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Hydrologic regimes of forested, mountainous, headwater basins in New Hampshire, North Carolina, Oregon, and Puerto Rico

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Abstract

This study characterized the hydrologic regimes at four forested, mountainous long-term ecological research (LTER) sites: H.J. Andrews (Oregon), Coweeta (North Carolina), Hubbard Brook (New Hampshire), and Luquillo (Puerto Rico). Over 600 basin-years of daily streamflow records were examined from 18 basins that have not experienced human disturbances since at least the 1930s and in some cases much longer periods. This study used statistical methods to systematically evaluate the relationship between precipitation and streamflow at a range of spatial and temporal scales, and draw inferences from these relationships about the hydrologic behavior of the basins. Basins in this study had fundamentally different abilities to store and release moisture at a range of time and space scales. These different hydrologic regimes are the result of different types of forest canopies, snow, and soils in the study basins. Through their influences on interception and transpiration, forest canopies appear to play a very important role in the hydrologic regimes at Andrews and Luquillo, but at Coweeta and Hubbard Brook, the current deciduous forest plays a more limited although seasonally important role. Because of the timing of melt and its interaction with soils, seasonal snowpacks at Hubbard Brook and Andrews have quite different effects upon streamflow and vegetation water use. A variety of water flowpath types in soil, from macropore flow to long flowpaths in deep soils or fractured bedrock, appear to operate at the four sites. Hydrologic regimes may help predict the temporal scales of biogeochemical cycling and stream ecological processes, as well as the magnitude and timing of hydrologic response to disturbance and climate change in headwater basins.

1. Introduction

The purpose of this study is to examine how hydrologic behavior varies among and within steep, forested basins, at multi-year to daily time scales, based upon analyses of long-term streamflow and climate records. Hydrologic behavior constrains key ecosystem processes such as productivity, nutrient cycling, population dynamics, and biological diversity, and depends upon the amounts and duration of water storage in vegetation canopies, soils, and stream channels.

In this paper we quantify and compare the distinct forms of hydrologic behavior that exist at the scale of headwater basins (e.g. [32]), as a step toward development of a classification scheme to predict and extrapolate hydrologic behavior across unmonitored basins. We define the hydrologic regime as the relationship between precipitation inputs and streamflow outputs in a basin, measured across a range of temporal and spatial scales. The concept of hydrologic regimes will help to define the geomorphic and ecological variables that act on the landscape [36] and may serve as a key index for assessing interactions between physical hydrology and biological processes in ecosystems [31,33]. Also, because hydrologic regimes express the spatial and temporal scales of hydrologic processes, they may contribute to evaluating and distinguishing short-term from long-term environmental change [29].

Because precipitation and streamflow are expected to vary at multiple temporal and spatial scales, and because many scales of hydrologic behavior may be important and interconnected, we incorporate both traditional and new measures of hydrologic behavior to construct ecologically meaningful hydrologic regimes. Hydrologic regimes integrate precipitation inputs at timescales from seconds to multiple years, with inherent basin properties shaped by environmental gradients and disturbance histories. The hydrologic regime reflects interactions among many biophysical features of the

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ecosystem, including soils, snow, and the vegetation canopy, which has both passive (interception) and active (evapotranspiration) roles [22]. Traditional hydrologic measures such as precipitation/streamflow ratios, estimates of evapotransipiration, and baseflow/quickflow separations, reveal some important aspects of hydrologic regimes. However, these measures are usually compiled at annual or multi-year timescales, and therefore provide limited insight into links among climate, hydrology, and ecology. We develop additional measures of the hydrologic regime, based on the variability and the timing of precipitation and streamflow at multiple temporal and spatial scales. The multi-scale approach bypasses the pitfalls inherent in a priori selection of a single "correct" scale for studying ecological processes [25], and facilitates the identification of different inherent timing of water and related fluxes among basins.

This study characterized the hydrologic regimes at four forested sites in Oregon, North Carolina, New Hampshire, and Puerto Rico based on long-term, continuous precipitation and streamflow data. We examined over 600 basin-years of daily streamflow records from 18 basins at the four sites. This analysis was restricted to "control" basins, i.e. basins that have been unaffected by most forms of human disturbances since at least the 1930s and in some cases much longer periods. All study basins have forest vegetation and mountainous topography, but they vary in climate (from tropical to maritime temperate to continental temperate climates) and the age and type of forest vegetation. Hydrologic regimes were compared to identify dominant inherent scales of variability and timing of precipitation and streamflow at each site, and to predict the likely response to vegetation disturbance and climate change at the four sites.

2. Methods

This study used statistical methods to quantify the variability in precipitation, streamflow, and streamflow-precipitation relationships, among and within sites, at daily to multi-year timescales, and drew inferences from these relationships about roles of vegetation canopies, snow and soils at the four sites. The study was conducted using data from four, forested, long-term ecological research (LTER) sites: the H.J. Andrews (AND), in Oregon, Coweeta (CWT) in North Carolina, Hubbard Brook (HBR) in New Hampshire, and Luquillo (LUQ) in Puerto Rico (Fig. 1). These sites represent a range of climates and forest types, and they had excellent hydro-meteorological datasets initiated by the US. Forest Service (Tables 1 and 2). Each study site was visited, and data for this study were collected on landscape characteristics, instrumentation, climate and

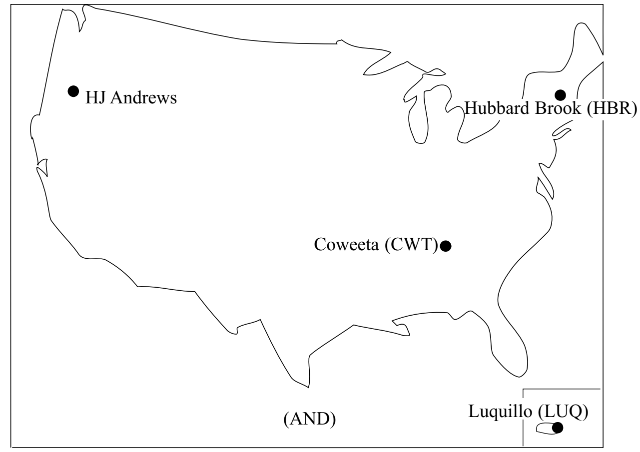

Fig. 1. Location of the four study sites: the H.J. Andrews (AND, Oregon), Coweeta (CWT, North Carolina), Hubbard Brook (HBR, New Hampshire) and Luquillo (LUQ, Puerto Rico) Long Term Ecological Research (LTER) sites.

streamflow, with particular emphasis on the 18 control basins (Table 2).

Analyses and comparisons were conducted at four temporal scales (average annual, inter-annual, monthly, and daily) and two spatial scales (within and across sites). Average annual analyses and comparisons were based upon data from all monitored basins at each site (32 altogether), including treated basins, but only for years without disturbance. Inter-annual analyses were based upon data from all control basins at each site (18 altogether; Table 2). Analyses at the monthly and daily timescales were based upon one or two selected control basins at each site: Andrews 2, Coweeta 2 and Coweeta 27, Hubbard Brook 3, and Luquillo 1.

2.1. Study sites

The Andrews Experimental Forest is located in the western Cascade Range of Oregon, in the northwestern United States (Fig. 1) (description based on [1,30,34]). We examined eight monitored basins, ranging in size from 9 to 101 ha (Table 2), with particular emphasis on three control basins: Andrews 2, 8, and 9. Detailed analyses were conducted using Andrews 2, whose hydrologic response is intermediate between that of Andrews 9 (low-elevation, steep, shallow soils) and Andrews 8 (high elevation, gentle slopes, deep soils). Streamflow records spanned 28–44 years (Table 2). Weir elevations range from 442 to 955 m. The climate is marine, with winter storms resulting from tropical marine air masses, and rare summer storms from convective processes. Mean monthly air temperature ranges from 1 °C in January to 19 °C in July. Average annual precipitation is 2200 mm at low elevations and 2500 mm at high elevations. Precipitation has a distinct winter maximum, with 80% falling between October and March. A sea-

Table 1
Characteristics of four forested, mountainous, long-term ecological research sites

	H.J. Andrews	Coweeta	Hubbard Brook	Luquillo[a]
Latitude	44°12′N	35°03′N	43°56′N	18°17′N
Longitude	122°12′W	83°25′W	71°45′W	66°45′W
Elevation (m)	410–1630	679–1592	222–1015	200–1075
Total area (ha)	6200	1626	3200	11491
Water year	Oct. 1–Sep. 30	May 1–April 30	June 1–May 31	Oct. 1–Sep. 30
No. of basins	8	17	8	3
Basin sizes (ha)	9–101	9–61	12–76	6–35
No. of control basins	3	7	5	3
Vegetation type	Evergreen needleleaf	Deciduous broadleaf	Deciduous broadleaf	Evergreen broadleaf
Dominant tree species	Douglas fir, western hemlock, western red cedar	Oak, pine	Beech, sugar maple, yellow birch	Tabonuco, palm, cecropia
Mean annual precipitation (mm)	2200	2300	1300	3600
Daily mean temperature range (°C)	1–19	3–22	−9–19	20–26
Snowpack	Transient	Rare to none	Seasonal	None

[a] All data for this study were collected at the Bisley basin, 200–450 m elevation, area ~50 ha.

Table 2
Characteristics of 18 selected control basins at four long-term ecological research sites

Site/basin	Size (ha)	Aspect	Forest type[a]	Year gaged	Years of record	Weir type[b]	Weir elevation (m)
Andrews							
Andrews 2	60	WNW	F	1952	44	A	548
Andrews 8	21	SSE	F	1963	33	A	993
Andrews 9	9	WSW	F	1968	28	A	432
Coweeta							
Coweeta 2	12	SSE	H	1936	60	B	709
Coweeta 14	61	NW	H	1936	60	B	707
Coweeta 18	12	NW	H	1936	60	B	726
Coweeta 27	39	NNE	H	1946	50	B	1061
Coweeta 32	41	ESE	H	1941	55	B	920
Coweeta 34	33	SE	H	1955	41	B	866
Coweeta 36	49	ESE	H	1943	53	B	1021
Hubbard Brook							
Hubbard Brook 1	12	SSE	N	1956	40	B	488
Hubbard Brook 3	42	SSW	N	1957	39	B	527
Hubbard Brook 6	13	SSE	N	1963	33	B	549
Hubbard Brook 7	76	NNW	N	1964	32	B	619
Hubbard Brook 8	59	NNW	N	1968	28	B	610
Luquillo							
Luquillo (Bisley) 1	7	NW	R	1987	9	C	263
Luquillo (Bisley) 2	6	NW	R	1987	9	C	269
Luquillo (Bisley) 3	35	NW	R	1987	9	C	268

[a] F: conifer; N: northern hardwoods; H: mixed hardwoods; R: tropical rainforest (see text).
[b] A: trapezoidal flume; B: v-notch; C: culvert.

sonal snowpack develops during winter at high elevations. Soils are fine-textured but porous and deep Inceptisols and Andisols developed on highly weathered andesite and basalt. The vegetation is conifer forest, dominated by Douglas fir and western hemlock, with some western red cedar.

The Coweeta Experimental Forest is located in the Smoky Mountains of North Carolina, in the southeastern US (Fig. 1) (description based on [4,41,44]). We examined 17 monitored basins, ranging in size from 9 to 61 ha (Table 2), with particular emphasis on the seven control basins: Coweeta 2, 14, 18, 27, 32, 34, and 36. The hydrologic response of these basins varied, and detailed analyses were conducted on Coweeta 2 (typical of low elevation basins with gentle slopes, deep soils, and low rainfall) and Coweeta 27 (typical of high elevation basins with steep slopes, shallow soils, and high rainfall). Streamflow records spanned 41–60 years (Table 2). Weir elevations range from 696 to 1061 m. The climate is humid marine, with winter storms influenced by subtropical marine air masses, and summer storms produced by local convective processes. Mean monthly air temperature ranges from 3 °C in January to 22 °C in July. Average annual precipitation ranges from 1870 mm at low elevations to 2500 mm at high elevations. Precipitation is relatively evenly spread throughout the year, with a slight maximum in March, and minimum in October. Snow contributes 2–10% to total precipitation. Soils are Inceptisols and Ultisols with a wide range of depths and textures, derived from highly weathered gneiss, sandstones, and schist. The vegetation is mixed hardwood forest, dominated by deciduous oak species, with an abundant evergreen understory consisting of rhododendron and mountain laurel shrubs.

The Hubbard Brook Experimental Forest is located in the White Mountains of New Hampshire, in the northeastern United States (Fig. 1) (description based on [7,26]). We examined eight monitored basins, ranging in size from 12 to 76 ha (Table 2), with particular emphasis on five control basins: Hubbard Brook 1, 3, 6, 7, and 8. Hydrologic response varied little among control basins, and detailed analyses were conducted using Hubbard Brook 3. Streamflow records spanned 28–40 years (Table 2). Weir elevations range from 442 to 619 m. The climate of the area is humid continental, with storms caused by convergence of polar continental and marine air masses. Mean monthly air temperature range from −9 °C in January to 19 °C in July. Average annual precipitation ranges from 1310 mm at low elevations to 1500 mm at high elevations and is evenly distributed throughout the year. The winter snowpack accumulates a water content of 200–400 mm in most years. Soils are coarse-textured, well-drained, shallow Spodosols derived from glacial till. The vegetation is deciduous northern hardwood forest (beech, sugar maple and yellow birch) with some conifers (balsam fir and red spruce) at high elevations or north-facing aspects.

The Luquillo Experimental Forest is located in the Luquillo Mountains of Puerto Rico (Fig. 1) (description based on [3,27,46]). In this study, we examined three monitored basins, ranging in size from 6 to 35 ha: Bisley 1, 2 and 3 (called Luquillo 1, 2, and 3 in this paper). These basins are all controls, because no treatments have been conducted. Hydrologic response varied little among control basins, and detailed analyses were conducted using Luquillo 1. Streamflow records spanned 8–9 years (Table 2). Weir elevations range from 262 to 270 m. The climate of the area is tropical marine, with frequent, low intensity storms produced by tropical marine air masses. Mean monthly air temperature ranges from 24 °C in December to 27 °C in July and August. Average annual precipitation is 3630 mm and is evenly distributed throughout the year. Soils are fine-textured Inceptisols and Ultisols developed on deeply weathered marine volcaniclastic rocks. The vegetation is tropical rainforest, dominated by broadleaf evergreen tree species (tabonuco, palm, and cecropia).

2.2. Conceptual approach

The approach taken in this study was to use statistical methods to systematically evaluate the relationship between precipitation and streamflow at a range of spatial and temporal scales, and draw inferences from these relationships about the hydrologic behavior of the basins. The relationship between precipitation and streamflow is

$$R = P - E - \Delta S, \tag{1}$$

where R is the streamflow, E the evapotranspiration, P the precipitation, and ΔS is the change in storage (including groundwater, soil, snow, and the vegetation canopy). Because the relationship between precipitation and runoff varies according to spatial and temporal scale, inferences could be drawn about the magnitude and timing of water storage in vegetation, snow, and soils, by examining the collected statistical analyses in conjunction with information about climate, vegetation, and disturbance history of each site.

Actual evapotranspiration (AET) was estimated as the difference between precipitation and runoff at the multi-year timescale, assuming that there is no net groundwater recharge, no net soil, snow or canopy. These results are shown in Table 3.

Baseflow and quickflow were separated using the Base Flow Index, as defined by the Institute of Hydrology [12]. Although this index has no direct physical meaning in terms of the pathways followed by the water within a basin [47], it is a useful device for comparing hydrologic responses across basins and sites. The minimum streamflow for all 5-day periods was calculated from the daily streamflow record, and the subset of 5-day minima that were less than 90% of adjacent 5-day minima were connected to create a baseflow separation line (Fig. 2). Streamflow above and below the line was defined as quickflow and baseflow, respectively. In cases in which the baseflow separation line exceeded total flow, baseflow was set equal to total flow.

2.3. Statistical analyses

Analyses consisted of estimating the variability in precipitation and runoff, and their relationships to each other, at various spatial and temporal scales. Two spatial scales were considered: the site (indexed $k, n = 4$), and the basin (indexed $i, n = 18$). Four temporal scales were considered: multi-year, annual (indexed i), monthly and daily (indexed t). At the multi-year timescale and site spatial scale, the relationship between precipitation and streamflow at the four sites (Andrews, Coweeta, Hubbard Brook, Luquillo) was

Table 3
Mean annual precipitation, streamflow, and evapotranspiration estimates for 18 selected control basins at four long-term ecological research sites

Site/basin	Mean annual precipitation (mm)	Mean annual streamflow (mm)	Streamflow/precipitation (%)	AET[a]	AET/precipitation (%)
Andrews					
Andrews 2	2257	1289	57	968	43
Andrews 8	2166	1185	55	981	45
Andrews 9	2267	1259	56	1007	44
Coweeta					
Coweeta 2	1761	807	46	954	54
Coweeta 14	1862	996	53	866	47
Coweeta 18	1931	1014	53	916	47
Coweeta 27	2404	1685	70	719	30
Coweeta 32	2206	1372	62	834	38
Coweeta 34	1996	1165	59	831	41
Coweeta 36	2227	1699	76	528	24
Hubbard Brook					
Hubbard Brook 1	1303	806	62	497	36
Hubbard Brook 3	1305	808	62	497	38
Hubbard Brook 6	1402	877	63	525	37
Hubbard Brook 7	1435	939	65	496	35
Hubbard Brook 8	1450	920	63	530	37
Luquillo					
Luquillo (Bisley) 1	3630	1805	50	1825	50
Luquillo (Bisley) 2	3630	1828	50	1802	50
Luquillo (Bisley) 3	3630	1842	51	1788	49

[a] Calculated from mean annual precipitation and streamflow, see text.

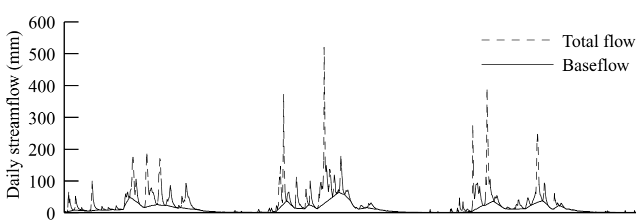

Fig. 2. Sample baseflow separation for Andrews 2, October 1959–October 1962.

$$R_k = a + bP_k + e, \quad (2)$$

where R_k is the mean annual streamflow at site k and P_k is the mean annual precipitationat site k, and e the errors; a the intercept of the fitted line, and b is the average proportion of mean annual precipitation delivered as runoff across sites. This line is designated as "all sites" in Figs. 3 and 4(a).

At the multi-year timescale and basin spatial scale, the relationship between precipitation and streamflow at the basins at each site was

$$R_{ik} = a_k + b_kP_{ik} + e_k, \quad (3)$$

where R_{ik} is the mean annual streamflow at basin i, site k and P_{ik} is the mean annual precipitation at basin i, site k, and e_k is the errors; b_k is the average proportion of mean annual precipitation delivered as runoff across the basins at a site. These lines and the points used to fit them, and hence the errors in model fit, are shown in Fig. 3(a). Mean annual streamflow for each basin was partitioned into quickflow and baseflow as described above; these values are shown in Fig. 3(b).

At the annual timescale and basin spatial scale, the relationship between precipitation and streamflow at each of the 18 control basins was:

$$R_{ij} = a_i + b_iP_{ij} + e_{ij}, \quad (4)$$

where R_{ij} is the annual streamflow at basin i in year j, and P_{ij} is the precipitation at basin i in year j, and e_{ij} is the errors, or unexplained residual variance at basin i in year j. The slope term b_i expresses the average additional streamflow from an increment in precipitation in basin i. The errors in the model indicate the variability of hydrologic response: the better the model fit, the more uniform is the response of annual streamflow to a change in annual precipitation at the basin. These fitted lines, and the points used to fit them, hence the errors in model fit, are shown in Fig. 4.

At the annual timescale and basin spatial scale, models similar to Eq. (3) were fit for quickflow and baseflow for each basin

$$Q_{ij} = a_{i1} + b_{i1}P_{ij} + e_{ij}, \quad (5)$$

$$B_{ij} = a_{i2} + b_{i2}P_{ij} + e_{ij}, \quad (6)$$

where Q_{ij} and B_{ij} are the annual quickflow and annual baseflow in basin i in year j, P_{ij} is the annual precipitation in basin i in year j, and e_{ij} are the errors. In this case the slope terms (b_{i1} and b_{i2}) depict the responses of

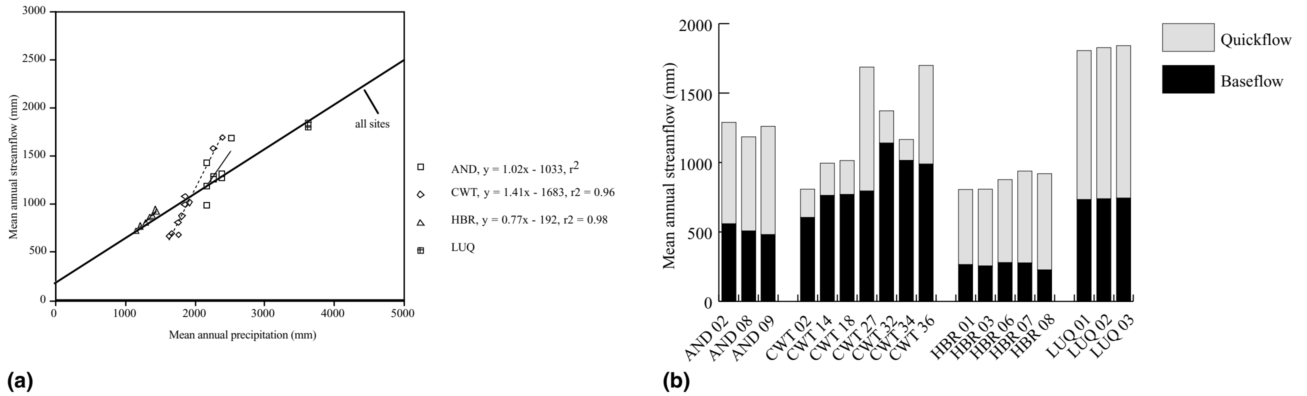

Fig. 3. Spatial variability in (a) mean annual precipitation vs. mean annual streamflow (Eq. (2)) and (b) baseflow and quickflow at 32 small experimental basins at the four study sites. Only 18 of the 32 basins in (a) are control basins; for the 14 treated basins calculations were based on only the pre-treatment years. The line designated as "all sites" is the fit using a single point (mean annual precipitation averaged across all basins and mean annual streamflow averaged across all basins) for each site.

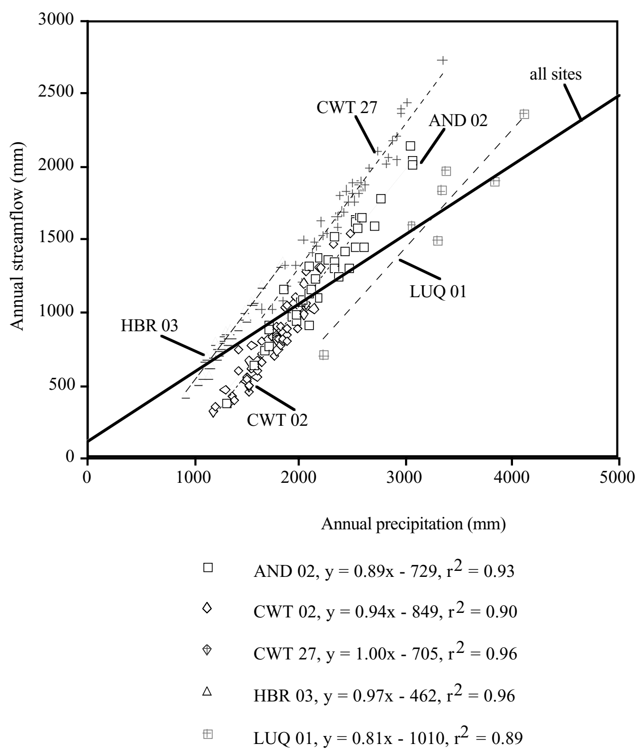

Fig. 4. Temporal variability at the interannual scale in streamflow vs. precipitation (Eq. (3)) at five selected basins: Andrews 2, Coweeta 2, Coweeta 27, Hubbard Brook 3, and Luquillo (Bisley) 1. The line designated as "all sites" is the fit using a single point (mean annual precipitation averaged across all basins vs. mean annual streamflow averaged across all basins) for each site.

quickflow and baseflow to an incremental input of precipitation in basin i. A high value of b_{i1} indicates that quickflow increases with increased precipitation; as b_{i1} approaches 1.0 as much as 100% of incremental precipitation is released as quickflow. A high value of b_{i2} indicates that baseflow increases with increased precipitation; as b_{i2} approaches 1.0 as much as 100% of incremental precipitation is released as baseflow. If $b_{i1} > b_{i2}$, quickflow is more responsive than baseflow; we interpreted this to mean that basin storage capacity is unable to absorb incremental precipitation, either because the storage reservoirs are small or because they are filled to capacity. If $b_{i1} < b_{i2}$, baseflow is more responsive than quickflow; we interpreted this to mean that storage capacity is able to absorb incremental precipitation, either because the storage reservoirs are large or because they are not filled to capacity. These slopes and some regression parameters are shown in Table 4.

Variability at the annual scale was compared to that at the monthly and daily timescale for a subset of basins (Andrews 2, Coweeta 2, Coweeta 27, Hubbard Brook 3, and Luquillo 1). Variability was quantified using the coefficient of variation (SD/mean) of precipitation, streamflow, and streamflow:precipitation ratios. These measures quantify the range of inputs that the basin receives, and the outputs that it produces. The CV for precipitation is a measure of the variability of the climate system at various scales. The CV for streamflow is a measure of the combined effects of precipitation variability and basin characteristics that dampen or accentuate the variability of precipitation inputs. The CV for streamflow:precipitation is a measure of the degree to which streamflow is a consistent proportion of precipitation, or how strongly coupled streamflow is to precipitation. Overall, the CVs illustrate the structure of the climate system, and the degree to which the basin serves as a capacitor, acting to dampen the variability of precipitation inputs in the process of converting them to streamflow outputs. Important differences among the sites are revealed by three kinds of comparisons: (1) among sites at a given timescale; (2) across scales for a given site; and (3) how CVs change with time scale among sites. CVs and their ranks by site are shown in Table 5.

Table 4
Regression relationships between annual precipitation (independent variable) and annual streamflow (dependent variable) for 18 selected control basins at four long-term ecological research sites (Eqs. (4) and (5))

Site/basin	Number of years	r^2	Intercept	Slope	Baseflow slope (%)	Quickflow slope (%)
Andrews						
Andrews 2	38	0.93	−724	89	32	57
Andrews 8	33	0.83	−672	86	33	53
Andrews 9	28	0.93	−711	87	34	53
Coweeta						
Coweeta 2	58	0.90	−849	94	64	30
Coweeta 14	54	0.92	−704	91	66	25
Coweeta 18	58	0.92	−883	98	67	31
Coweeta 27	48	0.96	−705	100	44	56
Coweeta 32	38	0.88	−599	89	70	19
Coweeta 34	33	0.90	−658	91	74	17
Coweeta 36	52	0.92	−728	100	52	58
Hubbard Brook						
Hubbard Brook 1	39	0.95	−437	95	21	74
Hubbard Brook 3	37	0.96	−463	97	17	80
Hubbard Brook 6	31	0.96	−421	93	21	72
Hubbard Brook 7	30	0.96	−350	90	21	69
Hubbard Brook 8	26	0.97	−416	92	17	75
Luquillo[a]						
Luquillo (Bisley) 1	8	0.89	−1010	81	43	38
Luquillo (Bisley) 2	8	0.90	−1236	89	45	44
Luquillo (Bisley) 3	8	0.92	−1190	87	46	41

Slope terms are expressed as mm of annual streamflow, baseflow, or quickflow associated with a 100 mm increase in annual precipitation, based on linear regressions.
[a] 1988 was excluded from the analyses for Luquillo.

Table 5
Coefficients of variation (CV) for precipitation, streamflow, and streamflow:precipitation ratios at daily, seasonal, and annual timescales, for 18 selected control basins at four long-term ecological research sites

	Daily		Seasonal		Annual	
Basin	CV	Rank	CV	Rank	CV	Rank
Precipitation						
Andrews 2	2.1	4	0.7	1	0.18	2
Coweeta 2	2.5	1	0.3	2	0.16	3
Coweeta 27	2.4	2	0.3	2	0.15	4
Hubbard Brook 3	2.3	3	0.3	2	0.14	5
Luquillo (Bisley) 1	1.8	5	0.3	2	0.28	1
Streamflow						
Andrews 2	1.8	2	0.9	1	0.30	3
Coweeta 2	1.0	5	0.7	3	0.34	1
Coweeta 27	1.3	4	0.5	4	0.22	5
Hubbard Brook 3	2.2	1	0.8	2	0.23	4
Luquillo (Bisley) 1	1.7	3	0.4	5	0.32	2
Streamflow:precipitation						
Andrews 2	2.6	3	0.9	1	0.15	3
Coweeta 2	2.0	5	0.5	3	0.21	1
Coweeta 27	2.0	4	0.3	4	0.08	5
Hubbard Brook 3	3.7	1	0.8	2	0.10	4
Luquillo (Bisley) 1	3.1	2	0.3	5	0.18	2

At the monthly and daily timescales, we calculated autocorrelation coefficients for precipitation and adjusted cross-correlations between precipitation and for a subset of basins (Andrews 2, Coweeta 2, Coweeta 27, Hubbard Brook 3, and Luquillo 1). Autocorrelations in precipitation measure the duration and spacing of precipitation inputs at a basin. We fitted autocorrelation models to precipitation data

$$P_t = a_1 P_{t-1} + a_2 P_{t-2} + \cdots + a_n P_{t-n}, \quad (7)$$

where a_1 is the correlation between precipitation in the current time period (t) and precipitation one time period in the past ($t-1$), and a_n is the correlation between precipitation in the current period and precipitation n time periods in the past. "Lag" is defined as the number of time periods (e.g. days, months) from time zero for a given autocorrelation coefficient. The resulting autocorrelation coefficients (one for each time lag) were connected with straight line segments and are plotted as curves of autocorrelation (Y axis) vs. lag (X axis), one for each site, in Figs. 5(a) (daily) and (b) (monthly).

Our interpretations of autocorrelation results are drawn from [6,24]. Significant autocorrelations were defined as those exceeding $2\times$ the standard error. The shortest lags at which positive significant autocorrelations occur (the left-most high point in the autocorrelation curve for a site) are a measure of the average duration of wet seasons (at the monthly scale) or precipitation events (at the daily scale) for that site. If a second set of positive, significant autocorrelations occurs, it is a measure of the average spacing between seasons (at a monthly scale) or precipitation events (at a daily scale). If significant negative autocorrelations occur (i.e., the curve falls significantly below zero), they are a measure of the average duration of periods without precipitation, i.e. dry seasons (at a monthly scale) or dry periods between precipitation events (at a daily scale).

Cross-correlations between precipitation and streamflow measure the time elapsed between a precipitation input and a streamflow output, or the strength and persistence of coupling between precipitation and streamflow, at a basin. We fitted cross-correlation models to streamflow and precipitation data:

$$R_t = c_0 P_t + c_1 P_{t-1} + c_2 P_{t-2} + \cdots + c_n P_{t-n}, \quad (8)$$

where c_0 is the correlation between streamflow and precipitation in the current period, and c_n is the correlation between streamflow in the current period and precipitation n time periods in the past. Lags at which positive significant cross-correlations occur indicate the average number of months or days between a precipitation input and a streamflow output. However, these

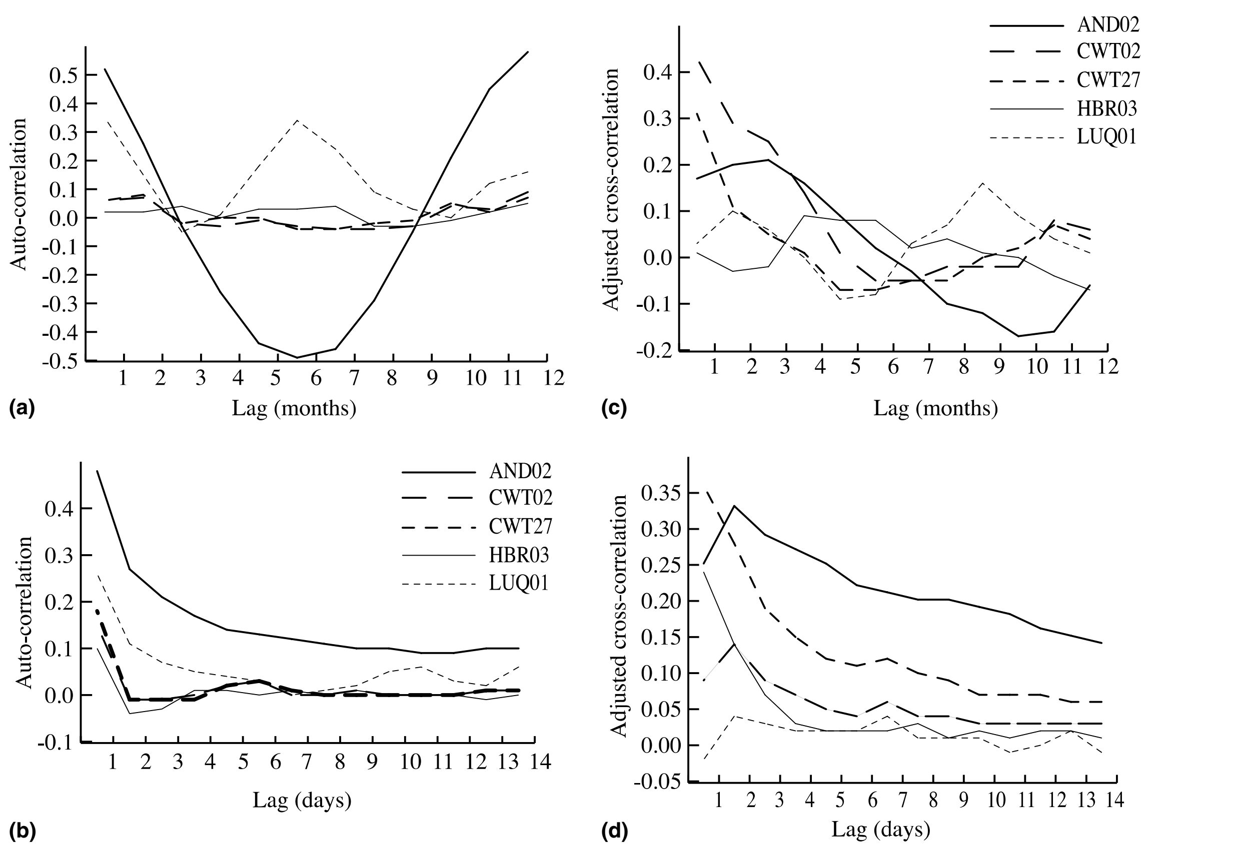

Fig. 5. Temporal variability shown by (a) and (b) plots of autocorrelation of precipitation (Eq. (6)) vs. time lag, and (c) and (d) cross-correlations of precipitation and streamflow (Eqs. (7) and (8)) vs. time lag. Correlations are shown at monthly timescales (a) and (c) and daily timescales (b) and (d) at five selected basins: Andrews 2, Coweeta 2, Coweeta 27, Hubbard Brook 3, and Luquillo (Bisley) 1. Auto- and cross-correlations were considered to be significant if they fell outside the 95% confidence interval around the null hypothesis of no correlation (i.e. zero), defined as 2 *times* the standard error of the correlation coefficients. These confidence intervals for monthly auto- and cross-correlations were: ±0.092 for Andrews 2; ±0.074 for Coweeta 2; ±0.082 for Coweeta 27; ±0.094 for Hubbard Brook 3; and ±0.2 for Luquillo 1. Confidence intervals for daily auto- and cross-correlations were: ±0.016 for Andrews 2; 0.014 for Coweeta 2; ±0.014 for Coweeta 27; ±0.016 for Hubbard Brook; and ±0.036 for Luquillo 1.

cross-correlations incorporate both precipitation patterns and the processing of precipitation by the basin. Therefore, to remove autocorrelation present in the precipitation record, we combined Eqs. (6) and (7) to define an adjusted cross-correlation term

$$c'_n = c - a \tag{9}$$

and c'_0 is a measure of the basin's capacity to store and release moisture from precipitation inputs.

These corrected cross-correlations (one for each time lag) were connected with straight line segments and shown as a curve, one for each site; in Figs. 5(c) (daily) and (d) (monthly). We interpreted lags at which positive values of c' occur to indicate the timing of net release of stored precipitation; the longer the lag, the greater is the duration of water storage between precipitation input and its release as streamflow.

3. Results

Hydrologic regimes for the four sites were constructed based upon measures of variability and timing of precipitation, streamflow and streamflow–precipitation relationships between sites vs. within sites, at multi-year, annual, monthly, and daily timescales. The hydrologic regimes are used as the basis for inferences about the roles of vegetation, snow, and soil, described in Section 4.

3.1. Multi-year timescales

The relationship between mean annual precipitation and mean annual streamflow differed within and among sites (Fig. 3(a)). Mean annual precipitation and mean annual streamflow were lowest at Hubbard Brook and highest at Luquillo. Mean annual streamflow at all four forested sites on average was about 50% of precipitation. Baseflow ranged from 25% of mean annual streamflow in basins at Hubbard Brook to 80% in high-elevation basins at Coweeta (Fig. 3(b)).

Spatial variability of streamflow was low at Hubbard Brook and Luquillo, and high at Coweeta and Andrews, but spatial variability of precipitation and baseflow/quickflow partitioning was low at all sites except Coweeta at the multi-year scale (Fig. 3). Control basins at all four sites range from 9 to 76 ha (Table 2), and maximum distances between control basins at each site are <0.5 km (Luquillo), 3.6 km (Coweeta), 4.7 km (Hubbard Brook), and 10 km (Andrews). Mean annual streamflow (at control basins and treated basins for untreated years only) varied by <100 mm among basins at Luquillo, roughly 200 mm at Hubbard Brook, 800 mm at Andrews, and 1200 mm at Coweeta (Fig. 3(a)). Mean annual precipitation varied among basins by a few hundred mm at Andrews, Hubbard Brook, and Luquillo, but by 800 mm at Coweeta (Fig. 3(a)). Baseflow varied over <50 mm among basins at Luquillo, <100 mm at Hubbard Brook and Andrews, and 600 mm at Coweeta (Fig. 3(b)).

Spatial variability in mean annual streamflow was closely related to precipitation at Hubbard Brook ($r^2 = 0.98$) and Coweeta ($r^2 = 0.96$) but not at the Andrews ($r^2 = 0.49$) (Fig. 3(a)). Mean annual streamflow was much more sensitive to differences in mean annual precipitation at Coweeta than at Hubbard Brook. A 100 mm increase in mean annual precipitation was associated with a 140 mm increase in mean annual streamflow among basins at Coweeta, but only a 77 mm increase at Hubbard Brook (Fig. 3(a)).

Evapotranspiration accounted for one-fourth to one-half of mean annual precipitation in control basins; much of this variability was among basins at Coweeta (Table 3). AET hardly varied among control basins within Hubbard Brook, Andrews, or Luquillo, but it ranged from 25 to 55% of mean annual precipitation in control basins at Coweeta.

3.2. Annual timescales

The relationship between annual precipitation and annual streamflow varied within and among sites (Table 4, Fig. 4). Overall, annual precipitation was closely related to annual streamflow over the periods of record at control basins at all four sites ($r^2 > 0.80$). Absolute values of intercept terms indicate that storage reservoirs were smallest at Hubbard Brook, largest at Luquillo, and intermediate at Coweeta and Andrews (Table 4, Fig. 4). However, annual streamflow was most responsive to changes in annual streamflow at Coweeta and least responsive at Luquillo. An increase of 100 mm in annual precipitation was associated with an increase of 100 mm in annual streamflow at Coweeta 27, 97 mm at Hubbard Brook 3, 94 mm at Coweeta 2, 89 mm at Andrews 2, and 81 mm at Luquillo 1 (Fig. 4, Table 4).

Streamflow response to increases in annual precipitation was dominated by baseflow at low-elevation Coweeta basins, by baseflow and quickflow at Luquillo and at high-elevation Coweeta basins, and by quickflow at Andrews and Hubbard Brook (Table 4). At the low-elevation Coweeta basins (Coweeta 2, 14, 18, 32, and 34) baseflow increased by 64 to over 70 mm for every 100 mm of incremental precipitation, but quickflow increased by only 15–30 mm. At the high-elevation Coweeta basins (Coweeta 27 and 36), quickflow and baseflow both increased by roughly 50 mm for each 100 mm-increment of annual precipitation. At Luquillo, quickflow and baseflow both increased by approximately 40 mm for each 100 mm-increment of annual precipitation. At Andrews, quickflow increased by roughly 55 mm, but baseflow increased by only about 30 mm for every 100 mm of incremental precipitation

(Table 4). At Hubbard Brook, quickflow increased by 70 mm or more, but baseflow increased by 20 mm or less for every 100 mm of incremental precipitation (Table 4).

3.3. Monthly timescales

Long-term monthly precipitation records reveal strong seasonality in precipitation at Andrews and Luquillo, and no significant seasonality at Coweeta or Hubbard Brook (Fig. 5(a)). Precipitation is significantly positively autocorrelated for months 1, 2, and 9–12 at Andrews, indicating the annual wet and dry seasons, and for months 1 and 6 at Luquillo, indicating two annual periods of relatively wet climate conditions.

Streamflow is significantly positively correlated with precipitation over lags of four months at Andrews and Coweeta 2 (low elevation), and for one month period at Coweeta 27 (high elevation). Streamflow was not significantly correlated with precipitation at any lag at Luquillo. At Hubbard Brook, streamflow was marginally significantly positively coupled with precipitation for a three-month period at a lag of four to six months (Fig. 5(c)). In basins at Andrews and at Coweeta low elevations, precipitation is stored and released as streamflow over a four-month period. At Coweeta the high-elevation basin stores moisture and releases it as streamflow over a one-month period. At Hubbard Brook, the basin has a capacity to store moisture without releasing it for several months, and then releases it as streamflow over a three-month period, four months later.

3.4. Daily timescale

Long-term daily precipitation records reveal longer, less distinctly defined precipitation events at Andrews and Luquillo, and shorter, discrete events at Coweeta and Hubbard Brook (Fig. 5(b)). At Andrews and Luquillo, the precipitation record was dominated by multiple-day events, with no single dominant scale or spacing. At Coweeta and Hubbard Brook, the dominant scale of precipitation events was 1–2 days, with a slight tendency for events to be spaced at a few days intervals.

Streamflow is significantly positively correlated with precipitation for at least two weeks at Andrews 2, Coweeta 2 (low elevation), and Coweeta 27 (high elevation), and for 4–6 days at Hubbard Brook and Luquillo (Fig. 5(d)). At Andrews and at Coweeta, the basins store and release moisture over a two-week period after a precipitation event, whereas storage and release occurs within less than a week at Hubbard Brook 3 and Luquillo 1. At basins with relatively shallow soils (Coweeta 27 (high elevation) and Hubbard Brook 3), streamflow declines steadily relative to precipitation, but at basins with relatively deep soils (Andrews 2, Coweeta 2, and Luquillo 1), streamflow peaks on the second day after a precipitation input.

3.5. Relative scales of variability from annual to daily

Overall, variability in precipitation and streamflow:precipitation ratios declined by an order of magnitude, and variability in streamflow declined by a factor of 5, from daily to annual timescales, but the five basins differed in their ability to preserve, dampen, or amplify the variability of precipitation inputs as they were converted to streamflow outputs (Table 5).

For precipitation, the decline in CV with increasing timescale is a measure of the relative importance of different aspects of the climate system at a site. For precipitation, this decline is steepest at Coweeta 2, Coweeta 27, and Hubbard Brook 3 (ranks decline by two units from daily to annual timescales) and gentlest at Luquillo 1 (ranks increase from 5 to 1) (Table 5). We interpret this to mean that precipitation inputs are dominated by convectional storms (daily events) at Coweeta and Hubbard Brook, but by large marine cyclones influenced by the ocean conveyor belt at Luquillo. Intermediate CV declines at Andrews 2 reflect precipitation inputs dominated by multi-day storms from tropical marine cyclones.

For streamflow, the decline in CV with increasing timescale is a measure of the relative importance, across timescales, of the combined influences of precipitation inputs and basin characteristics that dampen or amplify precipitation variability at a site. For streamflow:precipitation, the decline in CV with increasing timescale is a measure of how the tightness of coupling between streamflow and precipitation changes with timescale. For both streamflow and streamflow:precipitation, the decline in CV with increasing timescale is steepest at Hubbbard Brook 3 (ranks decrease from 1 to 4 from daily to annual timescales) and gentlest at Coweeta 2 (low elevation, ranks increase from 5 to 1) (Table 5). Of the sites in this study, Hubbard Brook has the most limited capacity to dampen fluctuations in daily precipitation, perhaps because of shallow, coarse-textured soils, whereas Coweeta 2 (low elevation) has the greatest capacity to dampen fluctuations in daily precipitation because of its deep, highly weathered soils. At the annual timescale, streamflow at Hubbard Brook is more strongly coupled with precipitation than at any other site, perhaps because shallow soils transmit winter precipitation inputs and spring snowmelt as streamflow during times when vegetation is inactive. In contrast, annual precipitation at Coweeta 2 is less coupled with annual streamflow than at any other site, perhaps because it contains deep storage reservoirs in soils that carry over moisture from one year to another.

Across all sites, the declines in CVs from daily to annual timescales are steepest for streamflow:precipitation, and gentlest for precipitation (Table 5). We interpret this to mean that basin characteristics that decouple streamflow from precipitation are most strongly expressed at the daily and seasonal timescales by such factors as moisture reservoirs in soil, snow, and vegetation, and least strongly expressed at the interannual timescale.

4. Discussion

Hydrologic regimes of headwater basins differ significantly among and within the forested sites we examined in Oregon, New Hampshire, North Carolina, and Puerto Rico (Table 6). Generally, each site is a combination of environmental gradients and disturbance histories that influence hydrologic regimes at various scales, and each site can be characterized according to the scales, from daily to multi-year, at which its hydrologic system is dominated. By comparing hydrologic regimes, we can draw inferences about the relative roles of forest canopies, snow, and soils at these four sites. Also, these varying hydrologic regimes have important implications for biogeochemical cycling, stream ecology, and hydrologic response to disturbance and climate change.

4.1. Hydrologic regimes

Headwater basins at Hubbard Brook had the simplest hydrologic regimes of the basins in this study: their hydrologic response was dominated by variability at two scales: daily and monthly (Table 6). Daily scale responses are attributable to the timing of precipitation inputs (dominated by single-day events spaced by relatively dry intervals) combined with the shallow, coarse-textured soils and relatively steep slopes, which appear to transmit most water inputs rapidly to stream channels. The monthly scale, lagged response (Fig. 5), and the strong coupling of streamflow to precipitation at the annual timescale (Table 5) are attributable to the accumulation and melt of a seasonal snowpack, combined with the tendency of the soils to rapidly transmit snowmelt to channels. The basins at Hubbard Brook are spatially homogenous in their hydrologic behavior, perhaps because they were shaped by recent (Holocene) glaciation.

Headwater basins at Luquillo (the Bisley basins) had a somewhat more complex hydrologic regime than Hubbard Brook: hydrologic response at Luquillo was dominated by variability at two scales: daily and multi-year (Table 6). The daily scale responses are attributable to short precipitation inputs, which include daily orographic storms, whose inputs are transmitted on the scale of hours to stream channels by shallow saturated flow through numerous macropores in the upper 0.5 m of soil in these small (<10 ha) basins (F. Scatena, pers. comm.). Annual and interannual scale responses are attributable to moisture storage in the very deep (9 m) clay soils, which appears to be slowly released into stream channels as baseflow. Multi-year variability also was expressed more strongly at Luquillo (Bisley) than at

Table 6
Summary of hydrologic regimes at four forested, mountainous, long-term ecological research sites

	Andrews	Coweeta low elevation	Coweeta high elevation	Hubbard Brook	Luquillo
Precipitation variability among basins	Moderate	High	High	Moderate	Low
Streamflow variability among basins	High	High	High	Low	Low
Baseflow variability among basins	Low	High	High	Low	Low
Annual baseflow response to precipitation	Low	High	Moderate	Low	Low
Annual quickflow response to precipitation	Moderate	Low	Moderate	High	Low
Dominant timescale of variability					
Precipitation	Seasonal	Daily	Daily	Daily/seasonal	Annual
Streamflow	Seasonal	Annual	Daily/seasonol	Daily	Annual
Streamflow/precipitation	Seasonal	Annual	Daily/seasonal	Daily	Daily/annual
Dominant temporal patterns, lags					
Precipitation event duration (days)	1–5	1	1	1	1–6
Months between wet and dry seasons	6	n/a	n/a	n/a	3
Streamflow response lag (days)	1–14	1–14	1–14	1–4	1–6
Lag of maximum streamflow response (days)	2	2	1	1	2
Seasonal storage lags (months)	1–5	1–5	1–2	4–6	n/a
Lag of maximum seasonal storage (months)	3	1	1	4	n/a

Each aspect of the hydrologic regime at a site was ranked as high, moderate, or low based on information in Tables and Figures. Precipitation and streamflow variability were ranked based on their ranges in Figs. 3 and 4; baseflow variability was ranked based on Fig. 3(b). Annual baseflow and quickflow responses to precipitation were based upon the slopes of regressions in Table 4. Dominant timescales of variability were based upon the highest ranking coefficients of variation in a given row in Table 5. Dominant temporal patterns and lags were based upon the statistically significant lags of autocorrelation and cross-correlation analyses in Fig. 5. The entry "n/a" means that there was no statistically significant correlation at any lag.

other sites; this may be attributable to variation in precipitation inputs associated with ocean and atmospheric dynamics that affect the periodicity of hurricanes. Basins at Luquillo (Bisley) are spatially homogenous in their hydrologic behavior, because they are spaced at less than 0.5 km from one another.

Headwater basins at Coweeta had more complex hydrologic regimes than Hubbard Brook or Luquillo, in the sense that hydrologic response varied both spatially and temporally among the monitored basins. Hydrologic response was dominated by monthly and multi-year variability at low elevations but by daily and monthly variabilities at high elevations. Much of the variability in hydrologic response is attributable to differences in rainfall amount, soil depth (soil water storage and release) and topography [17,19,44]. The low elevation response is attributable to the deep, relatively fine textured soils, which apparently require up to two days to transmit precipitation inputs to stream channels, and may continue to contribute water as baseflow for up to 5 months. The high elevation response is attributable to relatively shallow, coarser-textured soils that transmit precipitation inputs to the stream channel on average within one day, but only contribute baseflow for up to 2 months.

Headwater basins at Andrews had the most complex hydrologic regimes of the basins examined in this study, in the sense that hydrologic response varied both spatially and temporally at multiple scales. Hydrologic response was variable at daily, weekly, seasonal, and multi-year time scales. Daily variability is attributable to a network of ephemerally saturated zones (macropores) at shallow (<1 m) depths [14], which appear to transmit precipitation inputs to stream channels on average within a day. However, precipitation events often last for multiple days, and soils are deep and fine-textured, so they may store considerable moisture and release it over many days, weeks, and months after a precipitation input. Multi-day and monthly scale variation in streamflow at Andrews also may be due to the accumulation and melt of a transient snowpack (at low elevations) or a seasonal snowpack (at high elevations) [15,30] (see also Harr [16]). Seasonal variability of precipitation inputs (which does not occur at the other sites) creates pronounced seasonal variability in streamflow. Multi-year cycles in precipitation also are evident in the precipitation and streamflow record. In addition, spatial variability in hydrologic response is attributable to differences in the degree of weathering of underlying volcanic substrates, as well as to spatial variation in the types and styles of mass movements [42].

4.2. Forest canopy roles in hydrologic regimes

Forest canopies play different roles at the four sites; these can be distinguished according to the type of process (interception, evapotranspiration) and the timing (daily, seasonal, interannual). At Hubbard Brook, deciduous forest canopies play a dual hydrologic role. During the months when dominant forest vegetation is leafless, its hydrologic role is principally exerted through interception (primarily of snow), whereas during summer months, the interception role of the forest canopy may be less important than its water uptake (evapotranspiration). However, because of the short period when deciduous forest is in leaf, actual evapotranspiration accounts for less precipitation at Hubbard Brook than at any other site except Coweeta 27 (only 35–40% of precipitation on a mean annual basis).

Tropical rainforest canopies play an important role at daily and annual timescales at Luquillo. Evergreen broadleaf vegetation at Luquillo has a high leaf area to intercept precipitation, and is able to evapotranspire year-round because of uniform high air temperatures; hence actual evapotranspiration accounts for 50% of mean annual precipitation. The forest is regularly bathed in moist marine air masses, and intercepts over 40% of rainfall [35]. The Bisley basins have never been completely deforested but did support shade coffee 80–100 years ago and selective logging 75 years ago. Six hurricanes passed over Puerto Rico in the past century, two of which (in 1932 and 1989) passed directly over Luquillo [9]. In 1989 the basins were completely defoliated by the hurricane and were recovering during the period of this study [38]. The post-1989 hurricane forest canopy at Luquillo is irregular, with emergent tabonuco trees on ridgetops, and an understory of palms and woody vegetation with leaf area indices ranging from 2 in ravines to 12 on ridgetops [39]. During daily showers, forest canopies may intercept very large portions of precipitation inputs [39]), whereas on a multi-year basis they have an extremely rapid recovery of water use following natural disturbances such as hurricanes [38].

At Coweeta, deciduous forest canopies play an important, temporally and spatially varying role: in winter when canopies are leafless, their hydrologic role may be dominated by interception (possibly including some snow interception at high elevations), whereas in summer they exert a strong hydrologic influence through water uptake. Forests at Coweeta were affected by fire and windthrow 150 years ago, cultivation and grazing 80–100 years ago, and extensive logging 75 years ago [4,5], and the current second-growth forests are dominated by deciduous species. Because of soil depth and soil moisture availability, combined with the short period when the forest is in leaf, actual evapotranspiration accounts for only 25–40% of precipitation on a mean annual basis at high-elevation basins with shallow soils, but over 50% at the low-elevation basins with deep soils.

The conifer forest canopy at Andrews has a strong hydrologic role at daily and seasonal timescales, and its role varies with elevation. Forests were never cleared at the Andrews basins in this study, but they were affected by fire 450 and 150 years ago [45]. The forest canopy is structurally complex, and interception and transpiration may be controlled in certain seasons by deciduous trees (e.g. vine maple, *Acer circinatum*) and evergreen shrubs (e.g. *Arctostaphylus*, *Ceanothus* and *Rhodedendron* spp.) in understory gaps [10,13,40]. Canopy interception may be very important in fall and spring when rainfall events are relatively short, and during winter snow events, especially at high elevations. Also, in fall and spring, conifer canopies are actively transpiring and visibly influence soil moisture and streamflow. In summer, a period of soil moisture stress at Andrews, we infer that the forest canopy may be less hydrologically important than understory vegetation, perhaps because of greater sensitivity to vapor pressure deficits or low leaf water potentials.

4.3. Snow roles in hydrologic regimes

Snow plays an important role in the hydrologic regime at the Andrews and Hubbard Brook, but is not important or nonexistent at Coweeta and Luquillo. Snow accumulation and melt exerts an important influence upon the daily hydrograph at the Andrews [22] (see also Harr [16]), upon the seasonal hydrographs at Andrews and Hubbard Brook, and upon the interannual hydrograph at Hubbard Brook. At the Andrews and Hubbard Brook, seasonal snowpacks store and release soil moisture at a time closer to the time of summer vegetation physiological activity than would be possible otherwise, especially given the limited soil moisture storage capacities at Hubbard Brook. At the Andrews, transient snowpacks which accumulate and melt at daily or weekly timescales also contribute to net storage and delayed release of moisture.

4.4. Soil roles in hydrologic regimes

Soil properties and landforms exert important influences upon hydrologic regimes in the four study sites, through macropore flow, water storage in the soil matrix, and deep subsurface/groundwater flowpaths. Extremely rapid hydrologic responses at Luquillo and the Andrews are suggestive of rapid shallow subsurface saturated flow in macropores. Consistently rapid hydrologic responses at Coweeta 27, and inability to store snowmelt in basins at Hubbard Brook imply the existence of short flowpaths and relatively little groundwater storage in these basins. Intermediate responses, i.e. baseflow contributions for up to a month on average, at Coweeta high elevation and Andrews basins suggest that water may also be stored and drained from relatively fine-textured soil matrices. The most protracted hydrologic responses, i.e. water release over many months or even years at Luquillo, low-elevation Coweeta, and Andrews basins imply that these basins have the longest flowpaths through deep, fine-textured soil or fractured bedrock.

4.5. Implications for biogeochemical cycling and stream ecology

Based upon their hydrologic regimes, we offer some hypotheses about biogeochemical cycling behavior in headwater basins at the four sites. These are offered as hypotheses to stimulate intersite comparisons, because to our knowledge, formal work comparing the temporal scales of biogeochemical cycling has not been conducted. Hypotheses such as these, based on physical processes (water flow) can be considered null hypotheses, because chemical and biological factors would be expected to alter the expression of the hydrologic regime in biogeochemical fluxes (see e.g. [23]). At Hubbard Brook, the hydrologic regime implies that nutrient throughput would occur very rapidly, on the scale of days, or seasonally, via nutrient accumulation and flushing associated with deciduous canopies and seasonal snowpacks. At Luquillo, biogeochemical cycling could occur at timescales ranging from hourly to multi-year, associated with nutrient interception and retention in canopies, macropore flow, water storage and release from the soil matrix, and deep flowpaths in highly weathered soil. At Coweeta, cycling of nutrient inputs through headwater basins would be expected to occur at daily to monthly timescales (associated with shallow and deep soil drainage). Nutrient cycling at Coweeta would be expected to occur more rapidly at the higher elevation basins where soil flowpaths appear to be shorter than at low elevations. At Andrews, biogeochemical cycling pathways could be quite complex, with conifer forest canopies intercepting and retaining nutrients, soil path lengths varying from daily to seasonal, and snowpack storage and release at daily to monthly timescales, depending upon elevation.

Stream ecological properties differ at each of the four sites, in part because of their hydrologic regimes. Stream ecology at the Andrews is dominated by temporal and spatial patterns of hydrologic and geomorphic disturbances, including floods and landslides, and post-disturbance responses or recovery [11,43]. Ecological properties of streams at Coweeta are tied to strong seasonality of flow and litter inputs and their spatial variability in basins with slow (low elevation) versus fast (high elevation) hydrologic responses [21,28]. Ecological properties of streams at Hubbard Brook are tied to the relative timing of snowpack melting and leafout [8,20]. At Luquillo, stream ecology is dominated by high turnover rates and rapid recovery from hurricane disturbances [36,37].

4.6. Possible effects of climate change and vegetation shifts

The likely short-term effects of climate change (increases in mean annual temperature or precipitation) depend upon the importance of the affected storage reservoir at a given site. Short-term responses are those which precede vegetation responses to climate change. For example, an increase in mean annual temperature might produce quite different short-term responses at the northern sites, where snow reservoirs influence streamflow, compared to the southern sites, where snow is absent or not important. At Hubbard Brook and Andrews, higher temperatures might reduce snowpack accumulation; winter streamflow would increase but spring streamflow would decline, possibly limiting water availability and evapotranspiration by deciduous vegetation by late spring. At Luquillo and Coweeta, higher mean annual temperatures might increase evapotranspiration and reduce streamflow in all seasons (Luquillo), or only in the summer (Coweeta). On the other hand, an increase in mean annual precipitation might differentially affect basins with deep soils compared to those with shallow soils. In basins with large soil storage reservoirs at Andrews or Coweeta, additional precipitation could be stored and might augment streamflows months later. In contrast, in basins with shallow soils at Coweeta, and all basins at Hubbard Brook and Luquillo, additional precipitation would augment streamflow from within a few days to a month.

Short-term effects of changes in the temporal distribution of precipitation also can be predicted based on the coherence of precipitation with streamflow at each site. For example, streamflow at Hubbard Brook and the high-elevation Coweeta basins would be more affected than other basins in this study in response to a change in the timing and duration of storms, because most precipitation is converted to streamflow within a day at these basins.

If the forest canopy changes character in the long term, hydrologic responses will depend upon the importance of the canopy, soil, and snow reservoirs at each site. The most notable shift would be from broadleaf deciduous to needleleaf evergreen forest, or the reverse. Both Coweeta and Hubbard Brook are currently dominated by broadleaf deciduous forest, while Andrews is currently dominated by needleleaf evergreen forest and Luquillo is dominated by broadleaf evergreen forest. At Coweeta low-elevation basins, where soil moisture is rarely limiting, Swank and Crossley [41] reported that a shift from deciduous to evergreen forest canopy increased interception and evapotranspiration losses and reduced streamflow throughout the year, especially during seasons when deciduous forests were leafless. However, at Hubbard Brook, a shift from deciduous to evergreen might augment summer streamflow, if evergreen forest is more sensitive than broadleaf forest to summer soil moisture deficits. At Andrews, on the other hand, a transition from evergreen forest to broadleaf shrubs and trees was associated with a reduction in summer streamflow, apparently because the broadleaf species are less sensitive than needleleaf trees to summer soil moisture and vapor pressure deficits [2,18].

Hydrologic regimes at these four forested long-term ecological research sites reveal important links between climate, hydrology, and stream ecology. Different types and roles of forest canopy, snow, and soil reservoirs contribute to distinctly different hydrologic regimes. Different dominant scales of variability and coherence of water fluxes in the ecosystem in turn influence salient stream ecological processes and likely responses to global change at each site.

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References

[1] Bierlmaier FA, McKee WA. Climatic summaries and documentation for the primary meteorological station, H.J. Andrews Experimental Forest, 1972 to 1984. General Technical Report PNW-GTR-242. USDA Forest Service Pacific Northwest Research Station, Portland, OR, 1989.

[2] Bredensteiner KC. An investigation of vegetation–hydrology interactions in Watershed 1 at the H.J. Andrews Experimental Forest. M.S. thesis, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, 1998.
[3] Brown S, Lugo AE, Silander S, Liegel L. Research history and opportunities in the Luquillo Experimental Forest. General Technical Report SO-44. USDA Forest Service, Southern Forest Experimental Station, New Orleans, LA, 1983.
[4] Day FP, Phillips DL, Monk CD. Forest communities and patterns. In: Swank WT, Crossley DA, editors. Forest hydrology and ecology at Coweeta. New York: Springer; 1988. p. 141–9.
[5] Douglass JE, Hoover MD. History of coweeta. In: Swank WT, Crossley DA, editors. Forest hydrology and ecology at Coweeta. New York: Springer; 1988. p. 17–31.
[6] Errington JG. The effect of regular and random distribution on the analysis of pattern. J Ecol 1973;61:99–105.
[7] Federer CA, Flynn LD, Martin CW, Hornbeck JW, Pierce RS. Thirty years of hydrometeorologic data at the Hubbard Brook Experimental Forest, New Hampshire. General Technical Report NE-141. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, PA, 1990.
[8] Federer CA. Forest transpiration greatly speeds streamflow recession. Water Resour Res 1973;9(6):1599–604.
[9] Garcia-Monteil D, Scatena FN. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. Forest Ecol Manage 1994;63:57–78.
[10] Gray AN, Spies TA. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 1997;78(8):2458–73.
[11] Gregory SV, Swanson FJ, McKee WA, Cummins KW. An ecosystem perspective of riparian zones. BioScience 1991;41:540–51.
[12] Gustard A, Bullock A, Dixon JM. Low flow estimation in the United Kingdom. Institute of Hydrology Report 108. Wallingford, UK, 1992.
[13] Halpern CB, Spies TA. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol Appl 1995;5(4):913–34.
[14] Harr RD. Water flux in soil and subsoil in a steep forested slope. J Hydrol 1977;33:37–58.
[15] Harr RD. Some characteristics and consequences of snowmelt during rainfall in western Oregon. J Hydrol 1981;53:277–304.
[16] Harr RD. Effects of clearcutting on rain-on-snow runoff in western Oregon: a new look at old studies. Water Resour Res 1986;22:1095–100.
[17] Hewlett JD. A hydrologic response map for the state of Georgia. Water Resour Bull 1967;3:4–20.
[18] Hicks BJ, Beschta RL, Harr RD. Long term changes in streamflow following logging in western Oregon and associated fisheries implications. Water Res Bull 1991;27(2):217–26.
[19] Hoover MD, Hursh CR. Influence of topography and soil depth on runoff from forest land. Trans Amer Geophys Union 1943;part 2:693–8.
[20] Hornbeck JW. Storm flow from hardwood-forested and cleared watersheds in New Hampshire. Water Resour Res 1973;9(2):346–54.
[21] Huryn AD, Wallace JB. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology 1987;68:1932–42.
[22] Jones JA. Hydrologic processes and peak discharge response to forest removal, regrowth, and roads in small experimental basins, western Cascades, Oregon. Water Resour Res 2000;36(9):2621–42.
[23] Kirchner J, Feng X, Neal C. Fractal stream chemistry and its implications for contaminant transport in catchments. Nature 2000;403:524–7.
[24] Legendre P, Fortin MJ. Spatial pattern and ecological analysis. Vegetatio 1989;80:107–38.
[25] Levin SA. The problem of pattern and scale in ecology. Ecology 1992;63(6):1943–67.
[26] Likens GE, Bormann FH, Pierce RS, Eaton JS, Johnson NM. Biogeochemistry of a forested ecosystem. New York: Springer; 1977.
[27] Lugo AE, Scatena FN. Ecosystem-level properties of the Luquillo experimentalforest with emphasis on the Tabonuco forest. In: Lugo AE, Lowe C, editors. Tropical forests: management and ecology. Ecological studies, vol. 112. New York: Springer; 1995. p. 59–108.
[28] Munn NL, Meyer JL. Habitat-specific solute retention in two small streams: an intersite comparison. Ecology 1990;71:2069–82.
[29] National Research Council, 1991. Opportunities in the hydrologic sciences. Washington, DC: National Academy Press; 348 p.
[30] Perkins RM. Climate and physiographic controls on peakflow generation in the western Cascades, Oregon. Ph.D. dissertation, Department of Forest Science, Oregon State University, Corvallis, OR, 1997.
[31] Poff NL, Allan JD, Bain MB, Karr R, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. The natural flow regime: a paradigm for river conservation and restoration. BioScience 1997;47:769–84.
[32] Post DA, Grant GE, Jones JA. Ecological hydrology: expanding opportunities in hydrologic sciences. EOS 1998;79(43):517–26.
[33] Richter BD, Baumgartner JV, Wigington R, Braun DP. How much water does a river need?. Freshwater Biol 1997;37:231–49.
[34] Rothacher J, Dyrness CT, Fredriksen RL. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station; 1967, 54 pp.
[35] Scatena FN. Watershed scale rainfall interception on two forested watersheds in the Luquillo Mountains of Puerto rico. J Hydrol 1990;113:89–102.
[36] Scatena FN. Relative scales of time and effectiveness of watershed processes in a tropical montane rainforest of Puerto Rico. In: Costa J, editor. Natural and anthropogenic influences in fluvial geomorphology. Geophysical Monograph, vol. 89. Washington, DC: American Geophysical Union; 1995. p. 103–11.
[37] Scatena FN, Lugo AE. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. Geomorphology 1995;13:199–213.
[38] Scatena FN, Moya S, Estrada C, Chinea JD. The first five years in the reorganization of aboveground biomass and nutrient use following hurricane Hugo in the Bisley experimental watersheds, Luquillo experimental forest, Puerto Rico. Biotropica 1996;28:424–40.
[39] Schellekens J, Scatena FN, Bruijnzeel LA, Wickel AJ. Modeling rainfall interception by a lowland tropical rainforest in northeastern Puerto Rico. J Hydrol 1999;225:168–84.
[40] Spies TA, Franklin JF. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology 1989;70(3):543–5.
[41] Swank WT, Crossley Jr. DA. Introduction and site description. In: Swank WT, editor. Forest hydrology and ecology at Coweeta. New York: Springer; 1988. p. 1–16.
[42] Swanson FJ, James ME. Geology and geomorphology of the H.J. Andrews experimental forest, western Cascades, Oregon. Research Paper PNW-188. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, 1975.
[43] Swanson FJ, Johnson SL, Gregory SV, Acker SA. Flood disturbance in a forested mountain landscape. BioScience 1998;48:681–9.
[44] Swift Jr. LW, Cunningham GB, Douglass JE. Climatology and hydrology. In: Swank WT, Crossley DA, editors. Forest hydrology and ecology at Coweeta. New York: Springer; 1988. p. 35–55.

[45] Weisberg PJ. Fire history, fire regimes, and development of forest structure in the central western Oregon Cascades. Ph.D. dissertation, Department of Forest Science, Oregon State University, Corvallis, OR, 1998.

[46] Weaver PL. Bano de Oro Natural Area Luquillo Mountains, Puerto Rico. General Technical Report SO-111. USDA Forest Service, Southern Forest Experimental Station, New Orleans, LA, 1994.

[47] Young P, Beven K. Computation of the instantaneous unit hydrograph and identifiable component flows with application to two small upland basins – comment. J Hydrol 1991;129:389–96.