

## Climate variability at multiple spatial and temporal scales in the Luquillo Mountains, Puerto Rico

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Spatial and temporal variability in the climate of the Luquillo Mountains of eastern Puerto Rico is influenced by large-scale movements of air masses, extreme events, and regional and global climate change. Because of the long history of ecosystem research in the Luquillo Mountains, their status as a U. S. Dept of Agriculture (USDA) Experimental Forest, and their role as a source of drinking water for many communities, climate of the Luquillo Mountains has been a topic of interest for many different public and private entities. Long-term and spatially-diverse records of climate and simulation models suggest that climate is changing in the Luquillo Mountains. Precipitation is decreasing slowly in the lowlands of Puerto Rico and global models suggest that this trend will continue. Annual maximum and minimum temperatures are increasing slowly, and may be affected by accelerating urbanization around the Luquillo Mountains. Cyclonic storms are a major influence on community composition and ecosystem processes, and some studies have suggested trends in intensity and frequency of these storms. Cumulative effects of these changes may include a more pronounced dry season, changes in spatial distribution of species, shifts in the distribution of soil organic carbon, decreases in primary productivity, and increases in extreme rainfall events. Because predictions of the possible effects of climate change bear high levels of uncertainty, future research needs to focus on understanding the direction and magnitude of ecosystem responses to change. A coordinated effort to expand collection of meteorological data and to improve the quality of such data is a fundamental necessity if we are to understand the effect of future climate change on the Luquillo Mountains.

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Puerto Rico is centered on 18°N latitude and 66°W longitude, and serves as a geographic boundary between the Caribbean Sea and the North Atlantic Ocean. Two major mountainous systems on the island, one in the north-east corner (Luquillo Mountains) and one in the center (Central Mountains), reach just over 1000 m in elevation and create considerable climate variation on the island.

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Throughout the 1800s and until the 1950s, most of Puerto Rico was deforested to increase agricultural production. However, around 1950 Puerto Rico began to

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develop an industrialized economy, which resulted in a rural migration to urban centers, creating strong urban to rural gradients in population density, built environment, forest cover, and associated environmental factors (Fig. 1). Throughout the agricultural and industrial period, forest at high elevations in the Luquillo Mountains was never developed for agriculture and remains relatively undisturbed

by human activities. Conversely, San Juan, an urban center of nearly three million people located only 30 km from the Luquillo Mountains, continues to spread and affect landscapes. Spatial variability of land-cover/land-use types and the close proximity of San Juan create a valuable opportunity to study the effect of a rural to urban gradient on the climate of the Luquillo Mountains.

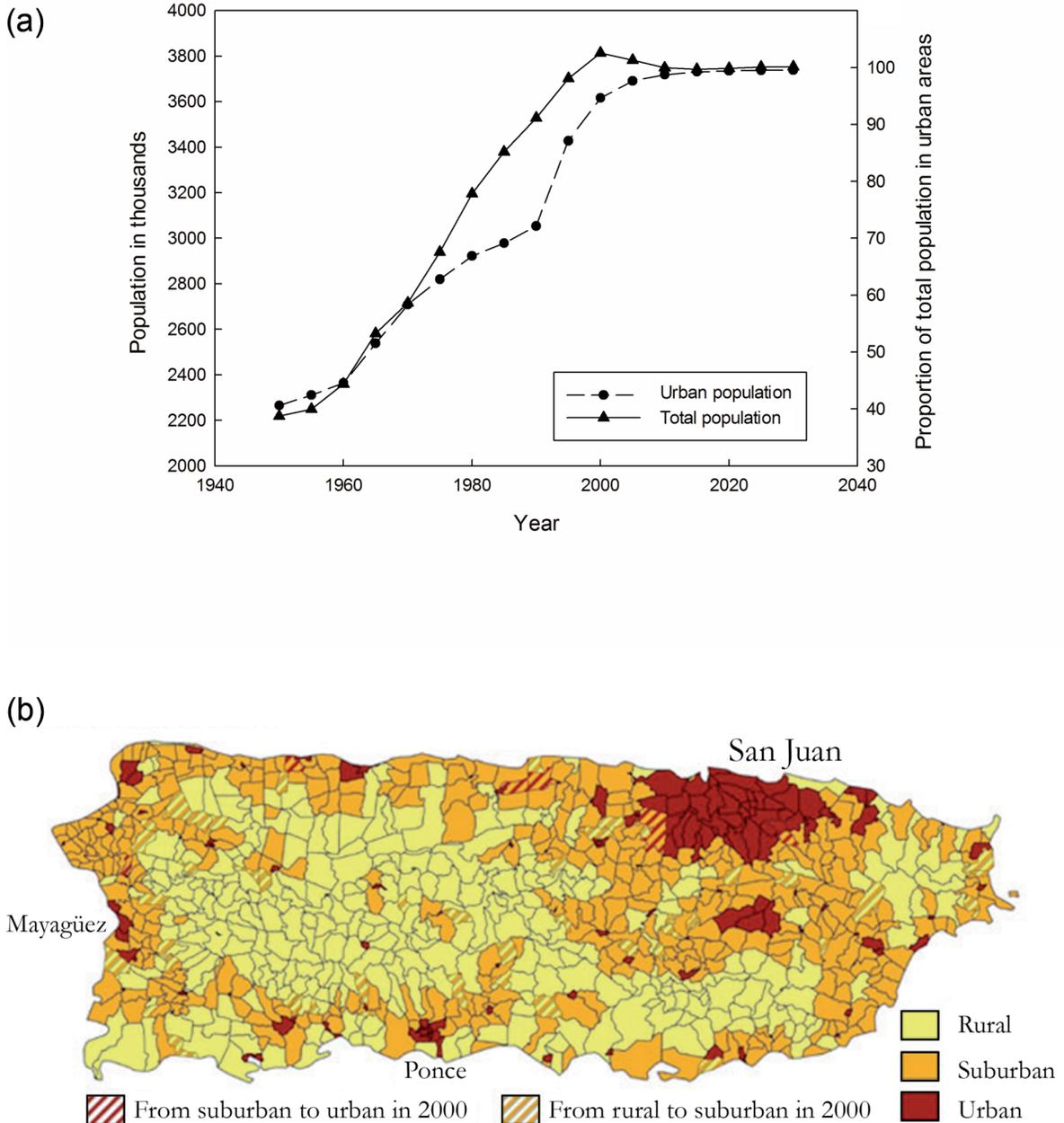


Figure 1. (a) Changes in the human population of Puerto Rico and the proportion of the population that is urban (source: UN – The World Population Prospects, the 2010 Revision and UN – World Urbanization Prospects, the 2011 Revision); (b) distribution of urban, suburban, and rural land uses of Puerto Rico (modified from Ramos et al. 2008).

## Goals

Here, we characterize the climate of the Luquillo Mountains by synthesizing information from a wide range of empirical studies, remotely-sensed data, and simulation models. Trends in long-term data sets are compared with predictions from local, regional, and global climate models to evaluate forecasts of climate change for the Luquillo Mountains. Trends in empirical and modeling data are discussed in the context of changing forcing functions to identify areas where additional measurements, research, or synthesis will improve understanding of the changing climate in the Luquillo Mountains. A discussion of the implications of trends in climate characteristics provides a link to the effect of changing climate on ecosystem services.

## Major influences on climate in the Luquillo Mountains

The sub-tropical latitude and persistent northeast trade winds are the predominant factors that determine the humid tropical maritime climate of the Luquillo Mountains. The climate of Puerto Rico and the Caribbean has been relatively stable compared to extra-tropical regions over millions of years (McDowell et al. 2012). Over seasonal to decadal scales, large-scale movements of air masses, extreme events, and coupled ocean-atmospheric patterns create temporal and spatial variability in weather patterns. The cumulative influence of these different elements defines a dynamic climate regime.

In Puerto Rico, and the Caribbean in general, seasonal weather patterns include dry (December–May) and wet (June–November) seasons. In the dry season in Puerto Rico, trade-wind orographic showers associated with high pressure systems dominate rainfall patterns in the absence of larger scale weather systems (Scholl et al. 2009). Deep moisture layer regimes occur year-round but are less frequent in the drier months. During this season, the trade-wind inversion layer (Gutnick 1958, Johnson et al. 1999) limits the vertical development of cumulus clouds.

During the rainy season, passing easterly waves and cyclonic storms provide much of the rainfall to the area. These synoptic systems have converging airstreams that deepen the moist layer and create the potential for shower and thunderstorm formation (Odum et al. 1970). Tropical storms passing to the north of Puerto Rico from June to November result in brief cloudless periods with light winds and high temperatures. Other large-scale atmospheric patterns include low-pressure troughs induced by temperate weather systems and winter cold fronts that reach into the tropics. Low-pressure polar troughs cause weak westerly flows and drier conditions on the eastern slopes of the mountains. Winter cold fronts produce strong north winds with steep lapse rates and heavy rains coupled with cool temperatures (Odum et al. 1970).

Isotopic analyses allowed Scholl et al. (2009) to estimate the contribution of different atmospheric patterns to total annual rainfall in the Luquillo Mountains. Trade-wind orographic rainfall combined with non-thunderstorm showers contributed 29% of annual rainfall. Rainy season atmospheric patterns (e.g. easterly waves, low pressure systems, and cyclonic storms) were responsible for 30% of the total. Fronts and troughs each contributed 14% of the total, and showers with thunderstorms added another 8%. Five per cent of total rainfall could not be attributed to a particular weather system.

Large scale, coupled ocean-atmospheric events (North Atlantic Oscillation [NAO], El Niño-Southern Oscillation [ENSO], Atlantic Multidecadal Oscillation) also have significant effects on the climate of the Luquillo Mountains at annual or longer time scales. Puerto Rico (Malmgren et al. 1998) and the Luquillo Mountains in particular (Greenland 1999) exhibit a strong and long-lasting temperature increase associated with El Niño events and a decrease in temperature corresponding to La Niña occurrences. The Luquillo Mountains also evidence a possible drying trend associated with El Niño (Greenland 1999). Throughout the Caribbean, El Niño events are associated with drier summers during the year of the events and wetter springs the following year (Gianini et al. 2001). In Puerto Rico, there is a significant positive relationship between rainfall and El Niño events but only for the month of May (Schaefer 2003). The NAO also affects rainfall patterns in Puerto Rico (Roy and Balling 2005). When the winter NAO index is high, the direction of winds becomes more northeasterly over Puerto Rico, resulting in lower than normal winter and annual rainfall (Malmgren et al. 1998). Local sea surface temperature can also have an important effect on insular climates in the Caribbean, including Puerto Rico. Ray (1934) detected a direct relation between air and sea surface temperatures in a 30-yr record. Local sea surface temperatures drive atmospheric temperatures in Puerto Rico, as expected in a small island with a maritime climate (Malmgren et al. 1998). Winter sea surface temperatures and summer NAO index are strongly related to rainfall totals in May, June, and July in Puerto Rico (Roy and Balling 2005).

## History of climate research in the Luquillo Mountains

Because of the location of the Luquillo Mountains, their status as a U. S. Dept of Agriculture (USDA) Experimental Forest, and their role as a source of drinking water for many communities, climate of the Luquillo Mountains has been a topic of interest for many different public and private entities. The percentage of water typically generated within the forest but diverted for use by local municipalities increased from 54% in 1994 to 70% in 2004 (Naumann 1994, Crook et al. 2007). Local residents use

the forest for recreation, and the Luquillo Mountains are a prime destination for off-island tourists.

Long-term and spatially diverse records of climate exist for the Luquillo Mountains and have prompted various spatial and temporal analyses. The Inst. of Tropical Meteorology, jointly operated by the Univ. of Chicago and Puerto Rico, conducted pioneering research on tropical synoptic systems during the early 1940s (Odum et al. 1970). An early summary of the climate of the Luquillo Mountains (Briscoe 1966) brought together information from various sources to examine spatial and temporal weather patterns. Wadsworth (1949) used long-term records to characterize the factors influencing forest productivity. Intensive meteorological measurements were conducted near the El Verde Field Station (EVFS; see Weaver and Gould 2013 for locations of field sites) in the 1960s and summarized as the backdrop for a study of the forest ecosystem (Odum et al. 1970).

More recently, the Luquillo Mountains have been the subject of a variety of research programs. The International Inst. for Tropical Forestry (IITF) has conducted research on forest productivity and services for decades. The U.S. Geological Survey (USGS) collects data on stream flow on several watersheds in the Luquillo Mountains and sponsors the Water, Energy, and Biogeochemical Budgets (WEBB) project that includes forested watersheds in the Luquillo Mountains. The Univ. of Puerto Rico-Río Piedras maintains a field station in the Luquillo Mountains and, along with the National Science Foundation and the USDA-Forest Service, supports the Luquillo Long-Term Ecological Research (LTER) project (Waide and Lugo 1992, Brokaw et al. 2012a). Scientists associated with the Luquillo Critical Zone Observatory (CZO) examine processes in landforms and watersheds underlain by granodiorites, volcanoclastics, and associated contact metamorphic rocks with the goal of understanding climate-landscape interactions. Researchers at the Inst. for Tropical Ecosystem Studies are using field measurements and modeling results to investigate how physico-chemical properties of African dust transported from the Sahara influence Caribbean cloud properties and precipitation in the Luquillo Mountains (Gioda et al. 2011). All of these research efforts focus strongly on the effects of changing climate and land-use on ecosystem structure, processes, and services, providing rich sources of information about climate in the Luquillo Mountains.

## Climate of the Luquillo Mountains

Long-term and spatially-dense meteorological records provide the basis for analyzing temporal and spatial variability within the Luquillo Mountains. Surface measurements are complemented by aircraft and satellite-based data collection. The most recent example of the application of these new technologies was the acquisition of Airborne Thermal

and Land Applications Sensor (ATLAS) data for eastern Puerto Rico in 2004 (González et al. 2007).

Efforts to understand the dynamics of climate in the Luquillo Mountains have produced a series of simulation models that provide insights into the causes of these dynamics. For example, Wang (2001) used simulation models to predict spatial and temporal variation in environmental conditions across the Luquillo Mountains. The strong influence of elevation and aspect on climate was evident in the modeling results of Lash-Marshall et al. (2013). Models were used to determine seasonal differences in elevational gradients of air temperature, transpiration rate, and solar insolation. Results from these models were then used to predict dynamics of primary production and soil carbon.

The Luquillo Mountains and surrounding areas have been subjected to strong, ongoing changes in land use/land cover that provide the opportunity to examine the effects of human disturbance on local and regional climate. The existing mixture of ground, air, and satellite-based measurements, coupled with the results of simulation models, allow analyses of climate variability from watershed to regional scales.

## Spatial variability

### Within watershed variability

The most intensive study of climate at the watershed or stand scale in the Luquillo Mountains was conducted at the EVFS from 1963 to 1966 (Odum et al. 1970). Measurements taken at 1, 16.5 and 27.6 m from ground level showed increasing mean temperature and diel range with height. Rainfall collected simultaneously from two towers < 100 m apart generally agreed in rainfall totals. However, 17% of the time, there were differences between the collectors, probably because of differences in the temporal development of passing rain showers.

Wind direction at the EVFS is generally from the southeast rather than the prevailing east to northeast trade winds (Odum et al. 1970). The shift in wind regime suggests the presence of a pressure trough on the leeward slopes of the mountain and results in conditions more favorable to evaporation. Wind speeds were higher above the canopy and at ground level than within the canopy at 16.5 m. Eddies and gusts detected above the canopy are buffered by the canopy structure and seldom affect air flow at ground level.

Microclimatic conditions near the forest floor vary little in closed-canopy forest (Odum 1970). Measurements of temperature and relative humidity along a transect from uplands through stream channels showed no significant patterns (Waide unpubl.), and microclimate at ground level may be more closely associated with the degree of canopy cover than topographic position.

The Bisley Experimental Watersheds (BEW), 12 km east of the EVFS at a similar elevation, are directly exposed to the northeasterly trade winds (Heartsill-Scalley et al. 2007). Windspeed varies little throughout the year, and averages  $1.2 \text{ m s}^{-1}$  at the BEW and  $1.3 \text{ m s}^{-1}$  at the EVFS (McDowell et al. 2012). Rainfall is aseasonal in the BEW and averaged  $3668 \text{ mm yr}^{-1}$  over a 21-yr period (Heartsill-Scalley et al. 2006). Despite a weak but significant decline in rainfall over the first 15 yr of the study, there was no significant trend over the whole period (Heartsill-Scalley et al. 2006). Throughfall averaged  $2168 \text{ mm yr}^{-1}$  and declined slightly from 1988 to 2008. During that 15-yr period, the BEW were affected by 10 named tropical storms and multiple prolonged dry periods (Heartsill-Scalley et al. 2007). Annual evapotranspiration in the BEW ranges from  $2.0$  to  $3.0 \text{ mm d}^{-1}$  (Wu et al. 2006a). Most rain events are small, but rain is frequent, occurring on average  $267 \text{ d yr}^{-1}$  (Schellekens et al. 1999). High annual rates of canopy interception (ca 40%; Bruijnzeel 1989) and evaporation result from frequent low intensity, short-duration rainfalls, net upward transport of evaporated moisture, and a relatively uniform canopy (Scatena 1990, Schellekens et al. 2000). Seasonal patterns of rainfall were similar between the BEW and the EVFS, but the BEW had significantly higher rainfall in April, May and October than the EVFS (Heartsill-Scalley et al. 2007).

### Landscape variability

Climatic variability within the Luquillo Mountains manifests as gradients that are correlated with elevation, slope,

aspect, or land use history. Efforts to understand spatial variability in the forest ecosystems of the Luquillo Mountains often invoke the existence of these gradients. Gradient analysis is defined as a conceptual system to examine the distribution, growth, and abundance of species or biological communities as a function of independently measured physical, chemical or biotic properties of their environment. For example, tree species within the Luquillo Mountains are each distributed by their independent responses to gradients of environmental conditions, and consequently communities at various elevations comprise species that happen to grow well there (Harris et al. 2012). Moreover, each species has a preferred distribution along gradients such as temperature, sunlight, wind exposure, upslope drainage, and soil moisture, which are strongly related to elevation and topographic position (Kessell 1977, 1979). Other chapters in this book employ gradient analysis to examine the distribution of species with elevation and associated landscape variability.

Lugo and Brown (1981) summarized environmental patterns over the elevational gradient in the Luquillo Mountains. Temperature, precipitation, and cloud formation are just a few of the characteristics that show trends with elevation. Temperature declines with elevation from a high of about  $26.5^\circ\text{C}$  at the coast to around  $20^\circ\text{C}$  at the mountain top (Fig. 2). The temperature range at lower elevations is greater than at higher elevations in all months. However, the annual variation in mean monthly temperature was similar at low (Río Blanco; 30 m a.s.l.) and high (East Peak; 1051 m a.s.l.) elevations ( $3.5^\circ$  and  $3.0^\circ\text{C}$ , respectively). Lower elevation sites have a greater diel temperature range ( $6.5^\circ\text{C}$ ) than do higher elevation

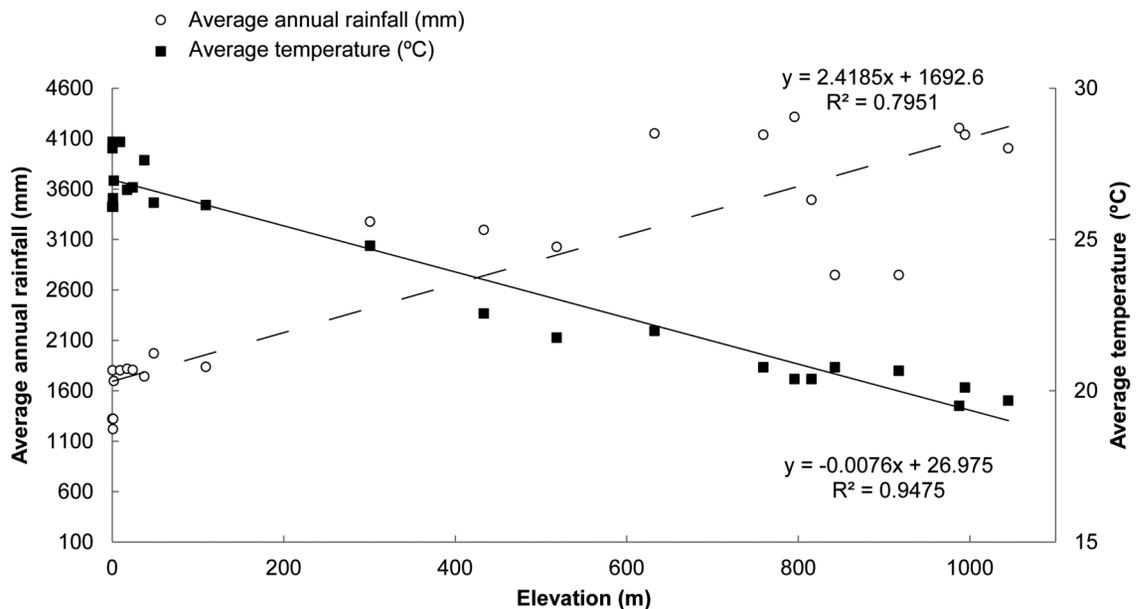


Figure 2. Changes in mean annual rainfall (open circles) and mean daily air temperature (closed squares) with elevation in the Luquillo Mountains. From González and Luce (2013).

sites ( $1.5^{\circ}\text{C}$ ). The annual pattern of relative humidity varies little with elevation, with the lowest values occurring from February–April at all elevations. At the highest elevation station, El Yunque Peak (1080 m a.s.l.), humidity is uniform throughout the year at around  $98\% \pm 2\%$ . Relative humidity decreases with elevation and from windward to leeward exposures. The lowest relative humidity and the maximum annual variation (63–75%) are found at the Cubuy station, located on an exposed shoulder southwest of El Yunque Peak. Significant daytime reductions in humidity (minimum = 50%) were observed at all stations but El Yunque Peak. Diurnal variation in relative humidity decreases with elevation from around 5% at El Yunque Peak to 20–30% at lower elevation stations. Nighttime humidity is uniformly high at all stations ( $> 74\%$ ) regardless of time of year. Wind velocity increases with elevation from  $0.42\text{--}0.83$  to  $2.22\text{--}5.00$   $\text{m s}^{-1}$ , and wind direction is more constant at higher elevations. Wind direction is generally from the northeast at high elevations, but tends to the southeast at lower elevation stations (Brown et al. 1983), perhaps because of a leeward pressure trough (Odum et al. 1970). Solar radiation declines with elevation from  $3.8\text{--}7.2$  to  $2.0\text{--}4.3$   $\text{kWh m}^{-2} \text{d}^{-1}$ .

Records from weather stations located within the Luquillo Mountains indicate a strong gradient in annual

rainfall with elevation (Brown et al. 1983; Fig. 2). Rainfall increases with elevation up to approximately 700 m. Annual rainfall ranges from  $2450 \text{ mm yr}^{-1}$  at lower elevations to over  $4000 \text{ mm yr}^{-1}$  at higher elevation stations. García-Martínó et al. (1996) found a positive relationship between elevation and mean annual rainfall and a negative relationship between elevation and average number of days per year without rainfall. A positive relationship between elevation of streamflow gages and mean annual runoff was stronger when watershed average elevation was substituted for gage elevation (García-Martínó et al. 1996). No horizontal spatial pattern in runoff was apparent within the Luquillo Mountains (García-Martínó et al. 1996).

Local topographical effects can override the general pattern of increasing rainfall with elevation. Holben et al. (1979) measured the spatial variability of rainfall above 500 m in the Río Espíritu Santo watershed using a grid of 20 bulk rainfall collectors (Fig. 3). Highest annual rainfall ( $4300 \text{ mm yr}^{-1}$ ) occurred at the highest station, El Yunque Peak. Lowest recorded rainfall ( $2670 \text{ mm yr}^{-1}$ ) occurred at about the same elevation on the southern boundary of the watershed. The relatively shallow gradient from east to west along the channel of the Río Espíritu Santo contrasts with the very abrupt decline in annual rainfall along the

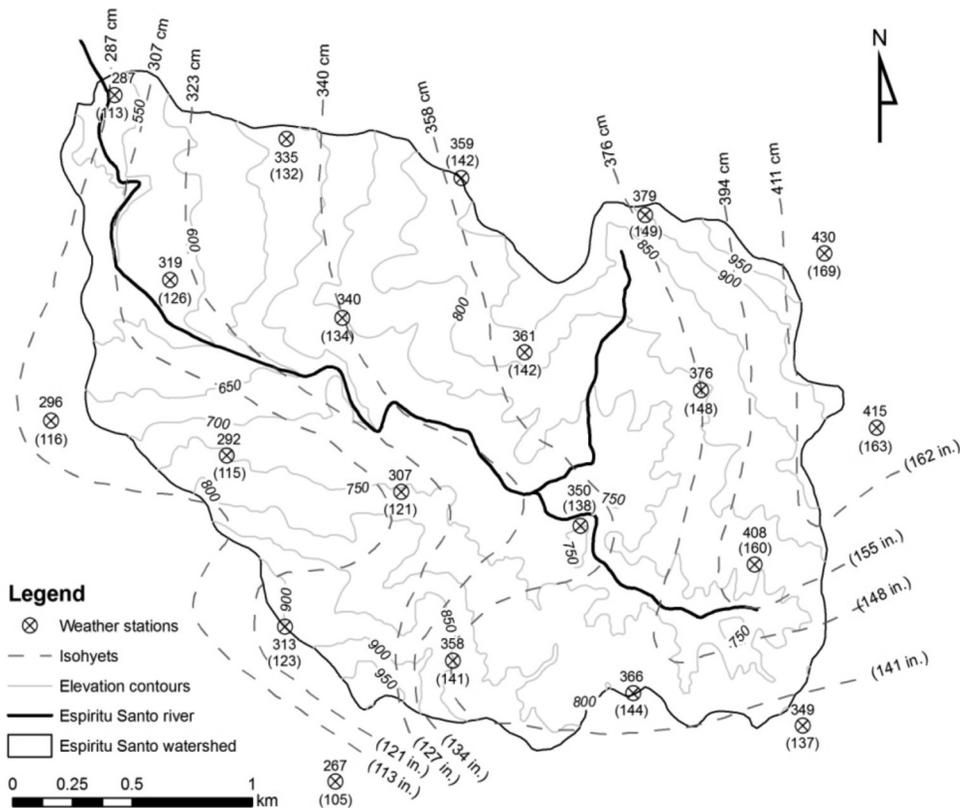


Figure 3. Annual precipitation from February 1976–February 1977 as isohyets superimposed on elevation contours for the Río Espíritu Santo Watershed (Holben et al. 1979).

southern border of the watershed. This decline in rainfall is attributable to a rain shadow associated with the highest peaks, heterogeneous topography along the southern border of the watershed, and perhaps the shift in direction of the prevailing wind discussed above. Location with regard to the northeast trade winds may also affect the pattern of annual rainfall. Long-term records from the BEW on the windward side of the Luquillo Mountains and the EVFS, just around the shoulder of the mountain from the BEW at a similar elevation, showed nearly identical average annual values (3482 vs 3393 mm yr<sup>-1</sup>), but the BEW had significantly higher rainfall in the months of May, June and October (Fig. 4; Heartsill-Scalley et al. 2007).

Rainfall distribution is highly variable above 700 m a.s.l. in the Luquillo Mountains (Fig. 5). From 1994–1998, rainfall averaged 4500 ± 143 mm yr<sup>-1</sup> over 12 stations in the upper elevations of the LEF. There was no trend in precipitation along the upper elevation gradient. The lack of a simple relationship between precipitation and elevation was likely due to a combination of localized effects of topography on rainfall and cloud input and horizontal precipitation, which are very difficult to quantify (Weaver 1972, Holwerda et al. 2006). The higher variability in precipitation between 740 and 900 m a.s.l. likely results from the variability in cloud input at these elevations.

Because of high rainfall, soil moisture is high and varies little among seasons at the EVFS (between 70 and 80% from August 1999 to July 2000; Ruan et al. 2004). Soil moisture responds to rainfall, soil characteristics, slope, aspect, and canopy cover, and therefore the spatial pattern of soil moisture can be complicated. For example, soil moisture in gaps did not differ from intact forest (Pérez Viera 1986), apparently because higher evaporation balanced lower transpiration (Silver and Vogt 1993). Soil moisture increases with elevation in both open and closed canopy sites (Fig. 6; McGroddy and Silver 2000), and soil moisture is generally less in open sites except at the highest elevation. The annual rate of daily soil moisture loss

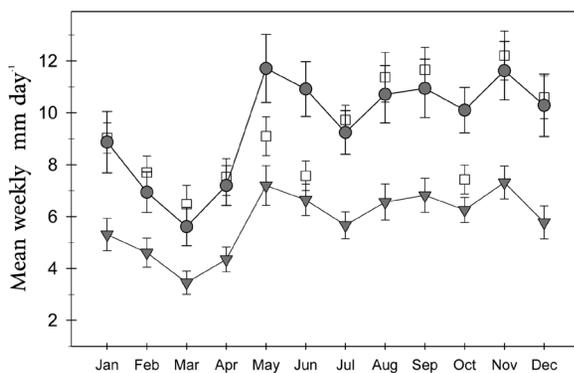


Figure 4. Monthly distribution of rainfall for EVFS (open squares) and BEW (gray circles) and throughfall for BEW (inverted triangles). Error bars represent one standard error of the mean. Redrawn from Heartsill-Scalley et al. (2007).

between the surface and 30 cm depth is about half the U.S. summer rate and low relative to temperate zones in general (U.S. Army Corps of Engineers 1960). At higher elevations and in valley bottoms, soil can remain saturated for long periods of time (Wadsworth and Bonnet 1951), resulting in low O<sub>2</sub> concentrations that affect root growth and greenhouse gas emissions (Silver et al. 1999).

Changes in cloud cover or cloud fraction may have important implications for climate. Predictions of cloud cover in the Luquillo Mountains, based on general linear models using three independent topographic variables (slope, aspect, and the difference between elevation and the lifting condensation level), showed a higher probability of cloud cover with elevation, and a higher probability of clouds at night (Wu et al. 2006b). Modeled probability of cloud cover decreased after sunrise until early afternoon, and then increased again for the rest of the day until night, and was correlated with the movement of the lifting condensation level (i.e. the height at which the relative humidity of air reaches 100% as it is cooled by adiabatic lifting).

Passing synoptic weather systems cause the rise and fall of the moisture layer, which controls cloudiness and shower frequency (Odum et al. 1970). When the moisture layer is deeper, weather conditions are characterized by heavy cloudiness, rain, low insolation, low temperature, and reduced evaporation. Fog forms as an advected cloud over a warm ocean and bathes the upper elevations of the Luquillo Mountains nearly 75% of the time during the day and over 95% of the time at night (Holwerda et al. 2006, 2011, Scholl et al. 2011). Under these conditions, cloud drip contributes 1–4 mm d<sup>-1</sup> to precipitation totals at the higher elevations of the Luquillo Mountains (McDowell et al. 2012). Because rainfall averages 15–30 mm d<sup>-1</sup> at high elevations, cloud drip represents a small fraction of total hydrologic input.

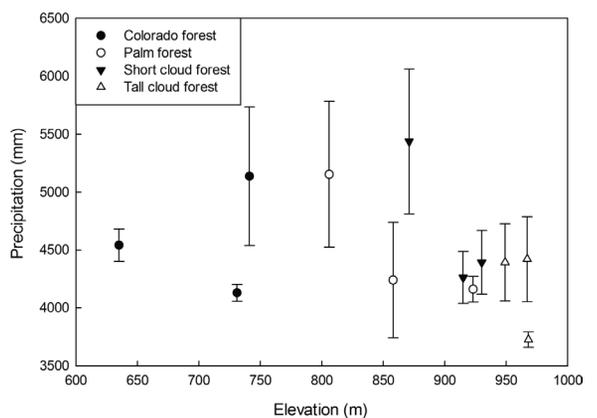


Figure 5. Mean annual precipitation ± one standard error for 12 stations from 635 to 968 m a.s.l. in the Luquillo Mountains (Silver unpubl.). Precipitation was measured continuously from 1994 to 1998 using small tipping bucket rain gages (Hobo Event data logger H7).

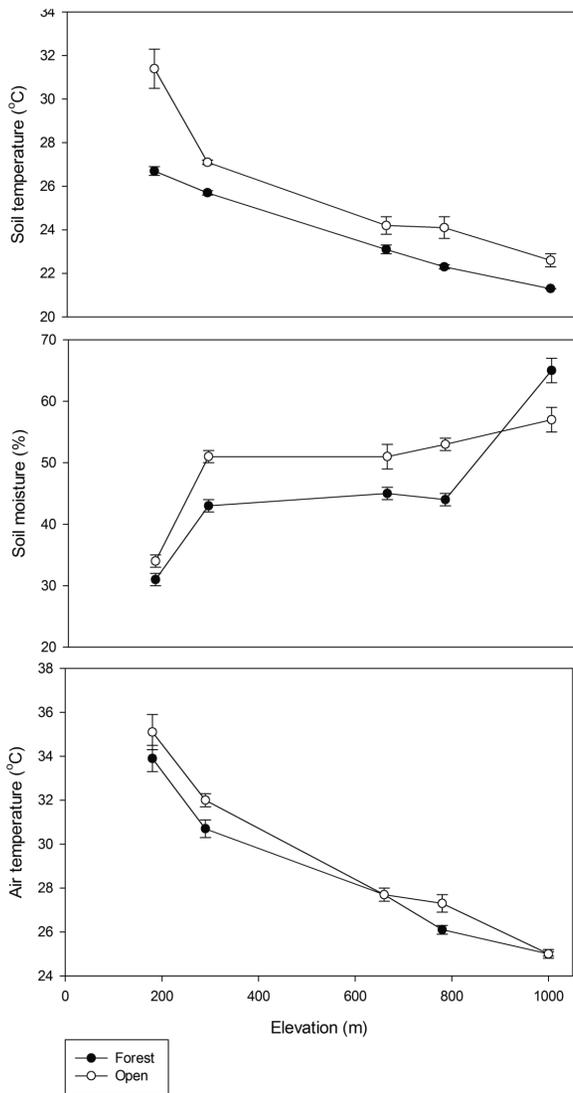


Figure 6. Comparison of soil temperature, soil moisture, and air temperature between open and forested sites at five elevations in the Luquillo Mountains. Error bars represent  $\pm 1$  SE. Data from McGroddy and Silver (2000).

When present, the lower limit of the fog layer is around 600 m a.s.l. (Lugo et al. 2012a), but many factors influence the elevation of the fog layer. For example, deforestation, storm-induced defoliation, urban heat island effects, or global climate change could modify temperature and humidity sufficiently to raise the fog base hundreds of meters (Scholl et al. 2009). After widespread defoliation occurred as a result of Hurricane Hugo in 1989, the cloud base in the Luquillo Mountains rose beyond the tops of the highest peaks (van der Molen et al. 2010). A rise in the fog base could lead to a decline in trade-wind orographic precipitation or a redistribution of precipitation (Scatena and Larsen 1991, Lawton et al. 2001, van der Molen et al.

2006), with significant effects on the climate of Luquillo Mountains.

### Regional variability

The NASA Airborne Thermal and Land Applications Sensor (ATLAS), which operates in the visual and infrared bands, was used on 13 February 2004 to collect 10-m resolution data from eastern Puerto Rico, including the Luquillo Mountains. The calibrated ATLAS data provide an excellent means to quantify the impact of changing land use on the surface energy budget. The ATLAS surface temperature data for eastern Puerto Rico (Fig. 7) represents a wide range of surface temperatures, from the coldest (black) clouds at about 10–13°C, the primary forest (purple/blue) at around 26°C, non-forested areas at the foot of the Luquillo Mountains (green) and the hottest urbanizing areas (yellow, red, white) including asphalt surfaces at about 42.7°C to roofs at over 53.5°C. The gradient in decreasing urbanization from San Juan to the Luquillo Mountains produces a gradient in surface temperature (Fig. 7).

We can compare how urbanization affects the surface temperature structure by comparing the frequency distributions of daily temperatures of the forest around the EVFS (Fig. 8) to the temperature frequency distributions of the urbanizing areas surrounding the forest (Fig. 8). Forest temperatures at the EVFS are normally distributed around 26°C. These forest canopy temperature distributions are similar to those reported by Luvall et al. (1990) from a tropical forest in Costa Rica using a similar aircraft-based remote-sensing technology. The cooler temperatures are represented by clouds and the warmest by roads and rooftops. The distribution of temperatures from urbanizing areas is skewed with a small vegetation component and a tail of much hotter temperatures resulting from the conversion of natural vegetation to surfaces covered by man-made materials.

Air temperature increases along the rural–urban gradient from the Luquillo Mountains to the center of San Juan (Murphy et al. 2010). Using data loggers placed at intervals along the rural–urban gradient extending from the forested mountains to San Juan (roughly 30 km), Murphy et al. (2010) demonstrated a pronounced nighttime urban heat island (UHI) with an average difference of 2.15°C between the urban reference station and rural stations during the wet season. During the dry season, there was a 1.78°C average difference (Fig. 9).

Generally, the UHI is expected to be more pronounced during the dry season, but according to Murphy et al. (2010), the actual weather during the wet season in which they collected data was somewhat drier than normal, while dry season measurements were somewhat wetter than normal. Nonetheless, the measurement of maximum UHI (i.e. the value of the UHI measured in

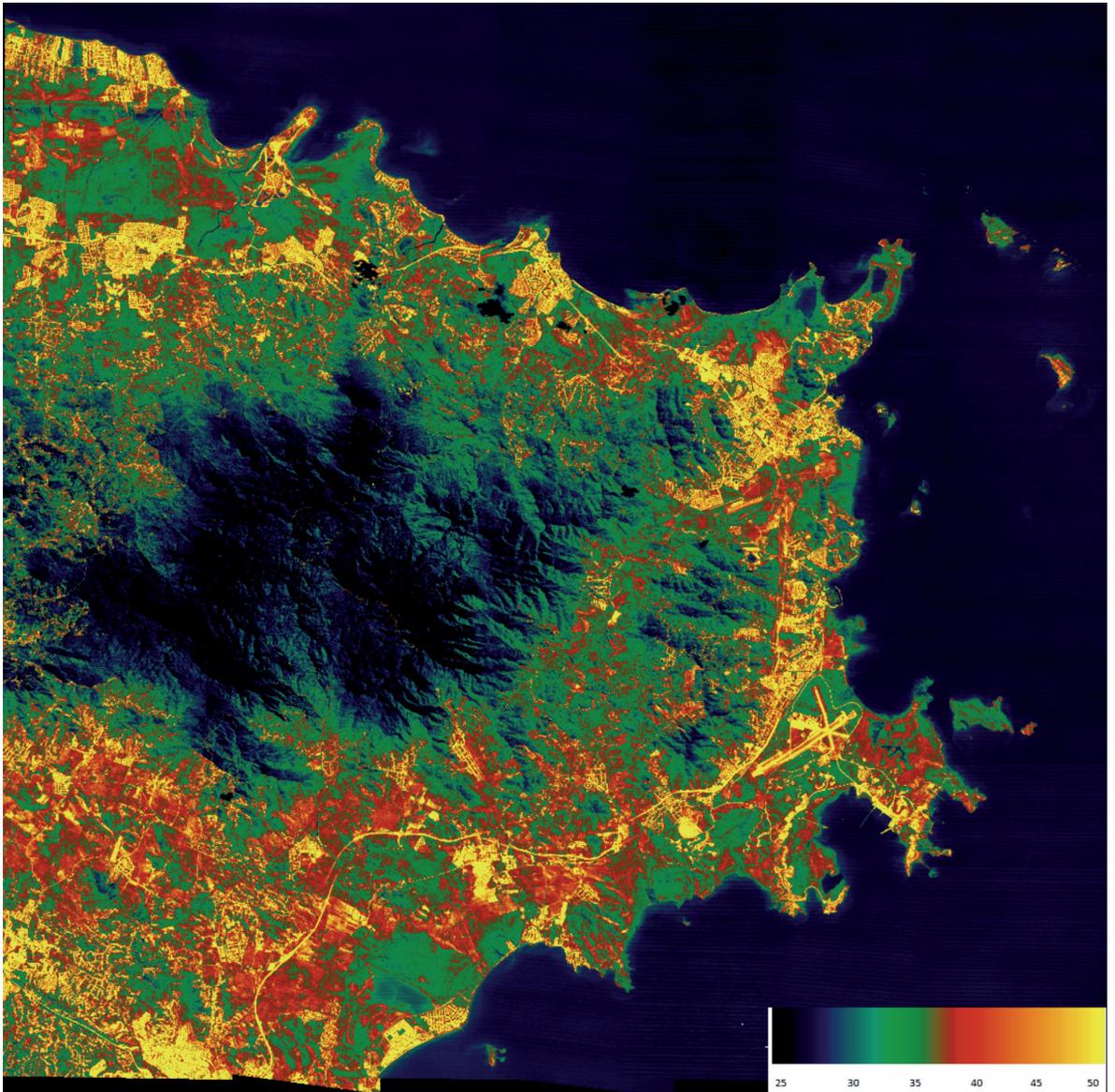


Figure 7. ATLAS 10 m resolution thermal image for the Luquillo Mountains and surrounding area of Puerto Rico. Warmer colors represent higher temperatures in °C.

periods with very low wind and few clouds that favor the formation of strong UHIs) resulted in a difference of 4.7°C between the urban reference and forest station. Other wet, tropical cities of like size show similar UHIs (Murphy et al. 2010). Temperature measured at stations along the urban–rural gradient between San Juan and the Luquillo Mountains was correlated with the percent vegetation cover upwind of the station (Fig. 10; Murphy et al. 2010). Thus, patches of vegetation provide the ecosystem service of reducing downwind urban heating effects.

## Temporal patterns

### Daily variation

Diel rainfall patterns in Puerto Rico result from interactions between orographic and convection processes. The daily heating cycle creates a mesoscale circulation over eastern Puerto Rico with rainfall maxima in San Juan at 04:00 and 15:00 h. As the land surface cools at night, the height at which adiabatic cooling produces clouds decreases.

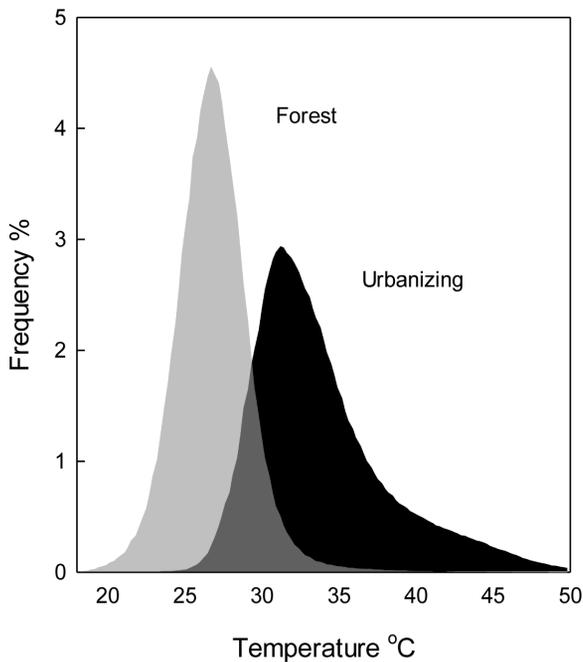


Figure 8. The ATLAS temperature frequency distribution of the forested area near the EVFS and the urbanizing area surrounding the Luquillo Mountains.

es. Nighttime orographic airflows lead to cloud formation on windward slopes at lower elevations (170 m or less) than does the daytime cloud formation caused by convective processes (Odum et al. 1970). An east-west gradient characterizes the timing of rainfall events, with the eastern part of the island (including the Luquillo Mountains) having a pre-dawn maximum (Roy and Balling 2005). These early morning rains are triggered by nighttime downslope movement of air converging with northeasterly and easterly trade winds.

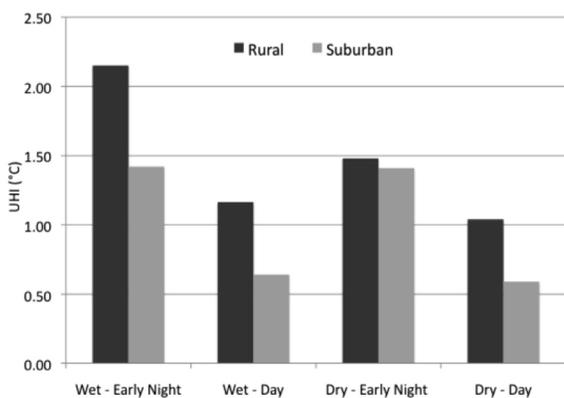


Figure 9. Temperature differences between the urban heat island (UHI) of San Juan and rural and suburban stations. Comparisons between wet and dry seasons and between day and night are shown. Reprinted from Murphy et al. (2010).

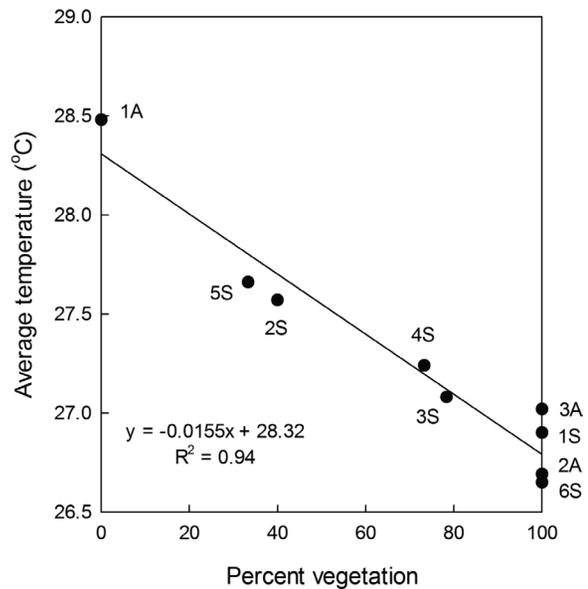


Figure 10. Relationship between average temperature during the summer of 2006 and the percent vegetation found upwind from the temperature gauge to a distance of 180 m. Gauges were located in the following habitats: 1A = urban reference, 5S = major road crossing, 2S = small urban center, 4S = residential, 3S = industrial, 3A = grassland mix, 1S = abandoned agricultural fields, 2A = old-growth forest, 6S = mowed grassland. See Murphy et al. (2010) for detailed descriptions of habitat types. The figure is reprinted from Murphy et al. (2010).

Most of the annual rainfall total (80%) results from high frequency, short duration precipitation events (Scatena 1995). Air temperature and solar radiation are greatest just after mid-day (Fig. 11). The nighttime lowering of the cloud base and higher wind speeds result in increased inputs of cloud water at night (Fig. 11; Holwerda et al. 2011). Persistent fog and clouds also affect the diel temperature range and solar radiation.

The formation and passage of cumulus clouds during the day cause variability in the light regime of the forest. At any point, an average 100 changes between full sun and cloud conditions occur daily, with greater numbers of changes in the summer (Odum et al. 1970). Diurnal temperature changes reflect changes in insolation, but the diurnal range in temperature is relatively small. Heating reduces relative humidity and accelerates evaporation and transpiration during the day (Odum et al. 1970). Diurnal variation in absolute humidity is less than daily variation.

### Seasonal variation

Rainfall shows the same seasonal pattern at all elevations in the Luquillo Mountains, with a relatively drier period from January–March followed by an increase in rainfall during

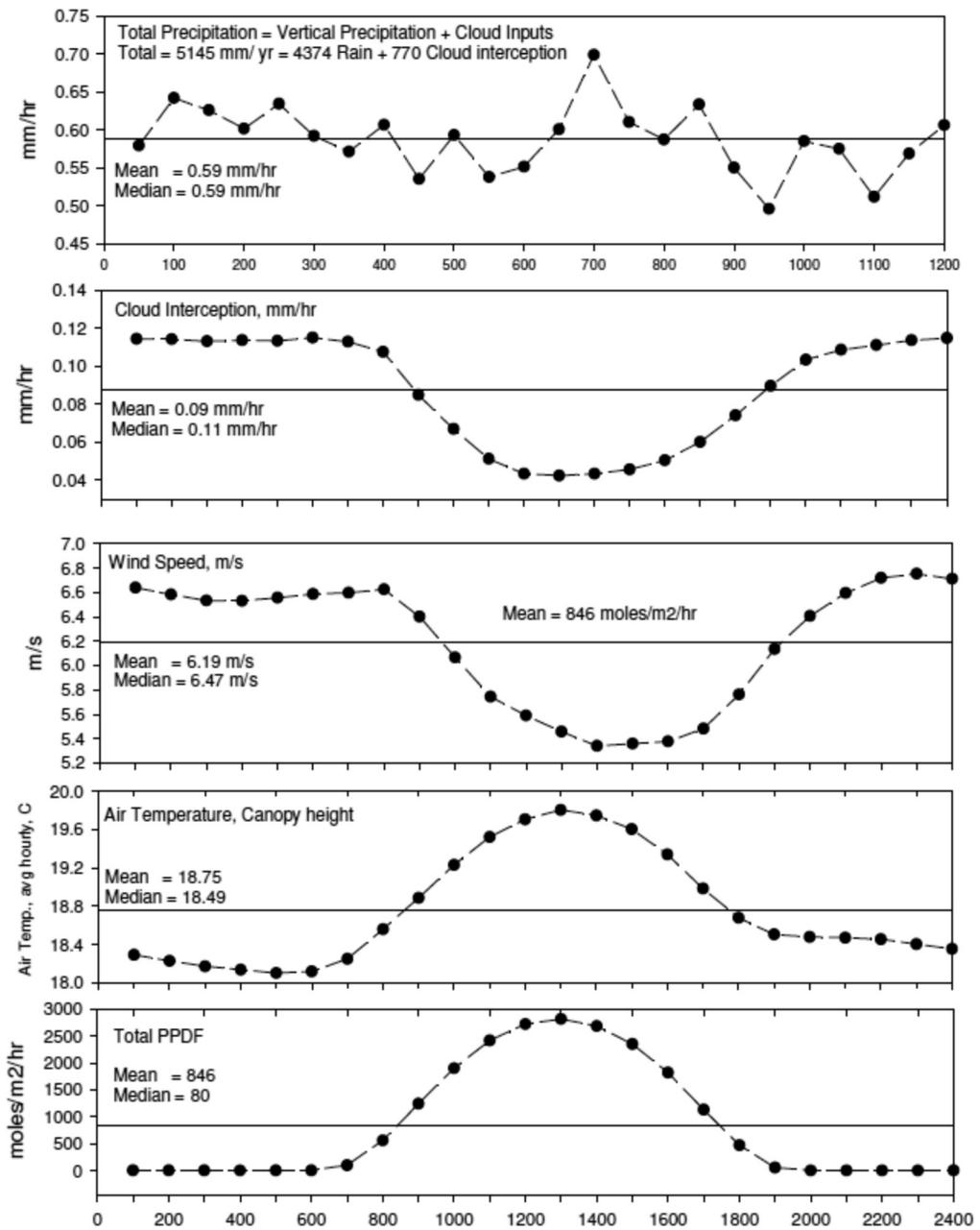


Figure 11. Diel patterns of micrometeorological characteristics at East Peak in the Luquillo Mountains. From Harris et al. (2012).

April–May. Rainfall declines at most stations in June and then is uniformly high during the rest of the year, with more uniformity in rainfall from April through November at lower elevations than at higher elevations (Brown et al. 1983). In general, rainfall is greater than 200 mm month<sup>-1</sup> except at lower elevations. Because rainfall is high even in the drier season, vegetation in the Luquillo Mountains does not experience seasonal stress.

Monthly temperature variation at the EVFS shows a typical pattern for Puerto Rico with maxima in June–

August period and minima in January–March (Fig. 12). Wind direction at the EVFS varies between north and east (Fig. 13). The annual pattern of total radiation is similar at different elevations, with maxima in July and minima in December–January (Fig. 14). Nonetheless, the intensity of radiation at the ground is less at higher elevations than at lower elevations because of more frequent and persistent cloud cover.

Data from the International Satellite Cloud Climate Project (ISCCP; <<http://isccp.giss.nasa.gov/>>) were used

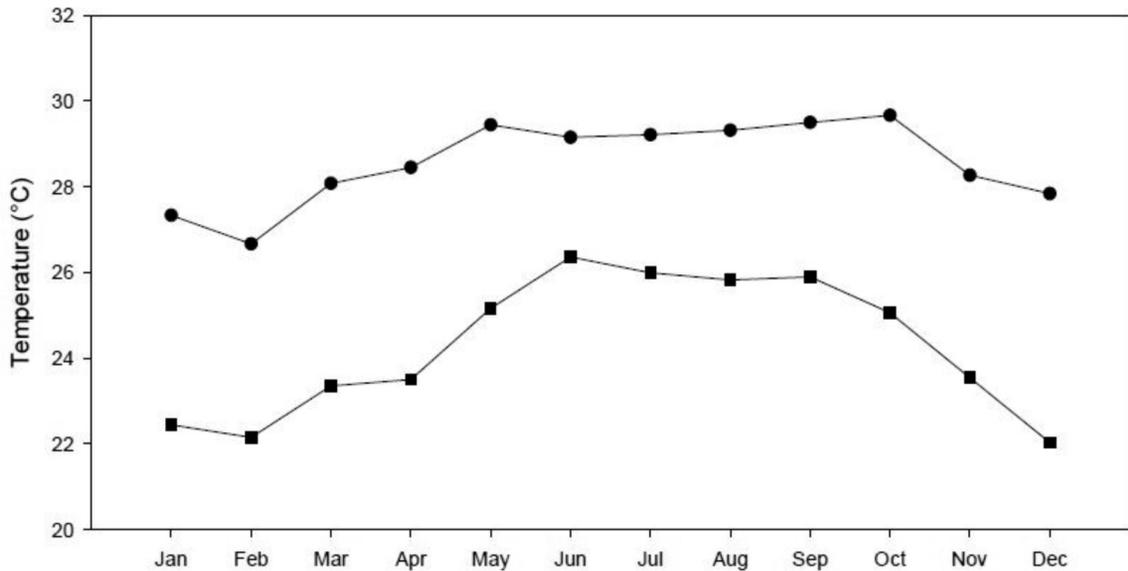


Figure 12. Average monthly maximum and minimum temperatures at the EVFS for the period 1975–2002. Data are from A. Ramirez and E. Melendez-Colom (pers. comm.).

to derive a monthly time series of cloud cover over Puerto Rico from 1983 to 2004. This data set provides reliable information for 130 parameters that exhibit and characterize the properties of clouds at the global scale and at 2.5° of spatial resolution (Rossow and Schiffer 1999). The seasonal distribution of deep convection clouds, the type of clouds with the greatest optical thickness and top pressure, is bimodal over the Luquillo Mountains (Fig. 15), paralleling the seasonal distribution of rainfall.

### Annual variation

Long-term records of rainfall are common for the Luquillo Mountains, but uninterrupted temperature series are less

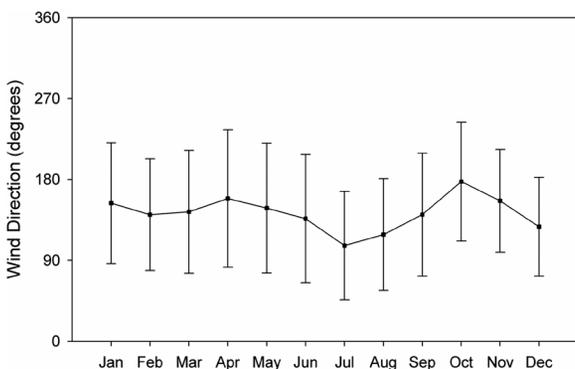


Figure 13. Monthly wind direction (degrees) for 2003 at the EVFS. Error bars represent one standard deviation. Data are from A. Ramirez and E. Melendez-Colom (pers. comm.).

common. Long-term records of temperature show similar patterns of annual variation at the EVFS and the BEW (Fig. 16). There is a direct relation between sea surface temperature and air temperature in the Caribbean (Ray 1934), but temperatures at the EVFS and the BEW do not show a strong relationship with sea surface temperature.

A detailed analysis of rainfall characteristics of a single weather station (La Mina) showed that annual rainfall totals over a period of eight years varied between 3730 and 6450 mm, and monthly totals between 310 and 1030 mm (Wadsworth 1949). An average of 269 d yr<sup>-1</sup> had at least 0.3 mm d<sup>-1</sup> of rainfall, with 53 d having at least 25.4 mm

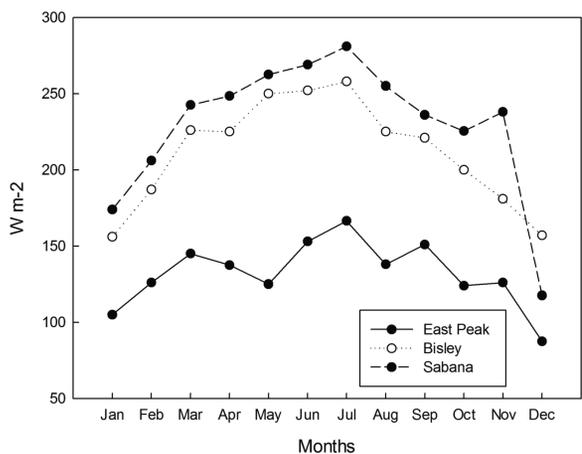


Figure 14. Average monthly total radiation at ground level at three different elevations from 2000 to 2002. Data are from F. Scatena (unpubl.) from the Luquillo Critical Zone Observatory and the Luquillo Long Term Ecological Research program.

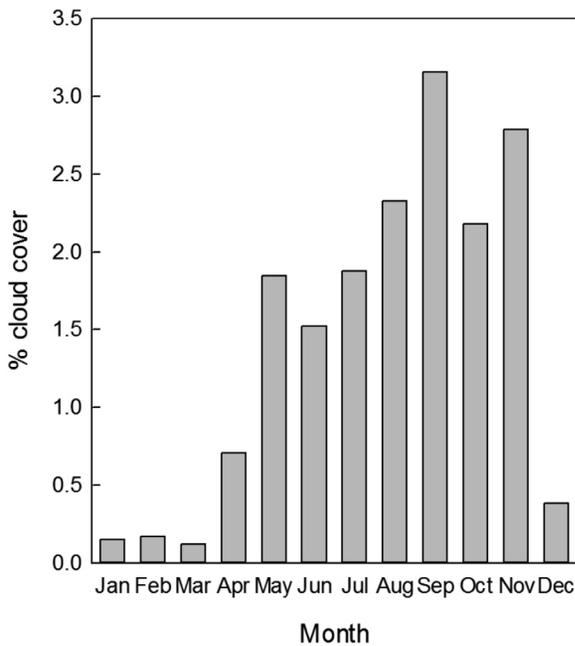


Figure 15. Monthly variation in the cover of deep convection clouds in the Luquillo Mountains from 1983 to 2004.

of rainfall. Over 1600 rain events occurred per year on average, with the mean duration of rainfall events being 19 min. Most rainfall (55%) fell during daylight hours (Brown et al. 1983).

Substantial year-to-year variability in rainfall is evident at the EVFS and BEW (Fig. 17). The four periods of drought and five hurricanes that have occurred since 1988 have produced differential consequences at these sites (Heartsill-Scalley et al. 2007). In 1989, moderate rains accompanying Hurricane Hugo were followed by three months of extreme drought, the combination of which resulted in an annual rainfall total near the long-term average. The 1991 drought affected the two sites similarly, but the 1994 drought was much more severe at the EVFS. In 1996, Hurricanes Bertha, Hortense, and Marilyn cancelled the effects of a drought, and in 1998, Georges, a very wet storm, resulted in a much larger than average annual rainfall. Despite high interannual variability, Heartsill-Scalley et al. (2007) also detected a weak but significant decrease in annual mean weekly rainfall at the BEW from 1988 to 2002. This pattern was part of a regional drying in the 1990s observed across Puerto Rico (Larsen 2000) and the Antilles (Díaz 1996), but at the BEW it was followed by several years of above average rainfall.

In the Luquillo Mountains, long-term streamflow records (> 20 yr) are available for eight USGS gauging stations. Because large water extractions for domestic use occur at over 35 water intakes located throughout the area, only three of these gauging stations (Río Canovanas, Río Icosos, and Río Mameyes) provide streamflow records un-

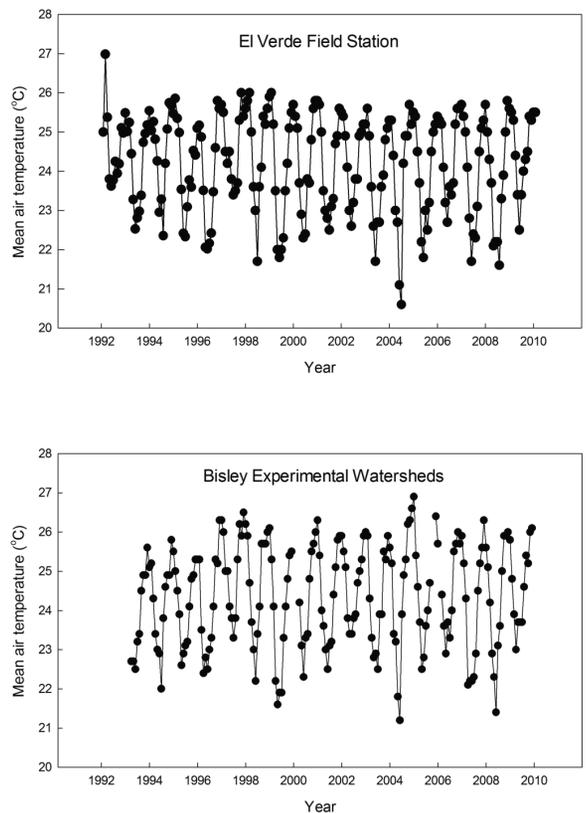


Figure 16. Variation in mean monthly air temperature at the EVFS and the Bisley Experimental Watersheds.

der natural flow conditions (Appendix 1). Historic rainfall data are available for three locations in the Luquillo Mountains: the BEW (285 m a.s.l.), the EVFS (350 m a.s.l.), and East Peak (1051 m a.s.l.). Historic streamflow and rainfall records from these stations were analyzed from 1989 to 2010 to assess temporal patterns in the proportion of the rainfall that becomes surface runoff in the Luquillo Mountains. The surface runoff that drains the Luquillo Mountains is a direct function of rainfall (Fig. 18). The proportion of rainfall that becomes runoff is known as the runoff coefficient. In the Luquillo Mountains, about 66% of the annual rainfall leaves the forest as surface runoff (Fig. 18; Appendix 2). This agrees well with previous estimates for the Luquillo Mountains (García-Martín 1996), but is higher than that in other tropical forests and for other locations in Puerto Rico. The annual runoff coefficient has been fluctuating over the last 22 yr around 66% (SD = 11%; Fig. 19). Assuming that underground water storage in the Luquillo Mountains is small, most of the remaining rainfall over the forest (34%) is lost through evapotranspiration. In general, low-rainfall years yield years with low runoff, whereas high-rainfall years will produce high runoff (Fig. 20). This is particularly true during extremely dry and wet years. During average years, the relationship

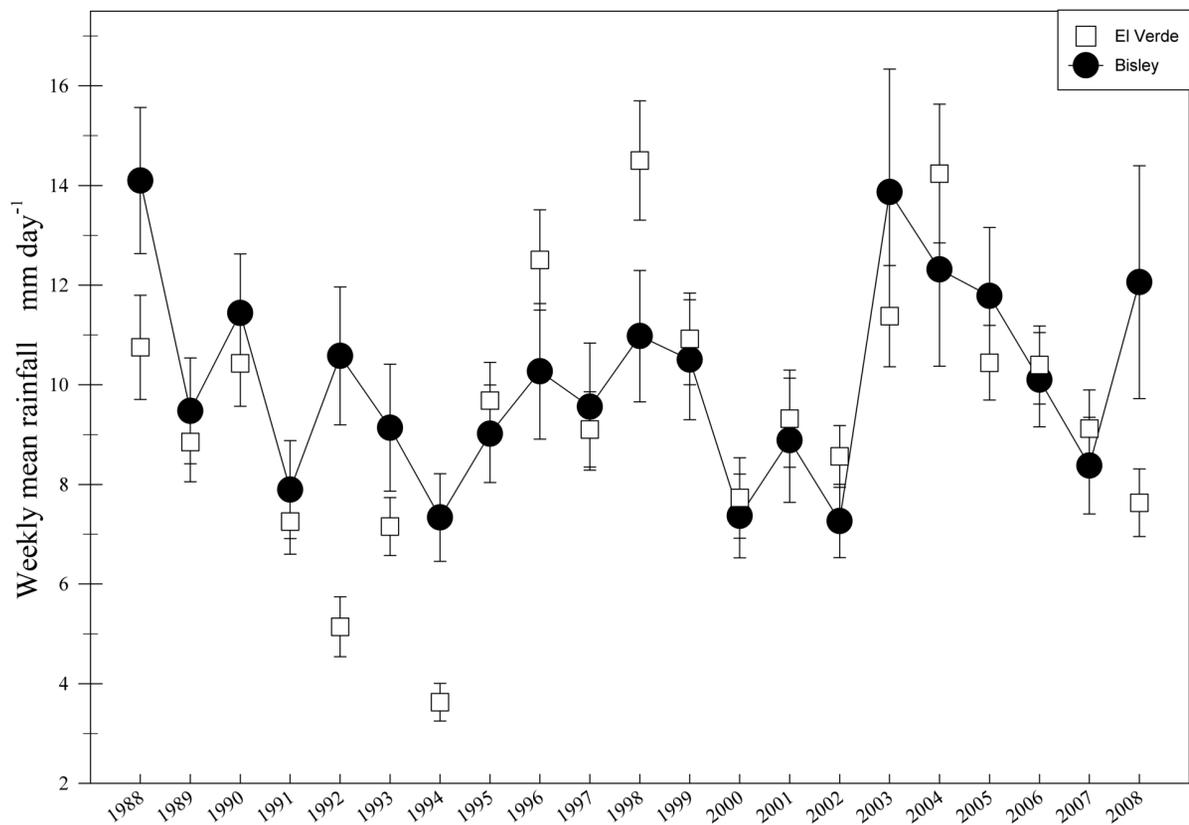


Figure 17. Mean ( $\pm$  SE) weekly rainfall per year for Bisley and the EVFS (data from Heartsill-Scalley 2006).

is not as strong. During the period 1989–2010, 2010 was the wettest year, while 1994 was the driest.

## Extreme events

Puerto Rico lies in an area with frequent hurricanes that bring extreme conditions of rainfall and wind. For the 20 named Puerto Rican storms between 1950 and 2000, median wind speed recorded at San Juan was  $17.5 \text{ m s}^{-1}$ , with a maximum of  $41.1 \text{ m s}^{-1}$  (Scatena et al. 2012). The median rainfall for these storms was  $40 \text{ mm d}^{-1}$ , with a maximum of  $225 \text{ mm d}^{-1}$  (Scatena et al. 2012). Approximately 51 hurricanes have passed over the island since the first recorded hurricane in 1515 (Schaefer 2003). Most hurricanes occur between July and November, and multidecadal changes in hurricane frequency have been observed over the past 300 yr in the Caribbean (Scatena et al. 2012), although the cause of these changes is not known. Globally, sea surface temperature, African monsoons and drought cycles, ENSO events, and patterns of thermohaline ocean circulation are related to hurricane frequency (Gray et al. 1997). On average, Puerto Rico experiences a direct hit from a hurricane once every 21 yr, and a hurricane will pass over the Luquillo Mountains every 50–60 yr (Scatena

1995). These events produce from three to  $225 \text{ mm d}^{-1}$  of rain depending on storm characteristics such as the intake of humid air, rotational wind velocity, forward speed, and the position of the storm relative to the measuring station (Scatena et al. 2012).

Other extreme rainfall events occur that are not associated with hurricanes. Since 1975, 82% of rainfall events greater than 100 mm have not been associated with cyclonic storms, but have instead resulted from convective cells or stalled low-pressure systems (Schaefer 2003). The greatest rainfall recorded in a 60 min period in Puerto Rico (150 mm) occurred at El Yunque Peak; the highest annual total (6452 mm) was recorded at La Mina (Colón Torres 2009). Such extreme events occur at any time during the year, but are most common from April–May and August–December. The occurrence of extreme events is important because high sediment loads in streams are associated with these events (Brokaw et al. 2012b).

Despite the high average annual rainfall, droughts also occur in the Luquillo Mountains. Severe and prolonged droughts in Puerto Rico occur every 10 yr on average, and the lower Luquillo Mountains typically experience 15 or more consecutive days without rainfall every 15 yr (Scatena 1995). These droughts can have a significant effect on rain forest organisms (Brokaw et al. 2012b).

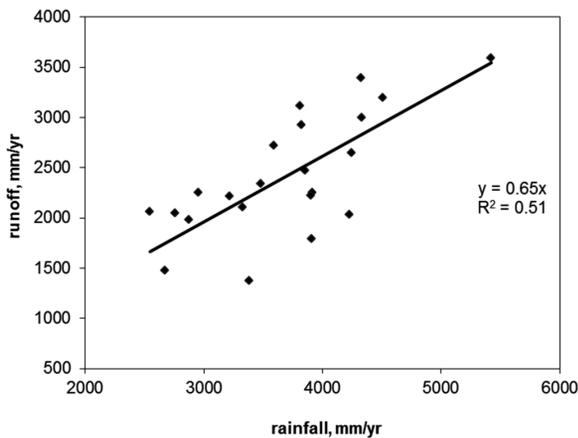


Figure 18. Relationship between annual rainfall and annual runoff for the Luquillo Mountains. The relationship is significant at the  $p = 0.001$  level. The Luquillo Mountains mean annual runoff was calculated as the arithmetic mean of three gauging stations with simultaneous streamflow data unaffected by water extractions or discharges. Mean annual rainfall over the Luquillo Mountains was defined as the arithmetic mean of annual rainfall data measured at three locations: Bisley (1989–2010), El Verde (2000–2010), and East Peak (2001–2009).

## Long-term trends

Long-term records and modeling suggest that climate may be changing in Puerto Rico. For example, rainfall declined over the island during the 20th century (Fig. 21; van der

Molen 2002, Bisselink 2003). The years 1991, 1994, and 1997 were among the driest recorded in Puerto Rico during the 20th century (Larsen 2000). The causes of this decline in rainfall are not clear. Increased cloud elevation in the Luquillo Mountains after Hurricane Hugo (van der Molen et al. 2010) suggests a possible relationship between foliage cover and rainfall. The long-term trend of declining forest cover that began in the 18th century in Puerto Rico provides a possible reason for the observed decline in rainfall. However, beginning in the 1940s, both forest cover and the area of impermeable surfaces in Puerto Rico increased as agricultural lands were abandoned and urbanization/suburbanization increased, suggesting that change in vegetation cover may not explain long-term rainfall patterns by itself. Moreover, an analysis of rainfall for the EVFS showed a 24% increase from 1957 to 1990 that was not statistically significant because of the high average annual rainfall (Greenland and Kittel 2002). Thus, local rainfall patterns may contradict the island-wide trend, suggesting that local and island-wide patterns are influenced by different factors.

A 62-yr record of temperature from the National Weather Service station in Fajardo, east of the Luquillo Mountains, shows a significant but small ( $0.024^{\circ}\text{C yr}^{-1}$ ) increase in annual maximum temperature and an even smaller ( $0.009^{\circ}\text{C yr}^{-1}$ ) decrease in annual minimum temperature (Greenland and Kittel 2002). Detrended standardized anomalies of annual temperature show a period of cooling from 1957 to 1978 followed by a period of warming. A similar analysis of rainfall shows a cyclic pattern at

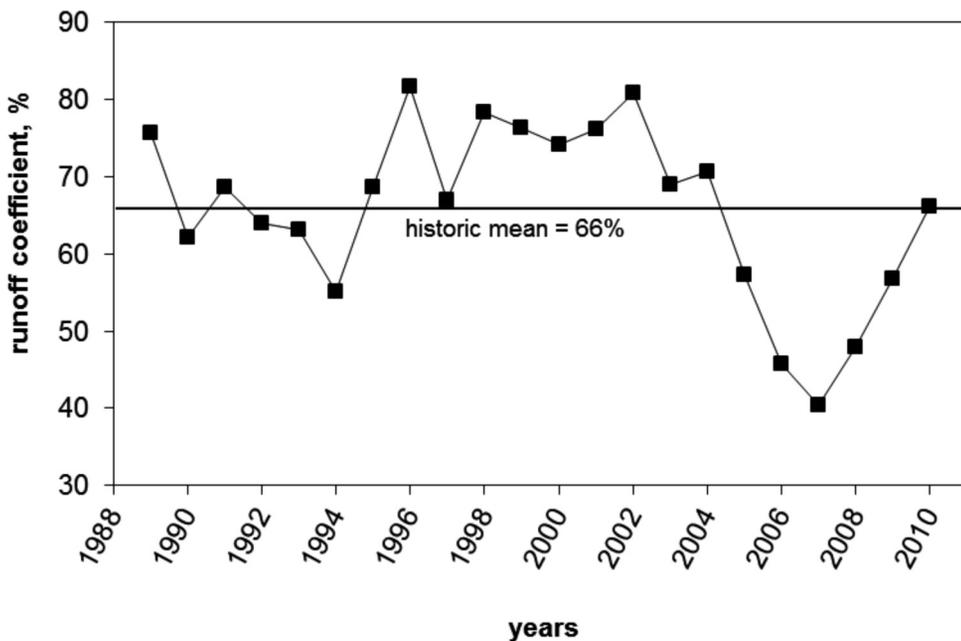


Figure 19. Annual variation in annual runoff coefficient in the Luquillo Mountains. Mean is calculated for the 22-yr period of measurement. The runoff coefficient is a dimensionless coefficient that relates the amount of runoff to the amount of precipitation that falls. Runoff coefficient varies inversely with infiltration rate, and thus is lower for permeable, well-vegetated areas.

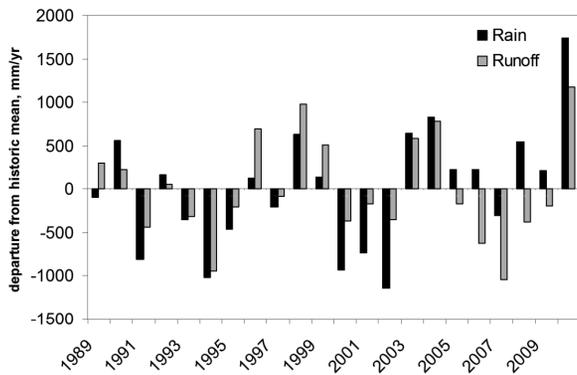


Figure 20. Comparison of the temporal variation in rainfall and runoff in the Luquillo Mountains.

roughly decadal intervals (Greenland and Kittel 2002). The urban heat island generated by the city of San Juan has led to a rapid increase in temperatures compared to nearby vegetated areas (González et al. 2007, Comarazamy et al. 2010, Murphy et al. 2010) and may have a stronger impact on local climate than changes predicted from global climate change (Comarazamy and González 2011, Comarazamy et al. 2012).

Empirical data and some models suggest that the frequency and intensity of hurricane disturbance are changing in the Luquillo Mountains (Emanuel 1987, 2005, Royer et al. 1998, Walsh and Pittock 1998, Webster et al. 2005). More intense hurricanes may lead to greater effects on forest structure, but given the demonstrated resilience of forests of the Luquillo Mountains to wind, the projected increase in hurricane wind speeds (5–12%; Knutson et al. 1998) may be of less importance than the projected increase in hurricane frequency (Scatena et al. 2012). Models have shown a strong relationship between hurricane frequency and forest structure (O'Brien et al. 1992). An increased frequency of disturbance would result in an increase in the proportion of earlier successional ecosystems, decreased forest biomass and height, and changes in community composition (Lugo et al. 2012b).

## Modeling

Models to predict climatic characteristics, evapotranspiration, river flow, carbon and soil dynamics, and above ground productivity have been developed as part of the Luquillo Long Term Ecological Research Program (Wooster 1989, Hall et al. 1992, Wang et al. 2002a, b, c, Wu et al. 2006a, b). Together, these models address spatial variation in major meteorological characteristics, energy balance, and ecosystem processes within the Luquillo Mountains. Regional simulations suggest that loss of forest cover can affect the cloud base of the Luquillo Mountains and decrease total

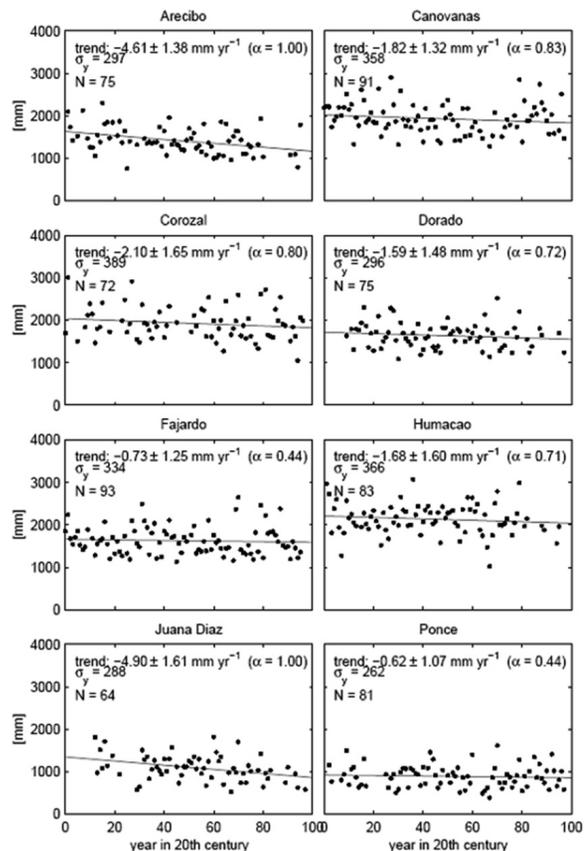


Figure 21. Trends in annual precipitation for eight stations in Puerto Rico. Data are from the National Climatic Data Center (1999). From van der Molen (2002).

rainfall (van der Molen et al. 2010). At the global scale, model simulations of future CO<sub>2</sub>-induced climate change indicate that Puerto Rico may experience changes in hurricane activity, decreases in soil moisture, and increases in dry season length (Hulme and Viner 1995). Global climate change may also have local effects, inducing higher cloud bases, less total atmospheric liquid water content, and reduced surface accumulated precipitation in the Luquillo Mountains and the Central Mountains of Puerto Rico (Comarazamy and González 2011).

Regional-scale atmospheric models, such as the Regional Atmospheric Modeling System (RAMS), are an important tool for simulation, forecasting, and study of meteorological phenomena at various temporal and spatial scales (Pielke et al. 1992, Cotton et al. 2003, Saleeby and Cotton 2004). Two RAMS scenarios were used to quantify the effect of land cover and land use (LCLU) on climate in the San Juan Metropolitan Area (SJMA) and over the Luquillo Mountains. The 'urban scenario' represented the current state of LCLU based on standard USGS surface characteristics updated with aerial photography and remote sensing. The 'natural scenario' represented natu-

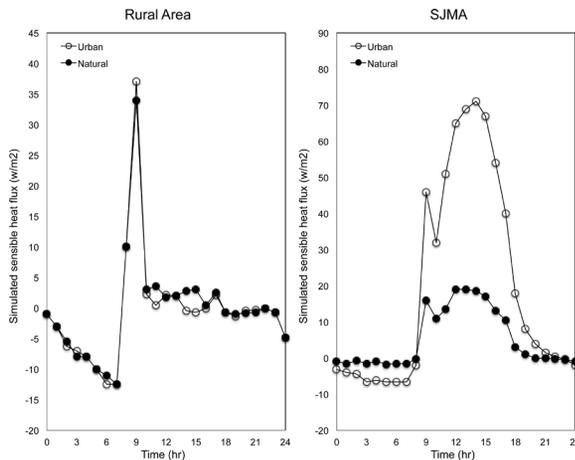


Figure 22. Simulated sensible heat flux (i.e. the conductive heat flux from the Earth's surface to the atmosphere) averaged over the Luquillo Mountains (Rural Area; left) and the San Juan Metropolitan Area (SJMA; right). Simulations were run for both Urban (open circles) and Natural (closed circles) conditions derived from land cover data for each location, for the 24 h period from 00:00 14 February to 00:00 15 February LST. Because Urban and Natural conditions are similar near the Luquillo Mountains, the simulated sensible heat fluxes for the rural location are nearly identical. The sensible heat flux for Urban conditions is much greater than for Natural conditions in the SJMA.

ral vegetation without urban influences by interpolating the surrounding vegetation. When run for the SJMA, the model revealed a pattern of slightly increased rainfall (ca 4 mm) southwest of the city in the urban scenario (González et al. 2007). Precipitation anomalies induced by the interaction of a large urban center with the region's climatology have been reported in previous studies for continental and coastal cities (Jáuregui and Romales 1996, Bornstein and Lin 2000, Shepherd and Burian 2003, Shepherd 2005). There are three main factors suggested as possible causes for urban-induced rainfall anomalies: 1) mechanical mixing resulting from increased surface roughness, 2) increased sensible heat due to the UHI, and 3) the release of anthropogenic atmospheric particles (AP) and aerosols (Jáuregui and Romales 1996).

A comparison of the surface sensible heat flux (i.e. the conductive heat flux from the Earth's surface to the atmosphere) for urban and natural simulations at two locations near the Luquillo Mountains and in central San Juan provides a better understanding of the mechanisms that lead to the observed rainfall anomaly (Fig. 22). The sensible heat flux over the SJMA for the natural run is similar to the fluxes for both runs over the Luquillo Mountains. The sensible heat flux is much greater in the urban run for the SJMA than in any of the other runs. In this scenario, the UHI causes warm air to rise rapidly, increasing the depth of the mixed layer. Low-level clouds then form with the

rising condensation level in the mixed layer, and these clouds are transported to the southwest by the prevailing trade winds. By this mechanism, the model produces slightly higher cloud cover in a region just southwest of the SJMA in the morning hours when differential heating occurs, and simulates increased accumulated surface rainfall over the same area.

Because urbanization and the heat island effect decline near the Luquillo Mountains compared to the SJMA (see above), the results from the two modeling scenarios are nearly identical. However, urbanization is increasing near the Luquillo Mountains, and construction of a new expressway flanking the mountains is accelerating this change. The increase in urbanization along the periphery of the Luquillo Mountains will likely cause a redistribution of rainfall (van der Molen 2002) as well as local or seasonal drying effects (Willig et al. 2012), but the magnitude of these changes cannot yet be predicted. Changes in cloud cover over the Luquillo Mountains need to be further explored to determine if they will reinforce or counteract directional changes resulting from global climate alteration (Comarazamy and González 2011). One of the major challenges for researchers studying the climate of the Luquillo Mountains is to integrate potential anthropogenic effects occurring at local, regional, and global scales (Willig et al. 2012).

## Conclusions

Climate is changing in the Luquillo Mountains. A report from the Intergovernmental Panel on Climate Change projects a drying trend in Puerto Rico over the next century as well as a trend towards more intense rainfall events (Christensen et al. 2007). Precipitation totals have already decreased significantly in the last century in the lowlands (Scatena 1998, van der Molen 2002), and modeling suggests that changing land-use has resulted in decreasing rainfall through links between vegetation cover and cloud development (Scatena and Larsen 1991, van der Molen et al. 2010). Annual maximum and minimum temperatures are changing, albeit slowly, around the Luquillo Mountains (Greenland and Kittel 2002). Ongoing increases in urban areas around the Luquillo Mountains may exacerbate and extend the strong temperature gradient radiating from the urban center of San Juan to areas that are more rural. Atlantic hurricane intensity has been increasing over the last 30 yr, although the cause for this increase is still being debated (Mann and Emanuel 2006, Emanuel et al. 2008, Wu and Wang 2008, Kossin and Camargo 2009). Hurricane frequency may also increase and potentially represents a more important factor in determining future changes in forest of the Luquillo Mountains.

The cumulative effect of these projected changes is hard to anticipate with certainty. Warming and drying

trends are likely to result in a more pronounced dry season and create conditions in which drought and potentially fire become more significant factors in structuring the communities and ecosystems of the Luquillo Mountains (Scatena et al. 2012). Drier conditions may also result in changes in the distribution of forest species along the elevational gradient (Scatena 1998, Scatena et al. 2012). Simulations predict that increasing temperatures would lead to a redistribution of soil organic carbon within the Luquillo Mountains (Wang et al. 2002a), and increasing CO<sub>2</sub> concentrations could result in decreased primary productivity (Wang et al. 2002b). Predicted increases in extreme rainfall events have the potential to increase soil erosion and transform the geomorphology of the Luquillo Mountains. The expansion of the UHI may affect temperatures within the forest, especially at the interface between forest and non-forested area. Such changes may make the forest more susceptible to fire, disease, and invasion by non-native species. Modifications in intensity and frequency of cyclonic storms could lead to changes in forest composition and structure, with concomitant changes in ecosystem processes and services.

Future research needs to address the uncertainty in predictions of the effects of changing climate. Specifically, manipulative experiments designed to anticipate and understand the effects of warming and drying trends are necessary. Expanded studies of the controls of key processes such as decomposition would provide additional understanding of predicted changes in the distribution of soil organic carbon. An emphasis on microbial control of decomposition is urgently required given the complexity of microbial communities and the present state of our understanding. Improved and more accessible simulation models could improve understanding of the possible effects of projected trends such as increased frequency of extreme events, the study of which is not amenable to field experiments. An emphasis on long-term monitoring of the interface between forest and non-forest habitats would provide the means for early detection of the effects of changes in land cover, particularly urbanization. A coordinated effort to expand collection of meteorological data and to improve the quality of such data is a fundamental necessity if we are to understand the effect of future climate change on the Luquillo Mountains.

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## Appendix 1

Inventory of USGS streamflow stations in the Luquillo Mountains unaffected by water extractions or sewage discharges.

USGS ID	River	Period of record (years)	Drainage area, km <sup>2</sup>	Annual runoff, mm	Elevation, m a.s.l.
50065500	Río Mameyes	1984–2010 (26)	17.8	2797	84
50075000	Río Icacos	1980–2004 (25)	3.3	3919	616
50061800	Río Canóvanas	1968–2010 (43)	25.5	985	69

## Appendix 2

Annual runoff coefficients for various tropical forested watersheds.

Site	Mean rainfall, mm yr <sup>-1</sup>	Mean runoff		Study
		mm yr <sup>-1</sup>	%	
Luquillo Mountains, Puerto Rico	3638	2412	66	This study
Luquillo Mountains, Puerto Rico	3529	2020	58	Lugo (1986)
Luquillo Mountains, Puerto Rico	3864	2512	65	Garcia-Martinó et al. (1996)
Puerto Rico	–	–	45	Giusti and Lopez (1967)
La Selva, Costa Rica	4716	2500	53	Sanford et al. (1994)
Barro Colorado, Panama	2424	969	40	Dietrich et al. (1990)
Okun, Southwest Nigeria	1719	387	22.5	Ogunkoya et al. (1984)
Amazon, French Guyana	3500	500–925	14–26	Roche (1981)