resulted in 10,592 out of 12,779 pulses. Because the FDA technique was used to primarily look at the shape of the pulses between AEF and LEF and a similar duration is needed to compare across pulses and across regions, each pulse was scaled to 40 h by dividing the time of each of the measurements by the pulse's total duration and then multiplying each by 40 h. Forty hours is about 10 h less than the average pulse duration across all sites. The functional observations (in this case, each individual discharge pulse) is fit with a model, which allows for determining average curves for each region and to investigate the potential differences between average curves. We completed B-spline transformations of each discharge pulse, which converts the observed discharge values in the pulse into a function that can then be averaged with other functions. For each discharge pulse, we smoothly transformed the discretely observed data into functional objects via a decomposition into a quadratic B-spline basis with 50 basis elements. Because we are not concerned with predicting discharge pulses and are only concerned with determining average shapes of the pulses, we were not concerned with overfitting each pulse. Functional data objects are then created and can be used to compute mean and standard deviation curves. A full detailed description of the FDA methods used for this analysis, including the equations used to develop functional objects, is included in Appendix 1.

4. Results

4.1. Discharge pulses between temperate and tropical using pulse metrics

Fig. 4 plots each of the nine covariates of hydrograph characteristics extracted from the yearly pulse data as boxplots, demonstrating some of the differences between the AEF and LEF. Tables A2.1 and A2.2 in Appendix 2 include the extracted hydrograph metrics for each basin for each water year and over the period of record used, respectively. LEF tends to have higher magnitude of pulses as a percent above historical mean and more discharge pulses, whereas AEF has greater average duration of pulses and greater variability in pulse duration (Fig. 4). The LEF streams average approximately 7 times as many discharge pulses each year as the AEF streams, but discharge pulses at AEF have an average event duration about sixteen times as long as those at LEF. The boxplots also indicate that LEF has higher variability in discharge magnitude and potentially higher skew compared to AEF (Fig. 4).

In logistic regression, only four of the nine covariates were needed to achieve perfect distinction between AEF and LEF: number of pulses (n), standard deviation of magnitude as a percent above historical mean (sd(Qmax)), average duration (D), and standard deviation of the duration (sd(D)). This means it is possible to determine whether a river is located in AEF or LEF using just number of pulses, variation in the normalized magnitude, duration, and the variation in duration. Specifically, in our study the AEF streams have fewer pulses, less variability in the normalized magnitude, longer average duration, and greater variability in duration than LEF streams (Fig. 4).

Table 3 shows the resulting LDA coefficients for each covariate. Larger values for covariates with positive coefficients increase the likelihood that the river will be LEF, and conversely, larger values for covariates with negative coefficients increase the likelihood that a river will be categorized as AEF (this relationship for individual covariates is true only when all other covariates are held constant).

The resulting LDA scores for our analysis were between −6 and 10 with non-overlapping density curves for AEF and LEF stations (Fig. 5). A clear divide between the two regions is located at around 0. The height of the density plot indicates how likely a station is to have a combination of hydrograph characteristics produce a particular score. LEF stations are centered near 2.5 and AEF stations near −2.5. LEF rivers show much more variability in scores with longer tails in the distribution than the AEF rivers. This greater variability implies that LEF rivers may be more variable in the combination of pulse hydrograph characteristics than AEF rivers.

4.2. Variations in discharge pulses with increasing drainage area between regions

In order to determine the associations between drainage area and the pulse metrics, we completed multiple linear regression as described in the methods section. The estimated models for the multiple regression analyses are included in Table 4, along with the coefficients (slope) terms describing the relationship between the metric and drainage area for each region. When analyzing the coefficients for each region individually, positive significant coefficients indicate that as the drainage area increases, the pulse metric increases (i.e., the coefficient is significantly different than zero); negative significant coefficients indicate that as drainage area increases, the pulse metric decreases. Significant interaction term coefficients indicate whether there is a different relationship between the metric and drainage area when compared between regions. Because of the form of the model, the exact p-value for LEF coefficients cannot be computed, but the significance of the relationship between the metric and drainage area for LEF can be inferred when looking at the relationship between AEF metrics and drainage area and the interaction term significance. For example, for the number of pulses metric, there is no significant relationship between number of pulses and drainage area for AEF, but there is a significant interaction term, indicating that the LEF coefficient for the relationship between number of pulses and drainage area is a significant relationship.

The significant relationships between drainage area and the pulse metrics correspond to the models with number of pulses, magnitude as a percent above the historical mean, standard deviation of magnitude as a percent above the historical mean, and average pulse kurtosis (Table 4). Therefore, the association between drainage area and these four pulse characteristics is different for each region. For AEF, there is no relationship between number of pulses and drainage area, but for LEF, there is a slight decrease in number of pulses with increasing drainage area (Fig. 6a). When considering magnitude as a percent above the historical mean, there is a slight decrease in magnitude with increasing drainage area in AEF and an increase in magnitude with increasing drainage area in LEF (Fig. 6b). The positive coefficient for

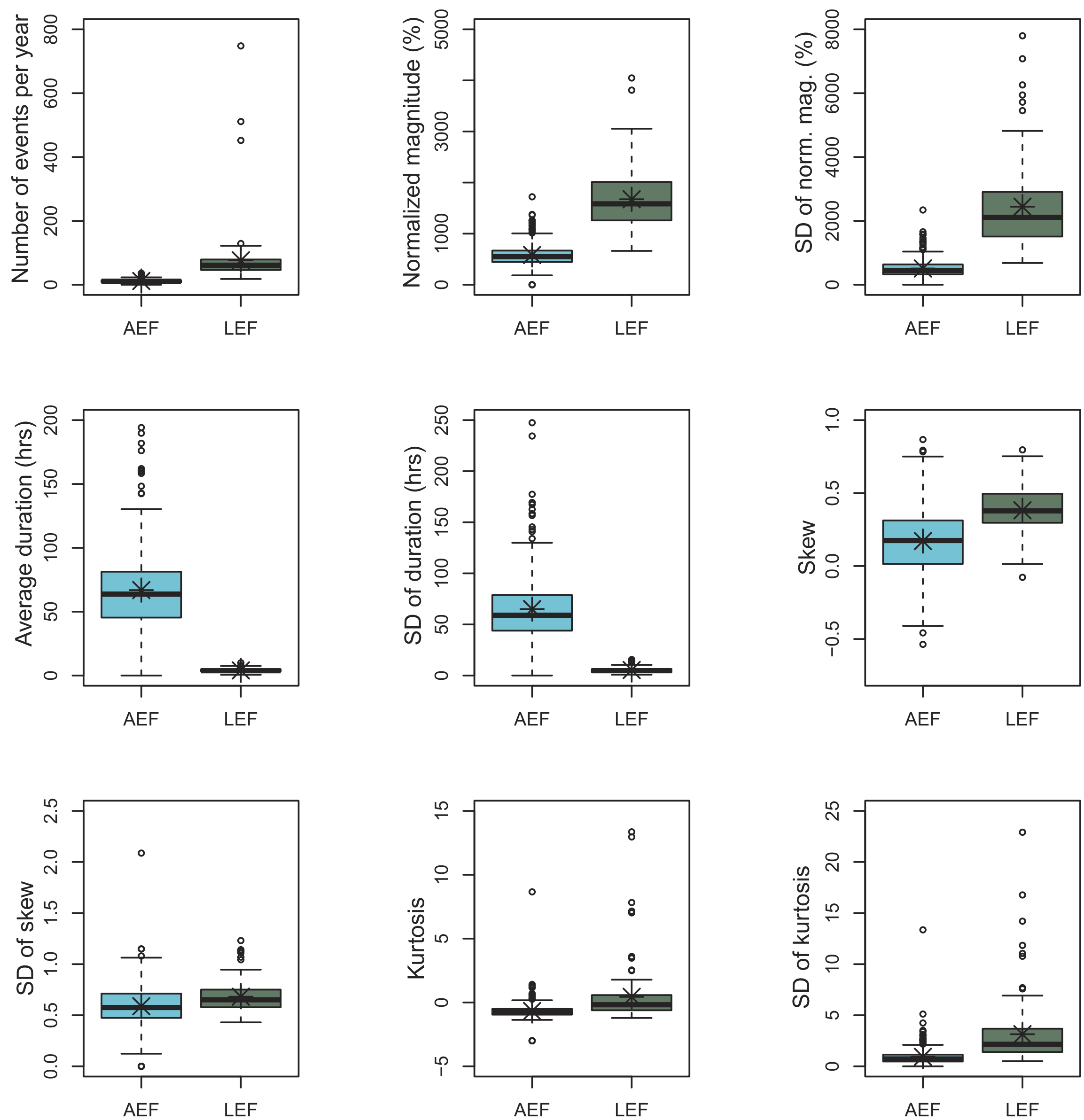

Fig. 4. The 9 metrics used for analysis for the AEF vs. the LEF stations. For boxplots, the star within the box indicates the mean value, the solid line within the box indicates the median value, the box ends are the upper and lower quartile, and the whiskers are the 10th and 90th percentile.

Table 3
Coefficients from the linear discriminant analysis (LDA) from each metric. Larger values for covariates with positive coefficients increase the likelihood that the river will be from LEF, and conversely, larger values for covariates with negative coefficients increase the likelihood that a river will be from AEF when all other covariates are held constant.

Metric	LDA coefficient
Number of pulses	1.016
Average magnitude as % above historical mean	1.879
Standard deviation of magnitude	−0.427
Average pulse duration	−0.772
Standard deviation of duration	−0.140
Average pulse skew	−0.034
Standard deviation of skew	0.153
Average pulse kurtosis	−1.009
Standard deviation of kurtosis	0.790

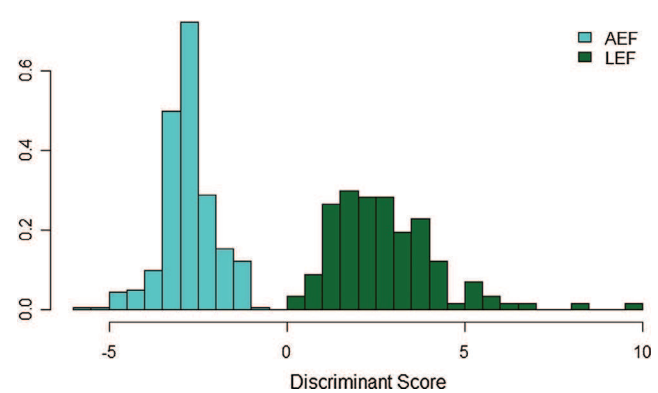

Fig. 5. The bars correspond to the LDA scores for all the AEF and LEF stations plotted on the same axis. Note that there is not only no overlap between the bars for AEF and LEF flows but also a gap between the bars showing clear separation between the two regions.

the normalized magnitude for LEF indicates a stronger increase in normalized magnitude with increasing drainage area compared to the small decrease in normalized magnitude in the AEF. Thus, the

Table 4
Estimated models for the multiple regression analyses to determine associations between drainage area and pulse metrics, including the interaction term for determining whether relationships between drainage area and pulse metrics are different between AEF and LEF. In each model, X_1 indicates drainage area, while $X_2 = 0$ for AEF and $X_2 = 1$ for LEF. Significant coefficients at alpha = 0.0055556 are bold (significance level is adjusted for multiple comparisons).

Pulse metric	Estimated model	AEF coefficient [p-value in brackets]	LEF coefficient [significance in brackets]	Interaction term coefficient [p-value in brackets]
Number of pulses[1]	$1.7916 - 0.0005X_1 + 1.2400X_2 - 0.0114X_1X_2$	−0.0005 [0.5220]	−0.0119 **[significant]**	−0.0114 **[less than0.0001]**
Magnitude as % above historic mean[2]	$24.1379 - 0.0432X_1 + 13.9538X_2 + 0.1722 X_1X_2$	−0.0432 **[0.0005]**	0.1290 **[significant]**	−0.1722 **[less than0.0001]**
Standard deviation of magnitude as % above historic mean[3]	$7.7123 - 0.0062X_1 + 4.7925X_2 + 0.0399 X_1X_2$	−0.0062 [0.1391]	0.0338 **[significant]**	0.0399 **[0.0035]**
Average pulse duration[4]	$3.9280 - 0.0001X_1 - 2.4980X_2 + 0.0074X_1X_2$	−0.0001 [0.9520]	0.0073 [not significant]	0.0074 [0.1440]
Standard deviation of duration[5]	$7.7375 + 0.0007X_1 - 5.7189X_2 + 0.0117X_1X_2$	0.0007 [0.865]	0.0125 [not significant]	0.0117 [0.4100]
Average pulse skew	$0.1633 + 0.0006X_1 + 0.1610X_2 + 0.0028X_1X_2$	0.0006 [0.1747]	0.0034 [not significant]	0.0028 [0.0766]
Standard deviation of skew	$0.5875 - 0.0001X_1 + 0.0974X_2 - 0.0001X_1X_2$	−0.0001 [0.8503]	−0.0002 [not significant]	−0.0001 [0.4891]
Average pulse kurtosis[6]	$1.4896 + 0.0014X_1 + 0.4278X_2 - 0.0085X_1X_2$	0.0014 [0.0401]	−0.0071 **[significant]**	0.0085 **[0.0002]**
Standard deviation of kurtosis[7]	$0.9158 + 0.0007X_1 + 0.3765X_2 - 0.0030 X_1X_2$	0.0007 [0.1241]	−0.0022 [not significant]	0.0030 [0.0588]

[1] Fourth root transformation applied to response variable to satisfy model assumptions.
[2] Square root transformation applied to response variable to satisfy model assumptions.
[3] Cube root transformation applied to response variable to satisfy model assumptions.
[4] Cube root transformation applied to response variable to satisfy model assumptions.
[5] Square root transformation applied to response variable to satisfy model assumptions.
[6] Square root transformation applied to response variable to satisfy model assumptions.
[7] Fourth root transformation applied to response variable to satisfy model assumptions.

normalized pulse magnitude metric indicates a slight dampening of the peak pulse discharge relative to the average value in the AEF, but an increase in LEF (Fig. 6b). The standard deviation of normalized pulse magnitude increases slightly in LEF with increasing drainage area, with no significant relationship in AEF (Fig. 6c), indicating that as drainage area increases, the variation in pulse magnitude increases at LEF. Finally, the average kurtosis of the discharge pulses decreases slightly in LEF with increasing drainage area, with no significant relationship in AEF (Fig. 6d).

4.3. Differences in shape of discharge pulses between regions

We used FDA to further investigate the average pulse shapes for each region. Fig. 7 shows the average curve and the standard deviation for each region, using the discharge pulses scaled to the same duration of 40 h. Clear differences in the mean curves indicate that LEF pulses peak at a much higher magnitude. In addition, the LEF pulses have a steeper receding limb of the pulses, while the receding limb of the AEF pulses is more gradual. The higher standard deviation of the LEF pulses indicate that there is greater variability in pulses in the LEF compared to AEF. The greatest variability in the pulses occur at the peak for both AEF and LEF.

5. Discussion

5.1. Hydrologic variations between regions and with increasing drainage area

Our results support the expectations that discharge pulses are more frequent (more events per year), of shorter duration, and of higher magnitudes relative to the historical mean in LEF compared to AEF (Fig. 4). These patterns are predictable from what is known of regional hydrographs; flow in the tropical streams generally pulse more frequently, for shorter periods of time, and at higher magnitudes than flow in the temperate streams, reflecting greater frequency of rainstorms, greater amounts of average annual precipitation, and more efficient transmission of water from hillslopes to streams (Brown et al., 1983; Post and Jones, 2001; Schellekens et al., 2004).

The LDA analyses indicate that some metrics of discharge pulses can provide a complete distinction between AEF and LEF: number of pulses, standard deviation of magnitude as a percent above historical mean, average duration, and standard deviation of the duration (Fig. 5). LEF pulses also have greater variability in magnitude relative to the historical mean and higher skew of discharge pulses. Plotting LDA scores is a useful tool to examine variability between basins and could be used as a more standard tool in hydrology to discriminate between basins. Potential applications of LDA analysis could include using it to identify outlier basins that have different hydrologic responses than nearby basins, help construct design pulses from reservoir releases to more closely match the characteristics of undammed basins nearby, compare different land management scenarios, or to compare discharge pulse characteristics pre and post disturbances (e.g., fire).

Our expectation that pulses in LEF will have a steeper falling limb relative to AEF is supported by the mean curves of discharge pulses from FDA analyses (Fig. 7). Normalizing the pulses to 40 h allows us to compare other aspects of the pulse, such as shape, without being overwhelmed by the already clear difference in duration. High infiltration rates in the AEF relative to precipitation rates (Jones, 2000) likely promotes a slower decline of discharge on the falling limb of the discharge pulse. In contrast, there is substantial macropore and overland flow in the LEF (Schellekens et al., 2004), which is common in the humid tropics (Chappell, 2010) and may contribute to the relatively steep receding limb in pulses due to preferential transport in hillslopes.

Variations in normalized magnitude with increasing drainage area also aligned with our expectations. We found a slight decrease in normalized magnitude in the AEF, but an increase in normalized magnitude in the LEF (Table 4 and Fig. 6b), which may be due to the rapid transfer of precipitation to streams in the LEF caused by overland and macropore flow, while the AEF has higher infiltration rates relative to precipitation (Harr, 1977; Jones, 2000; Schellekens et al., 2004). Thus, pulse attenuation with increasing drainage area is greater in the AEF compared to the LEF. The number of pulses increases with increasing drainage area at LEF, and does not change significantly with increasing drainage area in the AEF. The increase in the number of pulses with increasing drainage area could be a result of the larger drainage area sites receiving multiple pulses from incoming tributaries in a precipitation regime that experiences frequent, short duration precipitation compared to AEF (Scatena, 1995). AEF precipitation events many times result from broad, low-pressure systems that move inland from the Pacific Ocean (Post and Jones, 2001), potentially resulting in a spatially-extensive pulse throughout the AEF. In addition, there are a much larger number of pulses in LEF compared to AEF overall (Fig. 4), and the high infiltration rates at AEF may dampen and reduce the number of pulses within streams from storm events.

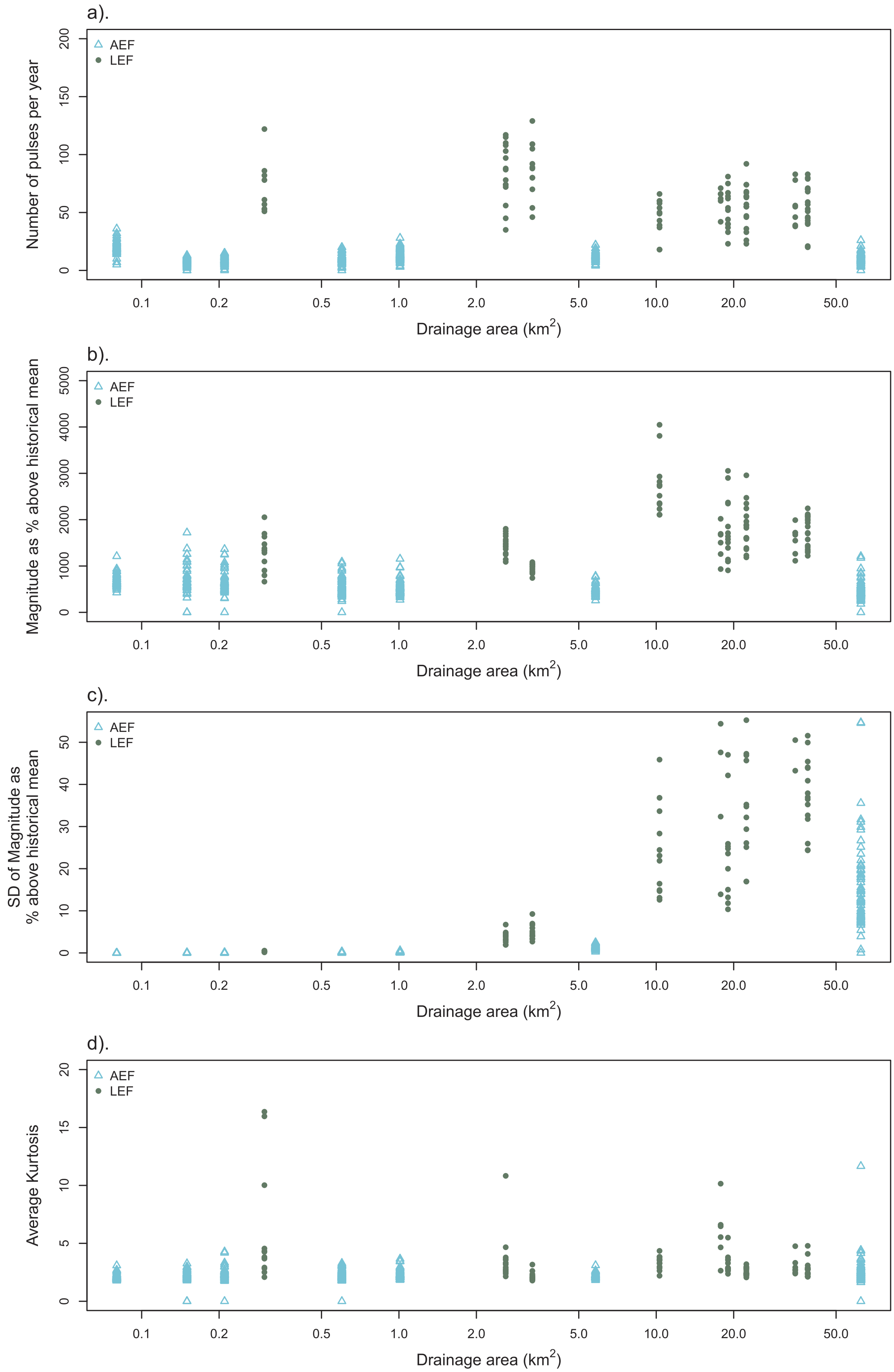

Fig. 6. Discharge pulse metrics with increasing drainage area (note log scale with increasing drainage area). Number of pulses (a), magnitude as a percent above historical mean discharge (b), standard deviation of magnitude as a percent above historical mean discharge (c), and average kurtosis (d). Each point is the average pulse metric for one water year at one site, and many points are overlapping, particularly at smaller drainage areas for plot (c).

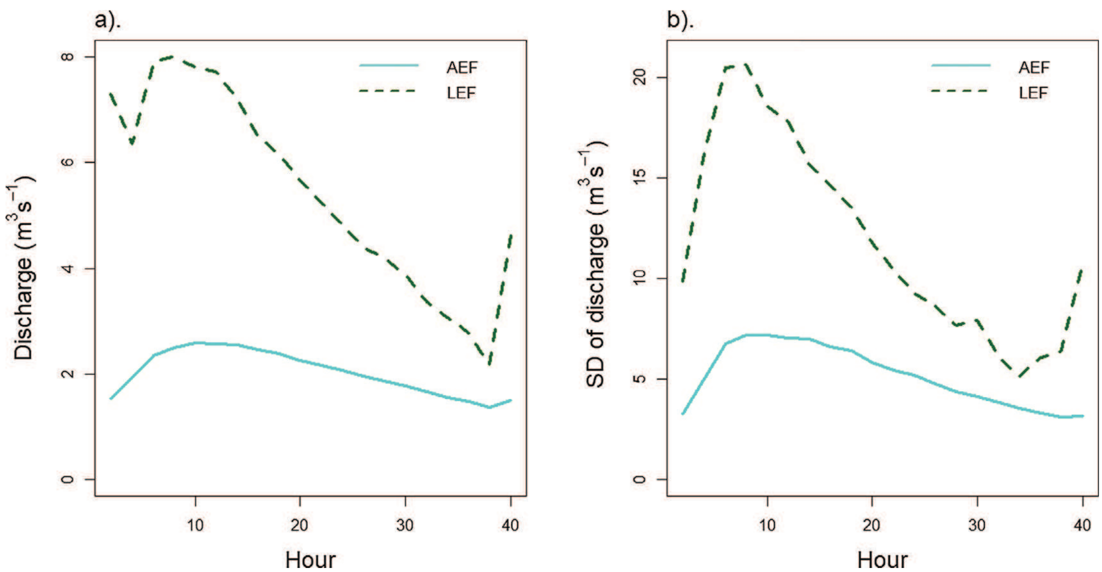

Fig. 7. The average curves for pulses for AEF and LEF scaled by pulse duration (a), and the standard deviation of the curves scaled by duration (b).

The standard deviation of the normalized magnitude also demonstrates a significant relationship with increasing drainage area, increasing slightly at LEF but lacking a significant relationship in the AEF. Similar to the number of pulses, the standard deviation of normalized magnitude in the LEF could increase with increasing drainage area due to short duration rainstorms occurring in different portions of the headwater basins, resulting in more variable pulse magnitudes at larger drainage areas. Finally, average kurtosis slightly decreases in LEF with increasing drainage area but has no significant relationship with drainage area in the AEF. Although somewhat difficult to interpret, kurtosis indicates how heavy-tailed a pulse is, and a slight decrease in kurtosis with drainage area indicates thinner tails for the pulse as drainage area increases. There is no thickening of the pulse tails with increasing drainage area due to attenuation at LEF, but the pulses become more peaked with thinner tails as drainage area increases. This could potentially be a consequence of increasing pulse magnitude as drainage area increases. However, the coefficient for kurtosis is quite small (Table 4), and thus the effect of increasing drainage area on kurtosis is likely weak.

The lack of significant relationships between the additional 5 pulse metrics (average and standard deviation of pulse duration and skew, and standard deviation of kurtosis) and drainage area may be due to the relatively small drainage areas across the entire study. In particular, we expected that the average duration of pulses would increase with increasing drainage area in the AEF due to attenuation of low flow with increasing drainage area, but no significant relationship exists (Table 4). Headwater streams many times do not display expected downstream trends in channel morphology due to the influence of local knickpoints, coarse sediment and debris inputs, direct connections to hillslopes, and limited floodplain development (Adams and Spotila, 2005). Because the stations in both AEF and LEF occur over limited drainage areas, the attenuation of pulse metrics through slowing of pulses and increasing duration likely does not occur.

5.2. Ecological implications of discharge pulses

Disturbances such as discharge pulses can physically move organisms along a stream, both through downstream transport and through increased hydrologic connection between different habitats. Transient states of discharge and stream substrate are particularly important to the survival rates of stream organisms, which must withstand the stresses imposed by conditions such as exceptionally high velocity and turbulence or rapid sedimentation on the streambed (e.g., Erman et al., 1988; Fausch and Bramblett, 1991; Johnson et al., 1998; Swanson et al., 1998; Zimmermann et al., 2014). Discharge pulses also temporarily reduce physical storage associated with obstacles to flow and zones of flow separation, and increase flow velocity, thus increasing the rate of loss of organic materials in stream ecosystems (Minshall et al., 1983).

The differences in discharge pulse characteristics between the AEF and LEF, along with differences in channel morphology, likely influence stream ecosystems. The high magnitude discharge pulses at LEF produce large values of shear stress and transport capacity that, in combination with rapid decay, limit retention of wood and other coarse particulate organic matter entering the streams. Thus, we expect that streams at LEF have relatively short residence times for organic matter. The lower magnitude, longer duration flow pulses present at AEF, combined with the greater capacity for storage of organic matter, indicate that streams at AEF likely have longer turnover times and distances for organic matter than streams at LEF, and generally greater stream retention. Relative to the AEF, minimal instream wood is present in the LEF (Pyron et al., 1999), and retention of organic matter occurs mainly in the interstices between coarse sediment or along channel margins in zones of reduced flow velocity. The exception to these relatively low wood inputs and limited retention occurs when large tropical storms and hurricanes create transient organic debris dams throughout the LEF (Wohl et al., 2019a). Measurements in Quebrada Bisley, a headwater tributary of the Rio Mameyes, however, provide a cautionary note. Merriam et al. (2002) found that only 37% of instream fine benthic organic matter was removed during a discharge pulse in which discharge increased more than twenty-fold. The frequency of such discharge pulses, as seen by the high number of pulses at LEF compared to AEF, however, suggests that organic matter is removed fairly effectively during most years, especially given the long travel distances noted by Merriam et al. (2002) for organic matter dislodged in Quebrada Bisley.

Although the discharge pulses analyzed here are not explicitly linked to ecological traits and species response, there is a need to move away from using only hydrologic metrics from daily discharge measurements towards a more complex understanding of hydrologic dynamics and associated effects (Arthington et al., 2018). Using discharge measurements at high temporal resolution, particularly in headwater streams, along with functional data to assess the entire shape of a discharge pulse, is an advancement towards measuring and assessing complex hydrologic processes and determining the potential impact on ecological processes in headwater stream.

6. Conclusion

We find that discharge pulses taken from sub-daily discharge measurements in headwater streams are distinctly different when comparing the AEF and LEF regions. The differences in discharge pulses are likely the result of differences in precipitation regimes, runoff processes, and the relationship between precipitation rate and infiltration rates. Treating the discharge pulses as functional data and averaging across all pulses allows for comparison of rising and falling limbs of pulses, as well as the variability in pulses between tropical and temperate sites. The drainage area and discharge pulse relationship differed between study regions for some of the pulse characteristics, shedding further light on runoff processes and attenuation in headwater streams across regions. Further work is needed across diverse temperate and tropical headwater streams to determine whether the differences between AEF and LEF apply elsewhere.

Characterizing regional differences in discharge pulses provides a useful starting point for understanding how physical differences in stream ecosystems can influence organic matter retention and ecosystem processes. Our results indicate that sub-daily, high temporal resolution discharge data can provide important insights into the hydrological patterns of stream discharge in small headwater streams. Fully quantifying differences between regions is also important in the context of management regimes and climate change, which may modify discharge pulses in the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2019.124236.

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