Chapter 17: Ecoregion Not Classified: Luquillo Experimental Forest, Puerto Rico

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Introduction

This chapter is a review and synthesis of research conducted at Luquillo Experimental Forest (LEF) on stream nutrients and biological responses. It is intended to inform national and regional water quality regulatory agencies, such as the U.S. Environmental Protection Agency (EPA) and the Puerto Rico Department of Natural and Environmental Resources, about existing results of relevant scientific studies that are available at LEF, and to identify future field and synthetic research of potential use to regulatory agencies that might be conducted at LEF.

Site Description

LEF encompasses 11 500 ha within El Yunque National Forest in northeastern Puerto Rico (lat. 18.3º N, long. 65.8º W). Steep, mountainous terrain dominates LEF, with deep valleys separated by high, knife-like ridges. Elevations in LEF range from valley bottoms at ~200 m to El Toro Peak at 1065 m. Rainfall is high with a strong elevation gradient ranging from 2500 mm/yr at lower elevations to ≥4500 mm/yr at upper elevations. Air temperature ranges from 15 to 30 ^{o}C year-round (McDowell et al. 2012).

LEF is predominantly forested, with four tropical rainforest types present at different elevations or topographic positions. Tabonuco forest dominates at 300 to 550 m elevation, while colorado forest dominates from 550 to 800 m, and elfin forest dominates above 800 m. Sierra palm forests are found in valley bottoms and ridge tops at any elevation (Murphy et al. 2012). Land use has been closely monitored and tightly controlled for research purposes within LEF. In recent decades, many areas bordering LEF have experienced urban or suburban development, while other areas have been allowed to regenerate forest cover following cessation of agriculture (Gould et al. 2012).

Four main watersheds drain LEF: the Rio Mameyes in the north, the Rio Fajardo in the east, the Rio Icacos/Blanco in the south, and the Rio Espiritu Santo

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in the west (fig. 17.1). Because of the abundant year-round rainfall, a dense network of perennial headwater streams drain this landscape of steep mountain flanks. Hurricanes have strongly influenced the hydrology, biota, and nutrient cycling of streams at LEF. Streams in LEF are extremely flashy and have steep, often rocky or boulder-strewn channels (Murphy and Stallard 2012).

Bedrock is mostly Cretaceous, volcaniclastic, sedimentary, and marine-deposited, with intrusions of the Eocene Rio Blanco quartz diorite. Contact metamorphism surrounding intrusions produced harder hornfels-type rock that underlay the highest peaks (Murphy et al. 2012). Watersheds with quartz diorite bedrock have lower channel slopes and sandy, meandering channels. Upland soils on the quartz diorite consist of loam Inceptisols with high quartz content, while soils on the volcaniclastic bedrock largely consist of clay and clay loam Inceptisols and Oxisols, with little quartz. Soil water flowpaths through the volcaniclastic-derived soils tend to be shallow owing to high abundance of occluding clays (McDowell et al. 2012).

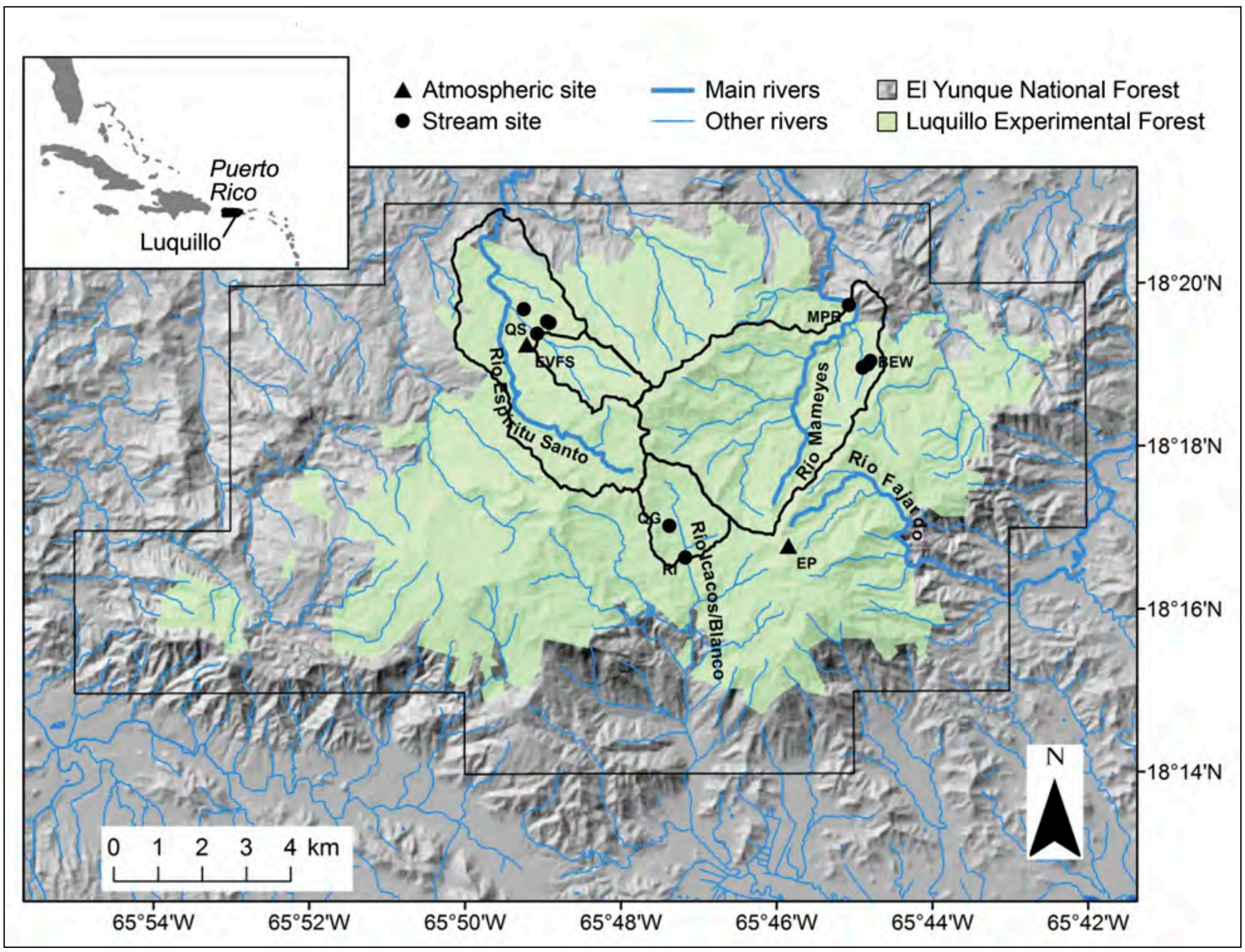

Figure 17.1—The Luquillo Experimental Forest, including locations of major reference watersheds (BEW = Bisley Experimental Watersheds; MPR = Rio Mameyes-Puente Roto; RI = Rio Icacos; QG = Quebrada Guaba; QS = Quebrada Sonadora) and atmospheric input monitoring sites (EP = East Peak; EVFS = El Verde Field Station).

Research History

The U.S. Forest Service (USFS) established LEF in 1956 to broaden the scope of research in tropical forestry, although natural history and forestry studies had been conducted at this site since the early 20th century. Previously, the Tropical Forest Experiment Station had been established in 1939 to provide a scientific basis for reforestation following several destructive hurricanes in the 1920s and 1930s, and was later renamed the International Institute of Tropical Forestry (IITF) (Wadsworth 1995). Work at LEF on sustainable forest production, including pine and mahogany plantations, produced important contributions to the literature on tropical forestry worldwide (Lugo et al. 2006, Lugo and Heartsill Scalley 2014, Wadsworth 1995).

IITF expanded from its original focus on forestry to conduct a broad range of continuing ecological and watershed studies in LEF. Studies of ecological structure and function, including water quality, hydrology, and watershed management, emerged from earlier forestry research (Brown et al. 1983, Lugo et al. 2006). Continuous stream gaging began in 1968, although sporadic flow monitoring had been conducted since the 1940s. Stream hydrology and chemistry studies began in the 1960s (Cuevas and Clements 1975). Modern ecological research in LEF also started in the 1960s, with 5 years of monitoring and experimentation on ecosystem processes as part of the Rain Forest Project supported by the U.S. Atomic Energy Commission (Odum 1970).

The U.S. Geological Survey (USGS) has a long record of hydrology and stream chemistry research at LEF. Water quality monitoring at USGS stations began in the 1960s and has continued to the present. As part of the Water, Energy and Biogeochemical Budgets (WEBB) program, USGS has published stream monitoring data from three LEF reference watersheds (Rio Mameyes, Rio Icacos, and Quebrada Guaba), along with two nearby watersheds with agricultural land use, in a 15-year study of watershed solute and sediment flux (USDI GS 2014).

In 1988, LEF became a member site of the Long Term Ecological Research (LTER) Network, sponsored by the National Science Foundation (NSF). As an LTER participant, LEF established regular stream nutrient monitoring as part of a program of multiscale, integrated ecosystem studies. In addition, LEF has been a member site in the NSF's Critical Zone Observatory (CZO) network since 2009, which has included studies of stream solutes, sediments, and nutrients.

Availability of publications and data—

For more details about the work at Luquillo LTER, including a detailed site description and a comprehensive list of publications, see LTER Network (2017a). Many datasets collected by LEF studies are on the LTER Network's online repository (LTER Network 2017b). Long-term daily streamflow and weather data from LEF that are formatted for ready comparison with other experimental forests and ranges, (EFRs) and LTER sites may be downloaded at the ClimDB/HydroDB website (LTER Network 2013). USFS publications on LEF and related journal articles can be downloaded from the IITF website (USDA FS 2017). The Luquillo CZO website (CZO 2017) also has an online data repository and a list of publications.

Biological Responses to Stream Nutrients N and P

Issues of Concern

Tropical and Neotropical forests have undergone the highest rates of deforestation and land use change of any forest type since the mid-20th century (Lindquist et al. 2012). Land use change in Puerto Rico over this period, outside of LEF, has largely run counter to trends elsewhere in the tropics, with substantial reforestation occurring on Puerto Rico's abandoned agricultural areas (Gould et al. 2012). Urban and suburban land development has also proceeded since the mid-20th century. Abandoned agricultural lands have either been urbanized or have naturally afforested with a mix of native and exotic species that together constitute a novel ecosystem (Lugo and Helmer 2004, Morse et al. 2014). LEF study basins are drained by rare and valuable examples of reference streams in tropical forests, against which streams draining urbanized and regenerating forest watersheds in Puerto Rico and elsewhere in the tropics can be compared (Heartsill Scalley and Lopez-Marrero 2014).

Urban development of watersheds downstream of LEF has caused increased nitrogen (N) and phosphorus (P) loading, as well as changes to other factors that may affect stream biota, including light availability, temperature, dissolved oxygen (DO), dissolved organic carbon (DOC), suspended sediment, channel structure, and streamflow (de Jesús-Crespo and Ramírez 2011, Potter et al. 2014, Ramírez et al. 2014, Santos-Román et al. 2003). Urban wastewater discharge from publicly owned treatment works and suburban/rural septic systems are major vectors of N and P enrichment to streams (Figueroa-Nieves et al. 2014). Excessive N and P loading can degrade water quality for beneficial uses such as drinking water, recreation, and aquatic ecosystem integrity.

Drinking water quality is of great concern for Puerto Rico's headwater streams, because streams that drain forested uplands are major sources of the island's clean drinking water. For example, more than 20 percent of Puerto Rico's population relies on drinking water primarily from streams leaving LEF (Scatena and Johnson 2001). Diversion of flow from streams leaving LEF has intensified recently, increasing from 54 percent in the 1990s to 70 percent in 2004 (Crook et al. 2007).

In addition to threatening local drinking water, excessive N and P loads can degrade water quality in sensitive downstream estuaries and coastal ecosystems, such as mangrove forests, seagrass beds, and coral reefs, which are important nurseries for many fish stocks and attractions for the tourism industry.

Atmospheric deposition of nutrients in precipitation, dust, and aerosols is a concern in many regions. Puerto Rico receives atmospherically deposited nutrients via long-range transport from distant sources such as dust originating from the Sahara Desert (McDowell et al. 1990, Pett-Ridge 2009).

Effects of global climate change on streams are also of concern in Puerto Rico. Hurricane-driven forest disturbance caused changes in N loading in LEF watersheds, and climate models predict intense hurricanes to become more frequent in the North Atlantic as climate warms (Emanuel 2013, Knutson et al. 2010).

Climate change may also cause impacts on LEF streams from drought, a concern that was recently highlighted by low rainfall in 2015. Despite wetter conditions in recent years in Hispaniola (Comarazamy et al. 2015), and in Puerto Rico from 2001 to 2013 (Van Beusekom et al. 2015), coupled climate-water cycle models predict a high likelihood that drought will become more frequent and severe in the Caribbean region owing to climate change (Prudhomme et al. 2014). Drought has complex impacts on stream biota, including indirect impacts via changing nutrient status. In dry periods, streams can experience low flows that concentrate nutrients as flow volume decreases, even if nutrient inputs remain constant. Reduced flows can also directly alter habitat for aquatic organisms by shrinking channel area and decreasing water available for transpiration by riparian plants.

Findings From Studies

Overall N and P conditions in streams—

Nitrate (NO_3^-)-N, ammonium (NH_4^+)-N, total dissolved nitrogen, and phosphate (PO_4^{3-})-P have been monitored weekly in LEF watersheds: Sonadora, Toronja, and Icacos since 1983, Bisley 1–3 since 1988, and Mameyes-Puente Roto and Prieta since 1989 (McDowell and Asbury 1994, Schaefer et al. 2000).

Concentrations and fluxes of N in LEF streams were higher than in most temperate forested reference watersheds, as is common in tropical and subtropical forests (Brookshire et al. 2012, Hedin et al. 2009, Lewis et al. 1999). Concentrations of NO_3^- were particularly high (≥100 μg NO_3^--N/L) compared to other forested reference streams. NO_3^- concentration was unrelated to discharge, indicating biotic control (McDowell and Asbury 1994, Shanley et al. 2011). Flux of NO_3^- was controlled by total runoff, which, in turn, is a function of the elevation gradient of precipitation (McDowell and Asbury 1994). Dissolved P concentrations and export were low to moderate, a feature common in other tropical forest streams. Iron and aluminum oxides in soils bind PO_4^{3-} strongly in soils, immobilizing P and delaying transport to streams via leaching (Liptzin and Silver 2009).

LEF is upwind of sources of air pollution local to Puerto Rico, which makes it an ideal site to monitor regional-to-global-scale atmospheric N inputs. The National Atmospheric Deposition Program (NADP) has been monitoring wet deposition of N at LEF since 1985 (NADP 2019). Stallard (2001) and Ortiz-Zayas et al. (2006) both reported a significant increase in wet N deposition from 1985 to 2003, but since then, N deposition has not increased (Stallard 2012). At current rates of 2 to 3.5 kg N/ha/yr, wet deposition of N is not considered a major vector of stream enrichment in Puerto Rico but might become an issue if atmospheric deposition of N increased in the future.

Data on dry deposition of N and P from windborne dust or aerosols are lacking for LEF and Puerto Rico in general, although throughfall, which is precipitation collected beneath the plant canopy, has been extensively studied. Throughfall washes the products of dry deposition off the canopy, and at LEF is significantly enriched in NO_3^--N, NH_4^+-N, and P compared to rain water collected in open areas (Heartsill Scalley et al. 2007, McDowell 1998, McDowell et al. 1990).

Enrichment with P is not considered a concern in headwater streams, such as those within LEF. Deposition of dust carried from the Sahara Desert across the Atlantic Ocean by the trade winds has been estimated to be a significant input of P to LEF watersheds, totaling 0.23 kg P/ha/yr, or slightly larger than the average input from bedrock weathering (Pett-Ridge 2009). Deposition from this transoceanic source is strongly seasonal, peaking in June and July (Stallard 2012). Although it is unclear how future P delivery from Saharan dust may be affected by climate change, at current levels, this source is not a major vector of P enrichment to streams.

Ability of streams to regulate N and P dynamics—

Organisms in LEF streams actively cycle N between the water column and benthic food webs. Uptake of the inorganic forms NH_4^+ and NO_3^- has been studied in detail. An enrichment study using isotopically tagged $^{15}NH_4^+$ showed that NH_4^+ uptake was dominated by nitrification rather than assimilation (Merriam et al. 2002). Trace amounts of $^{15}NH_4^+$ were continuously added over a 42-day period to a stream in an LEF watershed, Bisley 3. Detailed accounting of the fate of added ^{15}N showed rapid stream NH_4^+ uptake, of which 60 percent was due to nitrification. Over the study period, 65 percent of the isotopic tracer was exported in all forms, but only 1 percent was exported as $^{15}NH_4^+$, indicating that the stream actively processed 99 percent of the added $^{15}NH_4^+$. Fifty percent of added ^{15}N was exported as NO_3^-, 8 percent as DON, and 6 percent as particulate N. Of the 45 percent of added ^{15}N that was retained, most was in fine benthic organic matter and epilithon, which amounted to 10 and 6 percent, respectively, of the total amount added. Less than 1 percent of added ^{15}N was retained in leaves, wood, insects, shrimp, and crabs combined.

Potter et al. (2010) conducted isotopically tagged $^{15}NO_3^-$ additions lasting 24 hours in three LEF streams to quantify NO_3^- uptake and denitrification. Uptake was dominated by autotrophic rather than heterotrophic assimilation. Denitrification was a significant pathway, averaging a third of total uptake.

Although P dynamics have been less studied in LEF streams than N dynamics, Benstead et al. (2010) reported significant uptake of PO_4^{3-} in Bisley 3 and Prieta streams.

Consumers in higher trophic levels exert indirect influences on N and P dynamics in LEF streams. The most important consumers in LEF stream food webs are decapods consisting of three genera of freshwater shrimp (*Atya* spp., *Xiphocaris elongata,* and *Macrobrachium* spp.) and one genera of freshwater crab (*Epilobocera sinuatifrons*) (Covich and McDowell 1996; Pérez-Reyes et al. 2015, 2016; Zimmerman and Covich 2003). There are numerous reports of streams dominated by shrimp and crabs in tropical landscapes (Boulton et al. 2008, Jacobsen et al. 2008, Rincón and Covich 2014, chapter 18 on Hawai'i Experimental Tropical Forest). In early phases of their life cycles, shrimp species in LEF streams migrate to salt water and return upstream to mature and reproduce. Wright and Covich (2005) found that LEF shrimp fill important ecological niches that are often occupied by insect taxa in temperate streams, such as shredders, scrapers, filterers, and predators. In LEF streams, *Atya* spp. and *X. elongata* exerted top-down control over the benthic resource base, with indirect impact on N and P (Benstead et al. 2010, Crowl et al. 2001, Pringle et al. 1999). Grazing by *Atya* and detrital processing by *X. elongata* limited accumulation of N and P in autotrophic biomass and fine particulate organic matter standing stock. This grazing released nutrients for uptake and assimilation by autotrophs, and increased leaf litter decay rates. Greathouse et al. (2006) observed that reaches of streams above dams that excluded shrimp had far greater benthic organic matter and N standing stocks than did streams with shrimp.

Fish and snails are also important consumers in LEF streams, except in streams above cascades or steep waterfalls that are barriers to their upstream passage (Covich et al. 2009, Crowl et al. 2012, McDowell et al. 2012). Mountain mullet (*Agonostomus monticola*) are present up to ~400 m elevation and prey on shrimp, possibly releasing grazing pressure on autotrophs. Goby (*Sicydium plumieri*) are important algivores that can be found up to ~700 m elevation because they are capable of climbing dispersal barriers using suction-cup-shaped pectoral appendages. Herbivorous neritid snails (*Neritina* spp.) can climb the steepest inclines but generally are not found upstream of waterfalls, possibly because of short lifespans and the energetic demands of migration (Pyron and Covich 2003). Surveys have found the highest densities of shrimp upstream of the ranges of fish and snails (Covich et al. 2009, Greathouse and Pringle 2006, Hein et al. 2011).

Effects of N and P on LEF stream food webs and ecosystem processes—
To test N and P limitation on biofilm growth, Tank and Dodds (2003) deployed artificial substrates that diffused N and P, both separately and in combination, into LEF streams and monitored chlorophyll *a* production by epilithic and epixylic

biofilms. Bisley showed low chlorophyll *a* production in all treatments and no additional biofilm growth with added N or P; the P enrichment showed less growth than the control. No other LEF streams have been tested for N and P limitation of biofilms. No studies of the response of submerged or riparian vegetation to nutrients have been conducted at LEF.

Studies have also found no effects on decomposition and dissolved organic matter uptake in response to increased N and P availability in LEF streams. Tank and Dodds (2003) studied fungal biomass production on wooden disks with N or P enrichment. They found that ergosterol, a fungal biomarker, did not increase with N or P enrichment, providing evidence that wood-decomposing fungi are not limited by these nutrients. In a Costa Rican tropical forest stream, however, Rosemond et al. (2002) studied rates of leaf litter breakdown in a number of streams that constituted a natural P concentration gradient. They found that leaves broke down faster in the higher P streams, suggesting P-limitation of heterotrophic activity. No similar study has yet been conducted at LEF.

High NO_3^- concentrations in LEF streams have been attributed to high nitrification rates in soils and streams (Merriam et al. 2002). The watersheds on quartz diorite bedrock had high NH_4^+ concentrations in groundwater flowing through riparian zones, potentially supplying the stream with ample substrate for nitrification. In contrast, volcaniclastic watersheds had nearly undetectable levels of NH_4^+ in riparian groundwater. Riparian zones removed up to 90 percent of N from groundwater before it reached streams (Chestnut and McDowell 2000, McDowell et al. 1992). Where NH_4^+ was available to stream biota, nitrifying microorganisms using NH_4^+ as an energy source were able to compete with microorganisms using NH_4^+ as a nutrient (Merriam et al. 2002).

Other Factors Relevant to Biological Responses to Stream Nutrients N and P

Periods of drought in LEF have complex impacts on stream biota and food webs, causing accelerated rates of leaf senescence in terrestrial vegetation and litter delivery to streams, which, combined with a lack of flushing, leads to accumulation in streams of litter and organic debris. During the 1994 drought, pool depth decreased and aquatic habitat contracted, causing crowding and disrupting reproductive capacity among shrimp (Covich et al. 2003). Although these impacts on biota might be expected to alter stream N and P dynamics, no changes in LEF stream N and P concentrations were reported during the droughts of 1989, 1991, or 1994. Preliminary results from the drought of 2015 also suggest no change in N and P concentrations (McDowell, n.d.).

Frequent high flows in LEF streams might also be expected to affect biotic response to N and P. For example, scouring might limit periphyton biomass and thereby limit periphyton nutrient uptake, but Ortiz-Zayas et al. (2005) reported no decrease in periphyton biomass after high flows in an LEF stream. Relationships between discharge and concentration have been used in recent years to improve predictions of solute flux at high flows as well as to make inferences about watershed sources and sinks of solutes and suspended materials. The lack of response of NO_3^- concentration to discharge in LEF watersheds is thought to indicate that NO_3^- is under biotic control, likely a result of both terrestrial and aquatic immobilization (McDowell and Asbury 1994, Shanley et al. 2011).

Tank and Dodds (2003) observed that light availability at the stream surface was low (0.3 mol/m^2/d) beneath LEF's dense canopy. Consistent with low available light, undisturbed streams were highly heterotrophic. Even low-elevation reaches were predominantly heterotrophic, despite wider channel widths that permitted more light to reach the benthic surface (Ortiz-Zayas et al. 2005). In wider reaches, strong grazing pressure by shrimp may have limited autotropic standing crop, rather than available light.

Food webs in LEF streams depend heavily on litter inputs from riparian vegetation as a source of energy (Covich and McDowell 1996). High nitrification rates in Bisley have led to the hypothesis that NH_4^+ is also an important additional energy source to overall benthic metabolism and that energy demand regulates NH_4^+ uptake in these tropical forested streams (Merriam et al. 2002).

Water temperatures in LEF streams range from 17 to 30 °C. Stream temperatures generally decrease with altitude and show much less seasonal and diurnal variation than temperate forest streams (Brown et al. 1983, McDowell and Asbury 1994, Ortiz-Zayas et al. 2005, Stallard and Murphy 2012).

Reference Watersheds and Monitoring Sites

All LEF study watersheds have been formally designated as reference watersheds. They have been managed for minimal onsite human disturbance since LEF was established in 1956, and before that land use consisted of scattered, low-intensity agriculture, forestry, and mining. These LEF study basins are increasingly rare and valuable examples of well-studied reference conditions against which streams elsewhere in Puerto Rico and in the wet tropics worldwide can be compared. All of the research findings from LEF streams reported in this chapter are based on work done in these LEF reference streams.

Reference watersheds at LEF were selected on northeastern, northern, and southern flanks of the Luquillo Mountains to encompass the range of environmental conditions, particularly rainfall, which vary with aspect in response to the prevailing northeast trade winds.

The Rio Mameyes study watershed drains 1782 ha on the steep northeastern slope of the Luquillo Mountains, at 83 to 1050 m elevation. Mameyes was 99 percent forested when it was acquired by USFS in the 1930s, although parts of the basin had previously experienced selective logging and small-scale agriculture at lower elevations (Murphy et al. 2012). Agriculture was largely abandoned following a destructive 1899 hurricane (Scatena 1989). USGS has continuously measured discharge and rainfall at the watershed outlet since 1967.

The Bisley experimental watersheds, within the Rio Mameyes basin, have been managed as reference watersheds since their acquisition by the USFS in 1934. Bisley 1 watershed has an area of 7 ha, Bisley 2 an area of 6 ha, and Bisley 3 an area of 35 ha. Three gaged streams, two meteorological stations, soil and vegetation plots, and groundwater monitoring wells are located within the Bisley watersheds. Groundwater chemistry and hydrology in the riparian zone of Bisley 3 have been monitored intermittently since 1985 to the present. Rainfall and throughfall chemistry were monitored regularly at Bisley from 1988 to 2007.

Three reference watersheds are located at the El Verde research area within the Rio Espiritu Santo basin on the northern flank of the Luquillo Mountains. They consist of Quebrada Sonadora, with an area of 262 ha; Quebrada Toronja, with an area of 51 ha; and Quebrada Prieta, with an area of 31 ha. Wet deposition chemistry has been monitored at the El Verde Field Station since 1985 (NADP 2019).

Rio Icacos is a 326-ha reference watershed located high on the southern flank of the Luquillo Mountains at 620 to 832 m elevation. It is dominated by colorado forest with abundant sierra palm forest on ridges and in riparian zones. The Icacos basin had very little logging and no agriculture before acquisition by the USFS. USGS has continuously monitored stream discharge since 1968 and precipitation since 1989. Stream chemistry has been monitored weekly since the 1980s, and frequent event-based sampling was conducted by the USGS WEBB project in the 1990s and early 2000s. Groundwater chemistry and hydrology in the riparian zone of a small tributary to the Rio Icacos have been monitored intermittently from 1985 through 2010 and quarterly from 2011 to the present. Quebrada Guaba, another subwatershed of Rio Icacos, has had water chemistry monitored with weekly, continuous and event-based sampling. Meteorological data, wet deposition chemistry, and airborne dust chemistry are also monitored continuously at East Peak (1030 m), which flanks the Rio Icacos watershed.

Argerich et al. (2013) reported that over the period 1987–2007, Bisley 2, Bisley 3, and Sonadora all showed significant decreasing trends in monthly flow-weighted stream water NO_3^- concentrations. From 1997 through 2007, stream NO_3^- in these three watersheds, plus Bisley 1, also significantly decreased. They offered no explanations for these trends.

Cross-Site and Regional Studies

Streams in LEF have been included in numerous cross-site, regional, and global studies of stream nutrient flux because LEF has one of the most detailed stream chemistry records of any tropical or subtropical forest. LEF data were used to develop N and P criteria for water quality regulations across Puerto Rico. Sotomayor et al. (2011) made recommendations for N and P criteria using archived USGS water chemistry data from 57 stations across Puerto Rico that included six forested reference sites across Puerto Rico, three of which are LEF reference watersheds (Icacos, Mameyes-Puente Roto, and Sonadora).

Comparisons of developed vs. undeveloped watersheds in Puerto Rico have used LEF data. Santos-Roman et al. (2003) used water quality monitoring data from 15 sites across Puerto Rico, including two within LEF, and demonstrated that N and P concentrations were lower and overall water quality conditions were better in forested watersheds than urban watersheds. Stallard and Murphy (2012) compared stream chemistry findings from the USGS WEBB project for Icacos, and Mameyes, with two watersheds with historical or current agricultural influences. Concentrations and yields of NO_3^-, NH_4^+, and PO_4^{3-} were higher in the developed watersheds, which the authors attributed to agricultural activities and domestic waste disposal.

Biological communities in urban streams with high N and P, draining watersheds outside of LEF, have been compared to LEF streams. In the Rio Piedras watershed, in the San Juan metropolitan area, macroinvertebrate communities shifted from sensitive taxa, such as mayflies (Ephemeroptera) and caddisflies (Trichoptera), to tolerant taxa such as midges (Diptera: Chironomidae), with increasing urban density (de Jesús-Crespo and Ramírez 2011, Ramírez et al. 2009). These studies did not measure shrimp or crab populations, but did report sightings in the urban watersheds. Greathouse et al. (2006) reported that grazing by atyid shrimp kept rock surfaces clean even in streams with high N levels of 1.5 mg NO_3^--N/L. Native diadromous fish species, such as *A. monticola* that migrate between salt- and freshwater, also persisted in urban streams without physical barriers to fish passage (Ramírez et al. 2009). The presence of decapods and fish in urban streams outside LEF indicate that enrichment with N and P do not necessarily exclude them, although lack of population measurements prevented quantitative comparisons with reference streams.

Lewis et al. (1999) included data from Icacos, Sonadora, and Toronja in a multiregional analysis of stream N exports from 31 relatively undisturbed watersheds, consisting of 25 tropical streams from mostly American tropical forests and savannas, and six forested streams in California. Fluxes of all forms of N were found to be correlated with total runoff. Icacos ranked high in NO_3^- export among the studied watersheds owing to its high runoff.

Argerich et al. (2013) analyzed trends over time in NO_3^- and NH_4^+ concentrations in forested reference streams at seven EFRs across the United States, including four LEF catchments. The reference streams at some other EFRs, including Hubbard Brook Experimental Forest in New Hampshire (see chapter 3) and H.J. Andrews Experimental Forest in Oregon (see chapter 5) showed decreasing trends in NO_3^--N concentration as did the LEF streams. However, these EFRs have very different environments, and the authors did not speculate whether causes of these trends have anything in common among these otherwise dissimilar sites.

LEF has also been the site of two cross-site experimental studies of stream N cycling, the first and second Lotic Intersite Nitrogen eXperiments (LINX I and LINX II).) In LINX I, stable isotope enrichment experiments using $^{15}NH_4^+$ were conducted at 10 North American stream sites from Arctic tundra to tropical forest (see Peterson et al. 2001 for overview). The LEF was the only tropical stream in the study (Merriam et al. 2002). Nitrification in the LEF stream (Bisley 1) accounted for the largest fraction of total NH_4^+ uptake of any of the streams studied in LINX I, although the absolute rate of nitrification was higher in a North Carolina stream (Webster et al. 2003). Forest streams at LEF plus North Carolina and Oregon experienced no N or N + P limitation on biofilm growth. All three of these sites had very low average light availability (Tank and Dodds 2003), suggesting that light may commonly limit biofilm production in streams under heavy canopy cover.

Potter et al. (2010) reported the effects of $^{15}NO_3^-$ enrichments on streams at eight sites across North America that were part of LINX II. At each of the eight sites, streams were selected to represent reference, agricultural, and urban land use (Mulholland et al. 2008). In Puerto Rico, three LEF streams were used as reference sites and compared with three agricultural and three urban streams. As expected, ambient NO_3^--N and NH_4^+-N concentrations were lowest in the LEF streams and highest in the urban streams. Across all land uses, the Puerto Rican streams showed NO_3^- uptake that was strongly correlated with background NO_3^--N concentration, indicating that stream organisms/communities had some capacity to adapt to higher NO_3^- loads than under reference conditions by processing more NO_3^-. In addition, NO_3^- uptake was strongly correlated with gross primary productivity, suggesting that light exerts an indirect control on uptake where autotrophs are active. Denitrification in all Puerto Rican streams accounted for a third of total NO_3^- uptake on average, and denitrification rates were positively correlated with DOC concentrations.

Responses to Management and Natural Disturbance

Most LEF research on effects of forest management has focused not on streams but on forest biomass production. In the 1930s and 1940s, over 2300 ha of mahogany, teak, and pine plantations were planted at lower elevations of LEF, and timber production was monitored. Experimental studies examined the effects of cutting and herbicides on regrowth of vegetation. The Rain Forest Project (Odum and Pigeon 1970) examined effects of an experimental irradiation with radioactive cesium, which, at highest exposures, was lethal to vegetation on a 50-ha forest plot. Potential impacts of management practices on groundwater or streams have not been studied, nor have LEF research findings been used to develop any best management practices (BMPs) for water quality protection.

Hurricanes and landslides are the major natural causes of disturbances. As noted above, hurricane-related disturbance caused large increases in stream NO_3^--N concentrations that took years to decades to return to predisturbance baseline (McDowell et al. 2013, Schaefer et al. 2000, Shanley et al. 2011). No posthurricane increases in P have been observed. Following Hurricane Hugo in 1989, Shanley et al. (2011) showed that NO_3^--N exports from Icacos in the 1990s were roughly double those of the prehurricane 1980s. Groundwater N in hurricane-disturbed riparian zones showed a similar pattern to stream water NO_3^-, increasing for years to decades following disturbance (McDowell et al. 1996, 2013).

Hurricane disturbance of forests has long been recognized as a major driver of N dynamics in tropical forest streams, owing in part to research in LEF. Hurricanes affect stream N dynamics indirectly by wind-damaging trees, causing tree mortality, and by greatly increasing delivery of fresh leaf and wood litter to the forest floor and stream channel. Following Hurricane Hugo in 1989, loss of vegetative uptake and increased litter decomposition caused posthurricane increases in NO_3^--N concentrations and N export that took years to decades to return to prehurricane levels (Schaefer et al. 2000). A similar pattern was repeated following Hurricane Georges in 1998 (McDowell et al. 2013). Maximum posthurricane stream NO_3^- concentrations were 0.37 mg NO_3^--N/L, several times higher than prehurricane concentrations, but below the federal drinking water standard of 10 mg NO_3^--N/L. P dynamics showed no response to hurricane disturbance, either because mineralized P did not reach the stream or because mineralization of biomass-bound P was insufficient to raise stream water concentrations above background.

The Luquillo LTER Canopy Trimming Experiment (CTE) simulated the biophysical disturbances that accompany hurricanes (LTER Network 2015). Its purpose was to distinguish nutrient fluxes in soil solution caused by canopy opening vs. fluxes caused by wood and leaf debris. Neither canopy opening nor debris addition, on their own, produced elevated NO_3^--N flux in soil, but in combination they produced peaks in NO_3^--N concentrations lasting 18 months, which were similar to the posthurricane response of NO_3^- in streams (McDowell and Liptzin 2014). Levels in soil solution increased from 0.01 to 0.03 mg NO_3^--N/L to nearly 7.5 mg NO_3^--N/L over the first 10 months of the full hurricane simulation.

Both reduced vegetative N demand, and increased mineralization of organically bound N in litter appear to be necessary to produce a NO_3^- pulse in soil solution that was similar to the observed posthurricane pulse in stream water. Evidence from the CTE has strengthened the argument that regrowth of trees causes the hurricane-induced pulse of increased stream N concentrations to eventually decline to prehurricane levels. Dissolved PO_4^{3-} in soil solution did not respond to canopy trimming treatments.

Although direct effects on stream biota of a hurricane-induced N pulse have not been studied, posthurricane biological responses to increased channel inputs of plant litter have been reported. Shrimp populations temporarily increased in response to the abundance of litter inputs and debris dams from Hurricane Hugo, and then declined as prehurricane conditions returned over the following year (Covich et al. 1991). These temporary population booms may have altered nutrient cycling, considering that shrimp exert control on the benthic resource base, but any effects on N and P were not studied.

Reliability and Limitations of Findings

Research results and environmental monitoring datasets from LEF apply most directly to streams at other sites in Puerto Rico with relatively undisturbed forests, particularly where climate and geology are most similar to LEF's. At sites where these factors are dissimilar to LEF's, or where high accuracy is required, validation experiments or monitoring should be considered to test how well findings from LEF predict local conditions.

LEF streams have extremely flashy hydrology that makes study of stormflow conditions difficult and hazardous. As a result, most research has been conducted at base flow conditions, which may not detect the important processes that take place during stormflows. USGS used autosamplers during the WEBB project to obtain grab samples at higher runoff rates than any other studies previously published (Stallard and Murphy 2012), and sensors have recently been deployed at LEF to continuously record DO and conductivity. However, field experiments remain difficult and often dangerous during high flows, and the scarcity of stream data collected during high flow events has limited parameterization of models of nutrient effects on LEF stream biota at high flows.

Research Needs

The highest priority research question for the water quality regulatory community related to N and P that could be filled at LEF is, How does flow reduction owing to drought or water withdrawal affect stream biotic responses to N and P?

Filling this need would be important for the regulatory community because regulators require information on the capacity of stream biota to cope with the interactive effects of flow reduction and nutrient enrichment, especially considering predictions of increased drought frequency and severity. Compared to the impacts of hurricanes, relatively little is known about how drought conditions affect biological responses to N and P in rainforest streams. In periods of low flow, stream biotic processing of nutrients might mitigate the loss of dilution capacity by streams, or, alternatively, stream biota might be negatively affected by low flows and lose their natural capacity to process nutrients. If the latter is the case, stream nutrient levels would rise, perhaps making more costly wastewater treatment necessary in order to meet standards for protected uses. LEF shrimp survey data have been used to determine instream flow, the minimum required flow for preserving a given set of ecological functions (Scatena and Johnson 2001), but no study has considered the effect of low flow on nutrients. As discussed above, low flows during the drought of 1994 caused both crowding of shrimp and accumulations of leaf litter, suggesting a limit on the ability of shrimp to break down leaf litter, but the mechanism of this limit are not known (Covich et al. 2003). A better understanding of stream biotic response to drought might offer the potential to improve modeling for nutrient total maximum daily load (TMDL) models. If this research need were filled, water quality regulators might be better informed to decide when it might be necessary to modify nutrient endorsements during periods of low flows.

The following work would need to be done at LEF to fill this research need: (1) reanalyze existing LEF long-term rainfall, streamflow, and stream nutrient datasets to develop a quantitative model of drought effects on stream nutrient concentrations; (2) initiate focused monitoring of nutrient conditions and biotic surveys at low flows; (3) conduct nutrient uptake experiments during low flows; and (4) study biological responses to experimental flow reductions and drying of natural or artificially created streams.

Other relevant questions that might be addressed at LEF, but are of lower priority for regulators include the following:

- Can responses to global drivers such as climate change and atmospheric deposition of N and P be detected by monitoring LEF's forested, low-nutrient streams under reference conditions?
- How do N and P levels affect stream metabolism and biological oxygen demand export downstream?
- In LEF forested catchments, streams export a higher proportion of the total N load as dissolved organic nitrogen, while urbanized catchments

typically export a larger fraction as dissolved inorganic nitrogen. Do these differences reflect differences in N sources or differences in aquatic N cycling?

- Are the organic forms of N and P in LEF watersheds more or less labile than the organic N and P in urban watersheds or in wastewater?
- Is the marine environment a significant source of nutrients to tropical coastal streams via migrating shrimp and fishes? What fraction of stream N and P is delivered to streams from marine environments, how much is taken up in freshwater food webs, and how much returns to the ocean as stream flux?
- Do large floods alter stream nutrient conditions on an enduring basis?

Potential Utility to Water Quality Regulatory Agencies

Responses of ecosystems at LEF to disturbances, such as hurricanes and droughts, can be interpreted without the confounding effects of a complex land use history. In this context, watersheds at LEF might be useful to water quality regulatory agencies both as natural reference points for comparison with Puerto Rico's urban-impacted watersheds, and as sentinels of regional-to-global-scale drivers such as climate change and N deposition.

Long-term data on N and P concentrations and fluxes in LEF streams might be used to improve estimates of "best attainable" concentrations for the establishment of nutrient criteria for Puerto Rico streams. Nutrient criteria to protect biological and chemical integrity of inland waters in Puerto Rico are not in place but are in development (Sotomayor et al. 2011). LEF stream chemistry datasets might augment the datasets currently being used for this purpose. Similarly, LEF stream data might also be used to represent background "natural" nonpoint source loads for determining nutrient TMDLs for streams elsewhere in Puerto Rico.

Stream biological parameters, such as typical assemblages of aquatic organisms, and decapod and fish survey data, have been extensively studied at LEF. These data might be used to assist the development of indicators of stream biological integrity because detailed representations of unaffected biotic conditions are rare for Puerto Rican streams with low nutrient inputs.

Lastly, LEF research findings on the capacity of headwater streams and riparian zones to retain N might be used to establish BMPs for riparian buffer conservation. LEF findings demonstrate how important intact forested riparian zones and headwater streams are for protecting water quality and the biological integrity of streams in Puerto Rico and possibly elsewhere in the tropics.

Key points:

- LEF streams have characteristics typical of undisturbed tropical forests under natural conditions, such as relatively high N and low P concentrations.
- LEF stream biota have the ability to control N and P dynamics via microbial uptake of inorganic N and food web interactions, such as detrital processing and grazing on algae by shrimp that prevent accumulation of autotrophic biomass.
- Although food web effects on N and P have been extensively studied, many important questions remain unanswered about how N and P levels affect food webs.
- Low light conditions and scant DOC inputs to LEF streams limit energy available to biota and cause microbial nitrification of NH_4^+ to be an important energy source.
- From the perspective of the regulatory community, the highest priority research question that could be filled at LEF is, How does flow reduction owing to drought or water withdrawal affect stream biotic responses to N and P?
- Existing LEF datasets and research results might be used by regulators to establish nutrients criteria, to identify stream health bioindicators, and to develop BMPs for conserving riparian buffers for Puerto Rico.

Biological Responses to Stream Nutrients Other Than N and P

Issues of Concern

Nutrients other than N and P do not currently present issues of concern in Puerto Rico's streams, but their export and delivery to rivers, estuaries, and coastal waters may affect the functioning of those downstream ecosystems. For example, concentration and flux of silicone dioxide (SiO_2) are high in LEF watersheds relative to temperate forested streams, owing to rapid weathering of primary minerals in bedrock. In downstream estuaries and offshore marine environments, SiO_2 limitation of primary productivity by diatoms is common because diatoms require SiO_2 to grow their siliceous frustules, or shells. Changes in SiO_2 flux from uplands might alter diatom production at the base of food webs in estuaries and coastal ecosystems.

In Puerto Rico, urbanization and atmospheric deposition also add nutrients other than N and P to streams. Urbanization can increase chloride (Cl^-) two- to threefold above concentrations in reference streams. Atmospheric deposition of sulfate (SO_4^{2-}) is of concern because, in excess, it may acidify streams, although moderate-level SO_4^{2-} loading might alleviate sulfur limitation of terrestrial vegetation or aquatic microorganisms.

While not a nutrient for the purposes of this synthesis, DOC merits discussion because it is tightly coupled with nutrient cycling in aquatic ecosystems and can be an energy source for the base of aquatic food webs. DOC loads are low in LEF streams but are much higher in urban streams in Puerto Rico. Wastewater discharge can cause DOC enrichment and change the molecular composition of the DOC pool in streams (Figueroa-Nieves et al. 2014, Potter et al. 2014). Elevated DOC loads, especially more labile forms in wastewater, supports high stream bacterial populations and contribute to oxygen depletion.

Findings From Studies

Overall conditions of nutrients other than N and P—
Stream water calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), potassium (K^+), Cl^-, bromide (Br^-), SO_4^{2-}, and SiO_2 have been monitored on a weekly basis in LEF reference watersheds Sonadora, Toronja, and Icacos since 1983; Bisley 1–3 since 1988; and Mameyes-Puente Roto and Prieta since 1989 (McDowell and Asbury 1994, Schaefer et al. 2000). The dynamics of Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, Br^-, and SiO_2 are largely controlled by flow conditions, with strong dilution as flows increase. Additional controls also have been inferred from effects of hurricane-related disturbance on K^+, from spatial variability of dissolved SiO_2, and from the concentration-discharge relationships for SO_4^{2-}. Weekly monitoring for these constituents in wet deposition has occurred since 1985 at the El Verde site (NADP 2019). Wet deposition of SO_4^{2-} has increased in LEF precipitation, as has total acidity, since NADP monitoring began. Stallard (2012) attributed this increase to pollutants from temperate zone sources.

Bedrock weathering and sea salt aerosol inputs supply base cations to LEF streams (McDowell et al. 1990, McDowell and Asbury 1994). High SiO_2 concentrations (≥25 mg SiO_2/L) are a ubiquitous feature of LEF streams owing to high rates of bedrock weathering from year-round abundant moisture and warm temperatures.

Responses of stream biota to nutrients other than N and P have not been studied extensively in LEF streams. It is likely that none of these other nutrients are biologically limiting, because their stream water concentrations, driven by inputs from weathering and sea salt aerosols, are thought to be sufficient to support stream biological processes (Stallard and Murphy 2012).

Ability of streams to regulate dynamics of nutrients other than N and P—
Silica cycling by freshwater diatoms have not been studied at LEF. The role of terrestrial vegetation in the watershed SiO_2 cycle has been examined in the Icacos watershed. Studies have assessed sources of SiO_2 to the stream using a novel

geochemical technique, the ratio of germanium to silicon (Ge/Si) in stream water, soil solution, and minerals in soil and bedrock (Derry et al. 2005, Lugolobi et al. 2010). Previously, Derry et al. (2005) had applied this technique to Hawai'ian watersheds and shown that most of the SiO_2 in riverine flux had been cycled by terrestrial vegetation. At LEF, however, Lugolobi et al. (2010) found that terrestrial plants actively cycle only a small fraction of SiO_2 close to the soil surface, retaining it from streamflow.

The SO_4^{2-} concentration-discharge relationship is markedly different from Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, and SiO_2. Instead of strong dilution at higher flows, SO_4^{2-} concentrations show little response to changing discharge (McDowell and Asbury 1994, Shanley et al. 2011). This difference in the behavior of SO_4^{2-} from these other constituents suggests that biotic factors influence SO_4^{2-}, but the exact mechanism is unknown. Sulfur cycling within streams has not been studied in detail.

Other Factors Relevant to Biological Responses to Stream Nutrients Other Than N and P

Numerous other factors that might influence biotic responses have been measured at LEF. These are the same factors that were mentioned earlier in the chapter as possibly influencing responses to N and P: flow conditions, light, and organic matter. Low light levels, for example, probably exert strong influence on SiO_2 cycling, as light limitation of diatom growth can suppress SiO_2 demand in streams.

Streams in LEF have low DOC concentrations during base flows. McDowell (1998) attributed this condition to high sorption capacity in the clayey soils limiting supply to streams, and to high stream respiration rates that indicate DOC may be rapidly mineralized (Ortiz-Zayas et al. 2005). A strong positive concentration-discharge relationship holds, with DOC increasing from 2 to 20 mg DOC-C/L from low to high flows, except at highest flows when the relationship changes to a negative slope (McDowell and Asbury 1994, Shanley et al. 2011). LEF streams and groundwater are often supersaturated with carbon dioxide (CO_2), indicating that high soil respiration and high weathering rates supply CO_2 that eventually is exported as bicarbonate or degasses from the stream surface. Riparian zones retained large amounts of DOC from groundwater before it reached streams. Chestnut and McDowell (2000) estimated that without riparian processing, one headwater stream in the Icacos basin would have a fourfold higher DOC concentration. Some important aspects of stream carbon budgets have not yet been quantified at LEF, including the fraction of CO_2 produced by stream respiration, the amount of CO_2 lost from streams by evasion, and the contribution of autochthonous production to the stream DOC pool.

Cross-Site and Regional Studies

Monitoring data collected at LEF for nutrients other than N and P are used in regional and national analyses and maps of atmospheric deposition regularly produced by the NADP Network (NADP 2019). Stallard (2012) synthesized these data to analyze concentrations, loads, and trends in precipitation for the WEBB watersheds in northeastern Puerto Rico.

Stallard and Murphy (2012) reported stream chemistry findings from the USGS WEBB project for Icacos, Mameyes, and two other watersheds with both historical and current agricultural influences. Concentrations of Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, SO_4^{2-}, and SiO_2 were higher in the developed watersheds, which the authors attributed to agricultural activities and domestic waste disposal.

Studies of urban watersheds near LEF have elucidated the effects of urbanization on stream water Na^{+}, Cl^{-}, and DOC. Santos-Román et al. (2003) showed that among 15 watersheds across Puerto Rico, urban basins had higher Na^{+} and Cl^{-} concentrations than forested watersheds, including two in LEF. Potter et al. (2014) found that Cl^{-} and DOC concentrations in subbasins of the urban Rio Piedras watershed were positively correlated with spatial density of sewer pipes, suggesting that both constituents reach surface waters via leaks or illicit discharges. Chloride concentrations averaged 34 mg Cl^{-}/L with a maximum of 52 mg Cl^{-}/L. These concentrations were below EPA recommendations for aquatic life criteria of 200 mg Cl^{-}/L, but more than three times the highest concentrations in LEF reference watersheds. Concentrations of DOC were similarly enriched, with a maximum of 11 mg DOC-C/L.

Effluent from wastewater treatment in Puerto Rico significantly changes the DOC composition of streams, including some downstream of LEF (Figueroa-Nieves et al. 2014). Effluent shifts urban streams toward more labile DOC, which is more readily taken up by bacteria and respired, consuming DO in the process.

In a study of chemical weathering deduced from solute fluxes in stream water, White et al. (1998) found that Rio Icacos had the highest known weathering rates in the world for a granitic watershed, likely owing to high precipitation and a young pluton particularly susceptible to weathering (Stallard and Murphy 2012).

Responses to Management and Natural Disturbances

Concentrations and fluxes of nutrients other than N and P have been shown to be insensitive to hurricane disturbance in LEF, with the exception of K^{+}. In simulated hurricane treatments of the CTE, McDowell and Liptzin (2014) did not observe any response of DOC in soil solution.

The K^{+} cycle is an important biogeochemical marker of tropical forest disturbance and recovery. Stream concentrations and export of K^{+} were increased after hurricane disturbance of whole watersheds on a similar time scale to N (McDowell et al. 2013, Schaefer et al. 2000). This K^+ pulse was the result of mineralization of tree litter added to the soil by hurricane damage, as tree biomass was the largest K^+ pool in LEF systems (McDowell 1998). Schaefer et al. (2000) found that Hurricane Hugo had approximately doubled K^+ flux from LEF watersheds during the first year posthurricane. Although K^+ pulses in streams are probably a typical feature of whole-watershed responses to hurricane disturbances in the tropics, McDowell and Liptzin (2014) reported no K^+ pulse in soil solution in the CTE study, despite observing a NO_3^- pulse. They attributed the lack of an expected K^+ response to a lag in data collection that probably missed a rapid K^+ pulse in the first months after the simulated hurricane treatment.

Landslides occur frequently in LEF watersheds and often intersect the dense drainage network. Landslides directly affect LEF streams by delivering sediment to stream channels (Larsen 2012). Bhatt and McDowell (2007) attributed the higher concentrations of SiO_2 observed in springs at higher elevations to the exposure and weathering of fresh bedrock by landslides. Even in heavily forested LEF watersheds, the presence of roads increases the likelihood of landslides. Larsen (2012) found that 43 to 63 percent of landslide-related erosion in Icacos and Mameyes was associated with roads.

Reliability and Limitations of Findings

Scientific findings and monitoring datasets from LEF related to nutrients other than N and P probably apply to other watersheds in Puerto Rico with climate and land use similar to LEF. Where environmental factors differ from LEF, or where a high degree of accuracy is required, we suggest considering validation experiments or monitoring in order to test how well LEF results predict local conditions.

Research Needs

The highest priority research question for the water quality regulatory community related to nutrients other than N and P that could be answered at LEF is, Do tropical forested headwater streams actively process DOC, and does that processing affect aquatic food webs both in headwaters and downstream in second- and third-order streams?

Answering this question would be important for the regulatory community because DOC will either be used as an energy resource for stream food webs, as a source of mineralized nutrients, or be passively transported downstream to estuaries and coastal waters. The fate of DOC depends on its composition and on the environmental conditions and microbial communities it encounters in transit. If DOC is mineralized in streams, it will contribute to DO depletion and release organically bound nutrients. If DOC is not mineralized in headwater streams, background levels of DOC loading will probably be driven by riparian and instream DOC sources and by streamflow. Knowledge of DOC loading and active processing in headwater streams, such as those at LEF, might help water quality regulators better understand what background DOC would be in undisturbed streams for assessing effects of urban DOC enrichment from wastewater discharges.

The following work would need to be done at LEF to answer this question: (1) conduct assays of biodegradable DOC with incubations to determine DOC losses under different flow conditions; (2) conduct field or mesocosm enrichment experiments using different compositions of DOC, such as leaf litter leachate, glucose or acetate, and wastewater DOC; and (3) develop a quantitative model of DOC mineralization that incorporates effects of source and molecular composition.

Other relevant questions that might be addressed at LEF, but of lower priority for regulators include the following:

- Do tropical forested headwater streams exert any control on the SiO_2 cycle and downstream export from forested reference watersheds, or do they passively transport SiO_2 to downstream ecosystems?
- Do tropical forested headwater streams actively cycle SO_4^{2-}, or do they passively transport SO_4^{2-} to downstream ecosystems?

Potential Utility to Water Quality Regulatory Agencies

As noted above related to N and P, the LEF provides an invaluable background of conditions for nutrients other than N and P against which urbanized or other heavily managed streams may be compared, and also as a baseline for assessing responses to regional or global-scale drivers of change. Parallel to riparian processing of groundwater N, LEF-based findings that riparian zones retain groundwater DOC might provide a scientific basis for BMPs to mitigate DOC delivery to streams by conserving intact riparian zones. LEF also has extensive, long-term monitoring datasets on nutrients other than N and P that might be used by regulators should issues arise in the future concerning these other nutrients.

Key points:

- Potassium concentrations and fluxes increase greatly after hurricane-driven forest disturbance compared to prehurricane conditions.
- Silica can be a limiting nutrient in marine systems, and silica concentrations and exports are high in LEF streams owing to the high weathering rates of the underlying rocks.

- LEF streams carry low DOC loads, but nearby urban streams carry elevated DOC concentrations of labile forms from wastewater that may enhance DO depletion.
- The fate of DOC in headwater streams is a high-priority research need of water quality regulators that might be addressed by future LEF research.
- Continuous monitoring datasets of nutrients other than N and P from LEF watersheds from the 1980s to present are readily available for use by water quality regulators.

Overview and Synthesis

The LEF may be thought of as an island within an island, where largely intact, mountain forests are surrounded by a heavily urbanized landscape, all situated on an oceanic, tropical island. Free from the impacts of development, the green island of LEF has served for decades as an environmental laboratory for the study of important ecological functions, including processes that control the quality of water from these forest-dominated watersheds. Below, along densely populated coasts, the urban island of Puerto Rico is critically dependent on the green interior uplands to provide clean freshwater. These headwater streams also provide habitat that supports healthy communities of native aquatic species.

Research from LEF provides the most complete water quality baseline that exists for Puerto Rico and for tropical forest streams without confounding impacts from land uses. Past and future studies conducted at LEF may prove essential to disentangling the effects of global and regional drivers of change, such as drought and hurricanes, from the effects of local drivers such as urban development.

Many LEF studies discussed here have examined how streams process nutrients, showing that terrestrial inputs control fluxes of nutrients and organic matter in forest streams; that shrimp are the dominant organisms processing plant detritus in streams; and that natural disturbances, including hurricanes and landslides, strongly influence long-term stream nutrient dynamics. Fewer studies have addressed how stream biota respond to nutrients. Future work at LEF can broaden the scope of research to include more aspects of the responses of the biological community to stream nutrients. A better understanding of how LEF stream biota are affected by nutrients will undoubtedly be of use as regulatory agencies develop criteria to protect ecological function and maintain ecosystem services, such as providing clean water for the people of Puerto Rico.

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