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Caribbean

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The Setting

The United States Caribbean is an insular territory composed of a rich mix of the principal inhabited islands of Puerto Rico (including Vieques and Culebra) and the United States Virgin Islands (St. Croix, St. Thomas, St. John, and Water Island), over 800 smaller islands, and cays. It is a region of tropical humid and semiarid mountains, valleys, and coastal plains with a climate strongly influenced by the surrounding ocean. The rainfall distribution pattern on the islands surrounding the Caribbean is much more even than on most land areas within the Tropics (Ewel and Whitmore 1973). Yet precipitation in the United States Caribbean is mostly bimodal with an initial maximum around May, a relative minimum in June–August, and a second peak in September–October (Chen and Taylor 2002; Giannini et al. 2000; Rudloff 1981). Most of the precipitation in the region is orographic, given the diverse topography of the larger islands.

There are six ecological life zones in Puerto Rico and the United States Virgin Islands, ranging from subtropical dry through rain forest in the basal or sea level belt, and wet plus rain forest in the lower montane altitudinal belt (Ewel and Whitmore 1973). In general, the subtropical lower montane rainforest life zone occupies the smallest area, accounting for only 0.1% of the study region. Though subtropical moist forest is the dominant life zone, covering more than 58% of the area (Ewel and Whitmore 1973), Puerto Rico's topography results in a wide range of climatic conditions (from <850 to >5000 mm mean annual precipitation; Daly et al. 2003; Murphy et al. 2017) and ecosystem types (González et al. 2013b; Gould et al. 2006; Weaver and Gould 2013). A complex geologic history, which has given rise to alluvial, limestone, volcanic, and ultramafic soil parent materials, can be found in Puerto Rico and the United States Virgin Islands (Miller and Lugo 2009; Weaver 2006).

The ecological and geological diversity of Puerto Rico is also reflected in the diversity of its soils. Ten of the 12 soil orders established by the USDA Soil Taxonomy, the official system of soil classification of the National Cooperative Soil Survey, are present in Puerto Rico (Beinroth et al. 1996; Muñoz et al. 2018). Therefore, much of the diversity and predispositions typical of tropical soils around the world can be found within the United States Caribbean region.

The world's soils store 2–3 times more carbon (C) than the atmosphere and all terrestrial plant biomass combined (Houghton 2007). Soils play a fundamental role in the exchange of greenhouse gases with the atmosphere and in the cycling of biologically important elements (Trumbore 2009). Identifying controls on soil C storage and cycling across environmental gradients is crucial for improving predictions of feedbacks between the terrestrial biosphere and climate change. The US Caribbean has a long history of soils research, with a particular focus on understanding the role of different state factors in soil properties, biology, and ecological processes—as highlighted in the following sections.

History of Soil Surveys

The United States Government under the National Cooperative Soil Survey started soil surveys in the Caribbean region right after the United States acquired Puerto Rico during the Hispano-American war of 1898. The first soil survey in Puerto Rico was led by Clarence W. Dorsey and published in 1902. Since then, 16 formal initial and updated soil surveys have been completed covering Puerto Rico and the United States Virgin Islands. In 1928, the USDA Division of Soil Survey and the University of Puerto Rico Agricultural Experiment Station began in-depth surveys of the soils of Puerto Rico, which were published in 1942. Between 1965 and 2008, soil surveys at a scale of 1:20,000 for all of Puerto Rico were published as soil survey area reports (Table A1). Updated taxonomic classifications of the soils of Puerto Rico were later published by Beinroth et al. (2003) and Muñoz et al. (2018).

Historically, soil survey information was published in soil survey reports. Since 2005 this information has been available to the public in a digital format through the interactive application called Web Soil Survey. This digital format has substantially increased the demand for soils information at a regional scale. In addition, soil survey areas formerly were developed following political boundaries, mapped as islands, with different ages and survey crews. Recognizing the need to improve soil survey data and correct inconsistencies across soil survey areas, the Soil Science Division established major land resource areas. These areas are geographically associated land resource units. Today, the Caribbean Area National Cooperative Soil Survey, led by the USDA Natural Resources Conservation Service (USDA NRCS), manages eight Soil Survey Areas and four distinct major land resource areas. Land resource regions are a group of geographically associated major land resource areas. Identification of these large areas is important in statewide agricultural planning and has value in interstate, regional, and national planning (USDA NRCS 2006).

In 2012, the USDA NRCS implemented the Major Land Resource Areas Soil Data Join Recorrelation to address the need to improve soil survey data and reduce inconsistencies across soil survey areas. The Soil Data Join Recorrelation focused on the evaluation of map units to create a continuous coverage within the attribute database. This initiative reduced the number of map units and components in the database and improved soil properties and improved the accuracy of interpretations. This

Table A1 Soil surveys completed in Puerto Rico and US Virgin Islands

Soil survey area	Year published
Arecibo to Ponce Reconnaissance Survey	1902
St. Croix Island Reconnaissance Survey	1932
Puerto Rico Soil Survey	1942
Soil Survey of Lajas Valley	1965
Virgin Islands of the United States	1970
Soil Survey of Mayaguez	1975
Soil Survey of Humacao	1977
Soil Survey of San Juan	1978
Soil Survey of Ponce	1979
Soil Survey of Arecibo	1982
Camp Santiago and Fort Allen	2000
Soil Survey of United States Virgin Islands	2002
Caribbean National Forest and Luquillo Experimental	2002
Soil Survey of San Germán Area	2008
Soil Survey of El Yunque National Forest	2012
Soil Data Evaluation and Major Land Resource Area Soil Survey Updates	2012–Present

provided an opportunity to document decisions and identify future needs and projects[1]. In 2017, the Soil Data Join Recorrelation initiative evolved into the major land resource areas soil map-unit evaluations and major land resource areas-scale soil survey updates. New tools and data available such as geographic information systems and digital models are used to accelerate the evaluation and update process. All the changes in soil survey data become available to the public through the Web Soil Survey annual refresh each October.

The approximate total area for the distribution of the soil orders in Puerto Rico is 898,324.43 ha. Of the ten soil orders currently recognized in Puerto Rico, Inceptisols cover 29%, Ultisols 20%, Mollisols 15%, Oxisols 7.5%, Alfisols 5%, Vertisols 4%, Entisols 2%, Aridisols 1.5%, Histosols 0.5%, and Spodosols 0.2% of the total land area; the remaining 15.3% of land area is grouped in the miscellaneous soils category (Fig. A7).

For the United States Virgin Islands, the approximate total area for the distribution of the soil orders is 35,075.7 ha. Of the five soil orders currently recognized in these islands, Inceptisols cover 24.9%, Mollisols 63.6%, Alfisols 4.7%, Vertisols 3.1%, and Entisols 3.7% of the total land area (Fig. A8).

Soil Carbon Inventories in the United States Caribbean

Globally, 1576 petagrams (Pg) of C is stored in soils, of which about 506 Pg (32%) is found in soils of the Tropics. It is also estimated that about 40% of the C in soils of the Tropics is in forested soils (Eswaran et al. 1993). In the United States Caribbean, several efforts have quantified or mapped soil C. Beinroth et al. (1992) used the modern soil survey of Puerto Rico to estimate that overall, soils on the island contained 80 931 × 10^6 kg or 80.931 teragrams (Tg) organic C in the top 1 m of soil. Of the nine soil orders recognized at the time in Puerto Rico, Ultisols contributed 28.1% of total C, Inceptisols 25.5%, Mollisols 15.6%, Oxisols 13.1%, Histosols 6.4%, Entisols 4.8%, Alfisols 3.5%, Vertisols 2.8%, and Spodosols 0.2%. Average soil organic C (SOC) content by soil order ranged from 153.7 kg m^{-2} in Histosols or wetland soils to 6.5 kg m^{-2} in Spodosols. In between, soil orders did not vary greatly in soil C content, despite temperate-biased expectations that highly weathered soil orders like Oxisols and Ultisols would have very low C content. Soil OC content did not vary predictably by soil moisture regime (with the exception of Histosols), though clayey and silty soils appeared to contain more C than loamy and sandy soils (Beinroth et al. 1992).

In an assessment of SOC across the United States, Johnson and Kern (2003) used data from the National Soil Characterization Database and STATSGO (1994) from 229 forested sites in Puerto Rico representing 7 soil orders to map SOC in mineral and organic forested soils at depths of 0–100 cm. This national analysis aggregated all forest types in Puerto Rico into a Caribbean forest-type group. Mean SOC content for mineral soils was reported as 11.8 kg m^{-2}, compared to 10.7 kg m^{-2} in Beinroth et al. (1992). These values are comparable and on the high end compared to those summarized for nontropical forest types in the contiguous United States for the top 1 m (Johnson and Kern 2003). Highly weathered tropical soils are characterized typically by deep soil profiles, and these values would be consistent with overall greater SOC storage in mineral soils of the Tropics compared to mid-latitude mineral soils.

Effect of State Factors on Soil Carbon

Much research has been conducted in Puerto Rico to better understand the role of soil-forming factors, or state factors, on SOC dynamics. A state factor approach (sensu Jenny 1941) provides a useful framework for identifying the strength of environmental predictors—climate, biota (including vegetation and human activity), parent material, topography, and time—on the processes that contribute to SOC storage to improve estimates of SOC storage and geographic distribution at different spatial scales. For example, Silver et al. (2003) reviewed data from 29 studies of tropical forest soils of the United States (including Hawai‘i) for a total of 108 soil profiles. For the Puerto Rican soils, they reported a strong relationship between SOC and mean annual precipitation in wet and moist forests (≥2500 mm yr^{-1}). Mean annual temperature explained a low proportion of variability in SOC for the same sites. Including sites on the low end of the pre-

[1] Matos, M.; Rios, S.; Santan, A.; Anderson, D. 2016. Soil Data Join Recorrelation in the Caribbean area. [Presentation]. A healthy soil the key for a healthy environment; Southern Regional Cooperative Soil Survey conference; June 20–23, 2016; Rincón, PR.

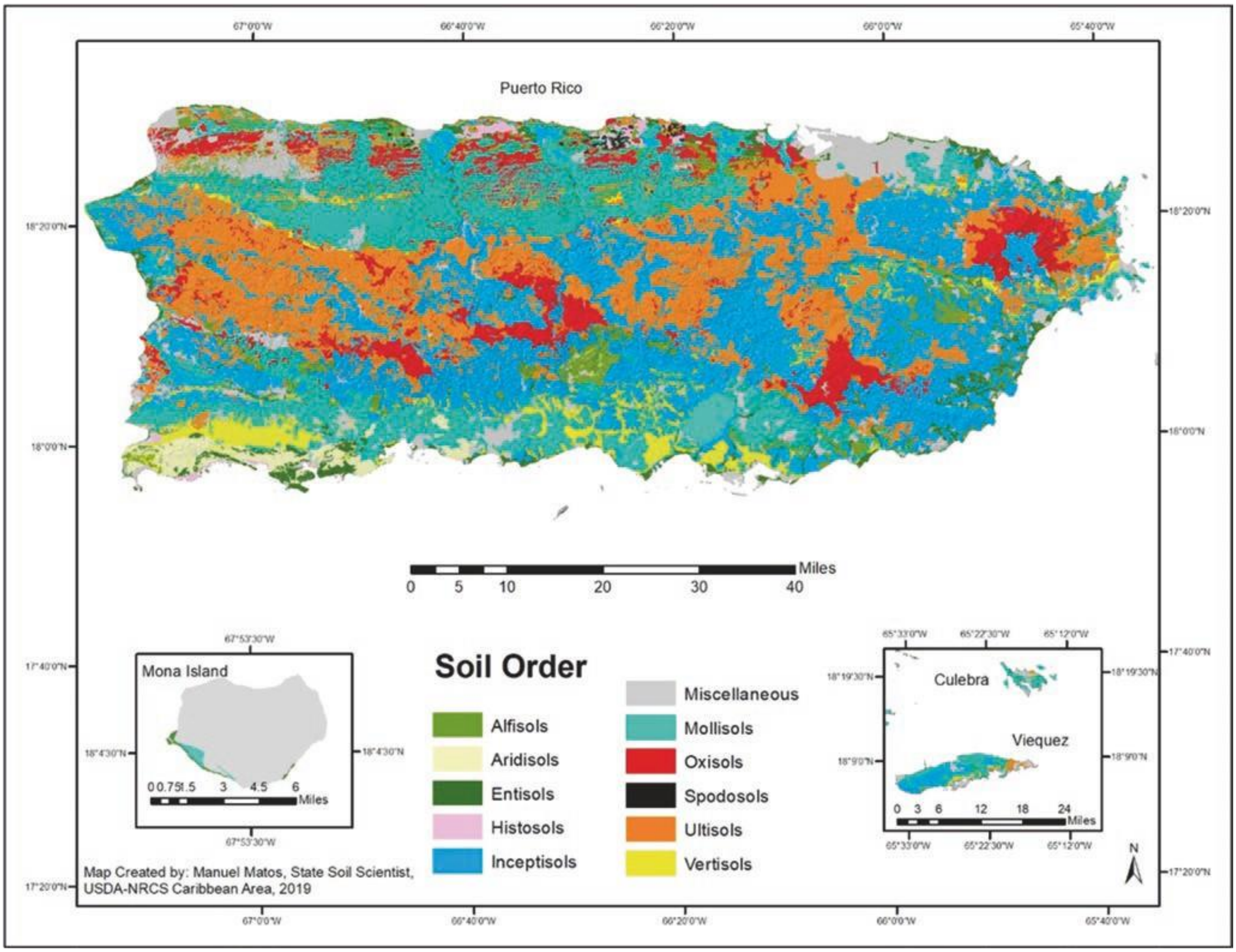

Fig. A7 Map of soil orders described for the islands of Puerto Rico

cipitation gradient weakened climatic relationships with SOC. Beinroth et al. (1996) demonstrated that the effects of climate and land cover on SOC were mediated by the role of soil mineralogy, highlighting the importance of parent material and weathering stage on C content and its response to environmental factors at the landscape surface.

More recently, the USDA NRCS surveyed 30 sites representing common soil series in Puerto Rico and the US Virgin Islands as part of the national Rapid Carbon Assessment project. Traditional predictors of soil C storage such as clay content and climate were poor predictors of regional soil C trends (Vaughan 2016). Soil OC stocks were not correlated with mean annual precipitation or mean annual temperature. Soil order and land cover were marginally significant predictors of SOC for a subset of the data with sufficient field site replication to test for the effect of these variables. Recognition of the heterogeneity of geologic substrates and weathering gradients in tropical regions and incorporation of a more mechanistic understanding can improve soil C modeling and land management decisions.

Different state factors become important at different spatial scales. In a study of 216 soil profiles in Puerto Rico's Luquillo Mountains differing in climate, topography, parent material, and forest type, only forest type and topographic position were significant predictors of soil C content in the top 80 cm (Johnson et al. 2015). These soils contained about 70% more C than the global mean for tropical forests down to a 1 m depth. Soil C storage in sandy, low-clay Inceptisols did not differ from highly weathered clay-rich Oxisols. Differences in soil C among forest types (colorado [*Cyrilla racemiflora*] > palm [*Prestoea montana*] > tabonuco [*Dacryodes excelsa*]) were attributed to differences in the ratio of C to N (C:N) of plant litter inputs and the accumulation of C in valley soils to depressed decomposition rates due to low oxygen (Johnson et al. 2015). In contrast, Johnson et al. (2011) reported greater SOC in hilltops than in valleys

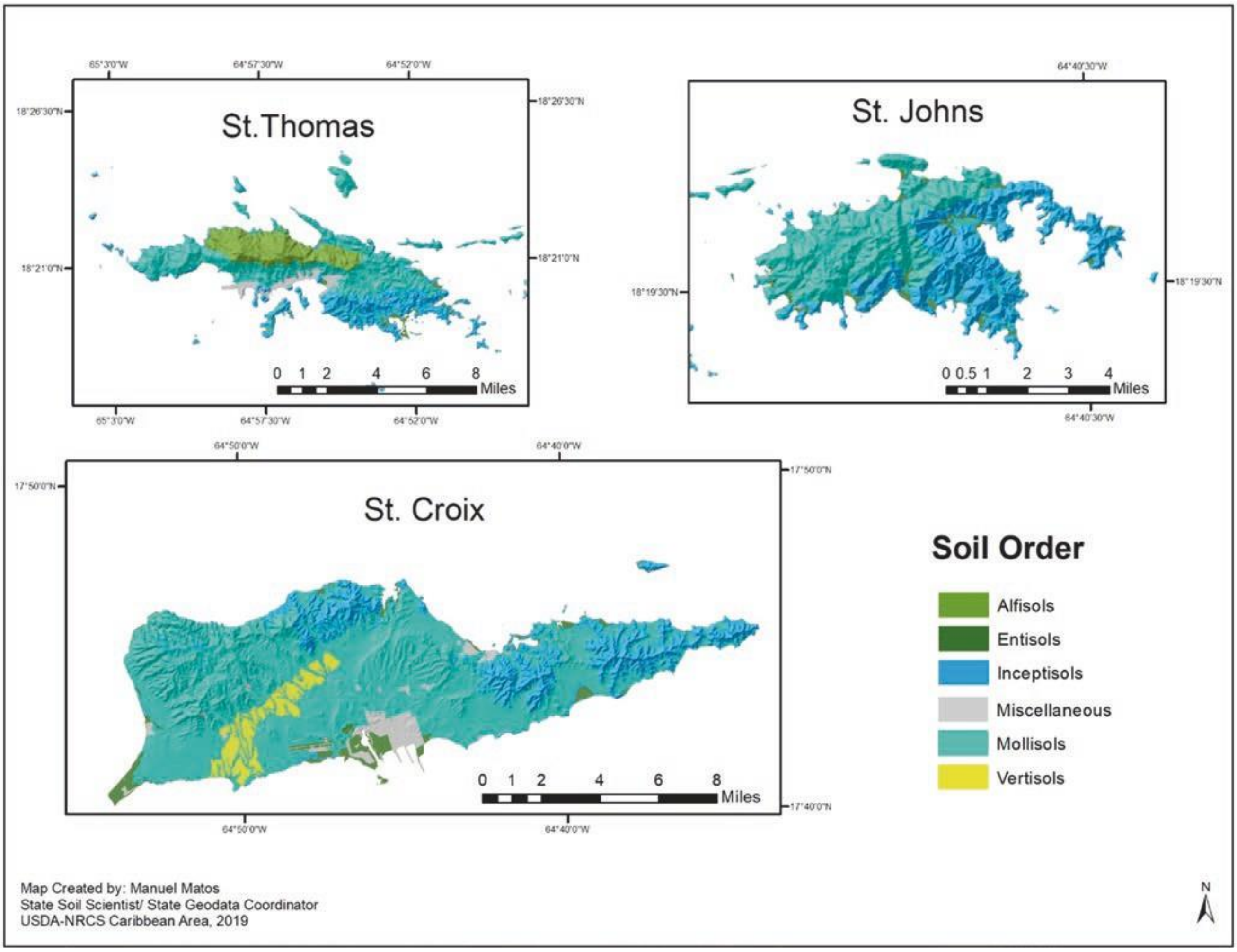

Fig. A8 Map of soil orders described for the US Virgin Islands

along steep forest soils across slopes. This atypical spatial distribution was best explained by differences in soil thickness and the concentration of iron and aluminum fractions.

Topography, climate, and parent material interact to influence organomineral assemblages and their role in SOC storage. Across a gradient of reducing soil conditions, decreasing litterfall inputs could not explain accumulation of SOC; instead, SOC stocks were correlated with concentrations of reduced iron (Hall and Silver 2015). This and other work (Hall and Silver 2013) conducted through the National Science Foundation-funded Critical Zone Observatory in Puerto Rico have focused on the role of redox in controlling SOC dynamics. These studies indicate that SOC in wet tropical soils is sensitive to fluctuations in moisture and reducing conditions, suggesting that future changes in precipitation under a warming climate have the potential to affect SOC storage.

Ping et al. (2013) studied soil properties, C distribution, and nutrient distribution along an elevation gradient in eight distinct forest types in eastern Puerto Rico. They found SOC and N stocks followed the elevation gradient: from 26.7 kg OC m^{-2} and 1.4 kg N m^{-2} in soils of the colder and wetter mountain tops to 12.3 kg OC m^{-2} and 1.0 kg N m^{-2} in soils of the lower elevation dry forests. Soil C:N ratio decreased from 20 to 11 as elevation decreased along the gradient. In addition, Ping et al. (2013) found that landscape movement on uplands through landslides, slumps, and fluvial and alluvial processes had a significant effect on variation of SOC stores, emphasizing the need to consider geomorphic processes when estimating C stores by landscape units. Coastal wetlands had exceptionally high SOC stores (>90 kg m^{-2}) due to their water-saturated and reduced environment. Soil OC content showed an inverse relation with soil bulk density and played a controlling role in cation exchange capacity, and nutrient distribution (Ping et al. 2013). Thus, Ping et al. (2013) concluded that elevation, through its influence on precipitation and temperature, exerts strong influence on the quantity and quality of terrestrial OC stores and on the depth-distribution pattern of C, N, and other nutrients.

Consistent with Gould et al. (2006), and Ping et al. (2013) showed total soil C was highest in saturated soils from upper and lower ends of the elevation gradient in northeastern Puerto Rico, that is, the roble de sierra-guayabota de sierra (*Tabebuia rigida-Eugenia borinquensis*; elfin forest) and palo de pollo or dragonsblood tree-golden leather fern (*Pterocarpus officinalis-Acrostichum aureum*) communities. Some of this C is in the form of calcium carbonate, and calcium levels are high in both the lowland dry and flooded communities. In addition, Gould et al. (2006) found that within the lowland and montane moist and wet forest communities, elevation was positively correlated with mean annual precipitation, the number of plant endemic species, total soil C, N, sulfur, C:N ratio, and organic matter content. Using a modeling approach, Dialynas et al. (2016) estimated different landslide erosion effects on SOC redistribution in two catchments with differing lithologies. This modeling study also found an effect of forest type on SOC replacement in eroding landscapes based on different net primary production rates.

Land Use Change and Management Effects

Determining management effects on soil C content can be challenging due to large background pools of organic matter and spatial heterogeneity across the landscape and with soil depth, in addition to the difficulty of identifying useful reference soils that have not been disturbed. Lugo-López (1992) provided a comprehensive review of the prior 50 years of research on soil organic matter in Puerto Rico from an agronomic perspective. He concluded that most soils maintained relatively consistent and high organic matter content despite cultivation and that when losses were observed, SOC accumulation rates post-disturbance could be very large. The review reported positive benefits of organic residue addition as a soil conservation practice to reduce erosion on steep slopes. In the lowlands, much research focused on soil improvement through remediation of alkalinity, salinity, and aluminum toxicity in soils affected by sugarcane cultivation and the rum distillery industry. In addition, past research on Puerto Rican soils identified the role of inorganic soil particles in the stabilization of soil aggregates and the protection of organic matter from microbial decomposition (Lugo-López 1992).

In a study of land use in Puerto Rico and the United States Virgin Islands, Brown and Lugo (1990) reported lower SOC in cultivated sites in wet and moist life zones than in the dry life zone relative to reference mature forest sites in each life zone. As reported for tropical soils globally, conversion to cropland resulted in greater losses of SOC than conversion to pasture. Recovery rates of SOC during postagricultural abandonment were faster in the wet and moist forests than in drier sites.

Lugo et al. (1986) in the 1980s resampled sites surveyed in Puerto Rico in the 1940s and 1960s to estimate rates of change with land use trajectories. The 1940s survey did not reveal differences in SOC (0–18 cm depth) by life zone or soil group, but according to the 1960s survey, moist and wet forests contained more SOC. The response of SOC to changes in land use in the moist life zone was more variable in gains and losses than for drier sites, yet all forest types exhibited general increases in SOC with reduced agricultural intensity. Recovery of SOC with reforestation of agricultural lands also occurred in all life zones. In addition, this study revealed the extent of urban development on former agricultural soils. Expansion occurred preferentially on the most fertile soils, resulting in greater SOC stocks in urban soils than in residual agricultural lands.

In a study of Puerto Rican and Hawaiian tree plantations established on former pastures or sugarcane (*Saccharum officinarum*) fields, more SOC accumulated under N-fixing trees than under eucalyptus (*Eucalyptus* spp.) (Resh et al. 2002). Using stable C isotopes, the authors attributed these results to greater retention of residual C derived from the past land cover, in addition to greater inputs of new tree-derived C under N-fixers; these trends were related to soil N levels in the plots. The Puerto Rican sites showed greater SOC stocks in the clayey Vertisols compared to the sandy Entisols. Soil C stocks in grasslands establishing after forest clearing contained only 70% of the soil C in surface soils (0–10 cm depth) of nearby secondary forests, regardless of whether reference forests were dominated by native or non-native tree species (Cusack et al. 2015).

Land management can affect not only the amount of SOC but also its bioavailability (Sotomayor-Ramírez et al. 2009). Conversion of sugarcane to eucalyptus or leadtree (*Leucaena* spp.) forests, pasture, and agricultural crops in a Vertisol in Puerto Rico produced differences in SOC, total N, and C cycling rates as measured by stable isotopes after a shift from warm-season to cool-season plant cover. In particular, the cropland sites had reduced SOC and microbial biomass, greater amounts of C respired during a short-term incubation, and the lowest enzyme activities.

Historical agricultural abandonment in the United States Caribbean has led to widespread forest regrowth, with potential for SOC sequestration (Silver et al. 2000). By the 1930s, much of the land area had been deforested for sugarcane, cattle, or other forms of agriculture. In Puerto Rico, up to 90% of forests had been cut down (Dietz 1986), yet by 1991 the area of wet forest had recovered by about 42% due to agricultural abandonment (Helmer 2004). The island of St. Croix, United States Virgin Islands, has experienced similar trends, with forest regrowth after sugarcane abandonment (Chakroff 2010; Daley 2010; Weaver 2006). Forest succession has the potential to restore soil ecosystem processes that were altered during deforestation (Powers and Marín-Spiotta

2017). The initial soil C content of a site and soil mineralogy can strongly influence the direction and magnitude of response of soil C to land use change (van Straaten et al. 2015).

Across Puerto Rico, secondary forests in the moist life zone contained more SOC (0–23 cm depth) than wet secondary forests (Weaver et al. 1987). At smaller scales, the effects of climate were mediated by parent material and forest successional stage. For example, on granitic soils, wet forests contained more SOC than moist forests. Topography also played an important role in SOC content, especially under coffee cultivation.

In a successional chronosequence of subtropical moist secondary forests on highly weathered Oxisols in Puerto Rico, select aboveground and belowground ecosystem components followed different successional trajectories over time, whereas others recovered in the same timeframe. Aboveground biomass C pools increased with secondary forest age and peaked in the oldest secondary forests (Marín-Spiotta et al. 2007), yet soil C storage appeared relatively stable with succession (Marín-Spiotta et al. 2009). More detailed analyses showed that certain soil organic matter pools were more sensitive to changes in land cover. Specifically, the free light fraction or particulate organic matter not associated with soil aggregates or mineral surfaces was depleted in the pastures and became replenished with reforestation, reaching levels of undisturbed forests in as little as 20 years, as did radiocarbon-based mean residence times (Marín-Spiotta et al. 2008). Stable C isotopes revealed that pasture-derived C was replaced by forest-derived C during reforestation (Marín-Spiotta et al. 2009). The greatest differences in microbial biomass, functional composition, and enzyme activities also occurred during the initial two decades of forest regrowth (Smith et al. 2014, 2015). Relative basal area and tree species richness matched those of primary forests in as little as 20 years (Marín-Spiotta et al. 2007). These data suggest that the recovery of ecosystem function to levels measured in reference forests may be rapid in postagricultural forests.

Yet into the future, it will be important to determine how the changing soil characteristics in the mountainous region of the island will intersect with management practices in the agricultural sector in the delivery of ecosystem services. Puerto Rico has been in economic crisis during the past decade and the government has decided to promote the agricultural sector. Despite the prevailing trend of reforestation for the island, significant areas of forest land are being converted for agriculture and pasture (Gao and Yu 2014). The net effect of deforestation in the central mountains of Puerto Rico may be a net increase in the water supply downstream but also a rise in large sediment discharges into streams and the ocean during large episodic rain events (Gao and Yu 2017). Ramos-Scharrón and Figueroa-Sánchez (2017) argued the combination of a topographically abrupt wet-tropical setting with the high level of soil exposure that typifies many sun-grown coffee (*Coffea* spp.) farms in Puerto Rico represents optimal conditions for high soil erosion rates, consistent with historical research (Lugo-López 1992).

Accelerated soil loss due to human land use is still one of the most critical environmental problems in tropical mountainous regions, as it can degrade soil function and downstream resources (Ramos-Scharrón 2018). Erosion in the Insular Caribbean can have detrimental effects on soils, nearshore coral reefs, and associated ecosystem services (Ramos-Scharrón 2018). In the island of St. John, United States Virgin Islands, geomorphic evidence indicates that plantation agriculture during the eighteenth and nineteenth centuries did not cause severe erosion. However, rapid growth in roads due to increasing tourism and second-home development since the 1950s has caused at least a fourfold increase in island-wide sediment yields; unpaved roads have been the primary determining factor (McDonald et al. 1997). Similarly, in a dry tropical area of Puerto Rico, unpaved road surfaces have the potential to generate runoff 2–3.5 times more frequently than under natural conditions and can produce sediment at rates 6–200 times greater than background (Ramos-Scharrón 2018). Thus, there is increasing evidence from United States Caribbean islands that an integrated approach to tourism, urban planning, and management requires the cohesive protection of soils and coastal habitats (Hernández-Delgado et al. 2012; Ramos-Scharrón 2018).

Hurricane Effects

Hurricanes can alter C dynamics and other biogeochemical processes through effects on tree mortality, increased deposition of woody debris and litterfall to the forest floor, and changes to soil microenvironmental conditions. For example, Hurricanes Irma and Maria in 2017 deposited a pulse of litter deposition equivalent to or more than the total annual litterfall (fallen leaves and fine wood) input with at least twice the typical fraction of woody materials across four forests in Puerto Rico (Liu et al. 2018). These enormous changes in quantity and quality of litter inputs to the forest floor are likely to alter soil food webs and biogeochemical processes, although the effects on nutrient cycling may be temporally variable and dependent on storm intensity and time since the last disturbance. For example, after Hurricane Hugo crossed Puerto Rico in September 1989, it took 60 months for the total litterfall to return to the prehurricane level in a tabonuco forest of the Bisley Experimental Watersheds (Scatena et al. 1996). After Hurricane Georges (1998), forest floor standing stocks and nutrient content increased in response to the large amounts of litter deposition, but levels returned to prehurricane values within 2–10 months (Ostertag et al. 2003). This latter response to hurricane differed by forest type. Upper elevation palm forest received the lowest litter inputs, but because of the slower decomposition at this site, forest floor recovered in the same amount of time as moist forest and tabonuco forest, which had greater amounts of litter and also greater decomposition rates.

The Luquillo Long-Term Ecological Research Network Canopy Trimming Experiment (hereafter, CTE) has been conducted since 2002 in Puerto Rico to disentangle effects of debris deposition and canopy opening on ecological and biogeochemical processes. This experiment was designed to simulate a hurricane and to separate the effects of changes in temperature, humidity, throughfall, and light (canopy opening) from debris deposition (changes in nutrient levels and the physical structure of the forest floor), in a study on the effects of an increasing frequency of storms, as a possible consequence of climate change (Shiels and González 2014; Shiels et al. 2014, 2015). In the CTE, a shift in dominance in fungal decomposers from basidiomycete macrofungi to microfungi was associated with increases in fungivore specialist groups: mites (order Acari), springtails (class Collembola), and booklice (order Psocoptera) (González et al. 2014; Richardson et al. 2010; Shiels et al. 2015). Furthermore, reductions in macroarthropod decomposers of litter and basidiomycete decomposer fungi that degrade lignin together were very likely responsible for reduction in rates of leaf decomposition in plots where the canopy was opened (González et al. 2014; Lodge et al. 2014; Richardson et al. 2010). Reduction of basidiomycete fungi was associated with reduced accumulation of phosphorus via translocation by fungal root-like structures, which could have contributed to slowing of leaf decomposition in plots where the canopy was opened (Lodge et al. 2014). In addition, González et al. (2014) found a negative correlation between the Margalef index of diversity of the litter arthropods and the percentage of mass remaining of mixed species of litter, suggesting that functional complexity is an important determinant of decay in the Luquillo Experimental Forest. Further, Prather et al. (2018) reported that although canopy presence did not alter consumers' effects in the CTE, focal organisms had unexpected influences on decomposition. Decomposition was not altered by litter snails (*Megalomastoma croceum*), but herbivorous walking sticks (*Lamponius portoricensis*) reduced leaf decomposition by about 50% through reductions in high-quality litter abundance and, consequently, lower bacterial richness and abundance. This relatively unexplored but potentially important link between tropical herbivores, detritus, and litter microbes in this forest demonstrates the need to consider autotrophic influences when examining rainforest ecosystem processes (Prather et al. 2018).

Also in the CTE, Gutiérrez del Arroyo and Silver (2018) found that 10 years after an experiment simulating the addition of hurricane debris, soil C and N were elevated relative to control plots in both surface and deep soils, and both light fraction organic matter and organic molecules complexed with minerals in the heavy soil fractions were elevated. Meanwhile, results from Liu et al. (2018) suggest that hurricane disturbance can accelerate the cycling of soil light OC on a timescale of less than 2 years but can elevate soil microbial biomass C for a longer period in this tropical wet forest.

Large quantities of coarse woody debris are generated periodically during tropical storms and hurricanes in the United States Caribbean. Among many ecosystem services provided, this dead wood serves as a temporary sink for atmospheric C and a source of soil organic matter (Harmon and Hua 1991; Torres 1994). Two recently published reviews have synthesized much of the current ecological research on the interacting factors of dead wood, soil biota, and nutrient dynamics in Puerto Rico's forests (González 2016; González and Lodge 2017). In the subtropical wet forests of Puerto Rico, decaying wood contributes to the spatial heterogeneity of soil properties, through its effect on soil organic matter and nutrient dynamics, further affecting the process of soil formation and nutrient cycling (Lodge et al. 2016; Zalamea et al. 2007, 2016). Zalamea et al. (2007) studied logs with contrasting wood properties, tabonuco and Honduras mahogany (*Swietenia macrophylla*), and at two different decay stages (6 and 15 years after falling). Soil under and 50 cm away from the decaying logs was sampled for soil organic matter fractions. They found decaying logs did influence properties of the underlying soil. The effects differed by species; more sodium hydroxide-extractable C was found in the soil associated with tabonuco logs, and more water-extractable organic matter was found in the soil associated with Honduras mahogany older logs. A higher degree of condensation of water-soluble fulvic acids and other related polyaromatic residues occurred in the soil associated with the youngest logs. More divalent cations were available in the soil influenced by younger logs; availability decreased as decomposition increased (Zalamea et al. 2007).

Consistent with Gutiérrez del Arroyo Silver' (2018) results in the CTE, work by Lodge et al. (2016) in the Luquillo Mountains showed that decomposing logs from two hurricanes spaced 9 years apart had a significant signature on the underlying soil as early as 6 months after the trees fell. Further, results from Lodge et al. (2016) indicate that 20% of randomly placed soil cores at a subtropical wet forest may fall on C- and N-rich hotspots that are the legacy of decomposed previously coarse woody debris. Thus, detailed studies within a variety of tropical forest types are important to better understand the complexity and uncertainty associated with global C pools, particularly given the long-term influence of both natural and anthropogenic disturbances on the functioning of these forested ecosystems (González and Luce 2013).

Climate Change Effects on Soils

Henareh Khalyani et al. (2016) assessed different general circulation models and greenhouse gas emissions scenarios of downscaled climate projections to inform future projections of climate and its potential impacts on the United States Caribbean. From that exercise, projections indicate a reduction in precipitation and increased warming from the 1960–1990 period to the 2071–2099 period of 4–9 °C air temperature (depending on the scenario and location) in the Insular Caribbean. Consequently, they projected a high likelihood of increased energy use for cooling and shifts in ecological life zones to drier conditions. The combination of decreased rainfall, increasing variability of rainfall, and higher air temperatures would lead to reduction of soil moisture and changes in soil organic matter dynamics. Soils in the Luquillo Mountains will be affected by the changing climate through increased variability in the decay of organic matter, changes to the patterns of soil oxygen concentrations, and changes in the availability of soil nutrients to plants (González et al. 2013a). In the Luquillo Mountains, soil oxygen content decreases with increasing mean annual precipitation (Silver et al. 1999). Aerobic soils support more plant biomass but less SOC and nutrient availability, whereas anaerobic soils become a net source of methane (Silver 1998). Methane consumption increases significantly during drought, but high methane fluxes post-drought offset the sink after 7 weeks (O'Connell et al. 2018). Thus, whether tropical forests will become a source or sink of C in a warmer world remains highly uncertain (Wood et al. 2012).

Climate change can affect SOC through changes in inputs and losses via alterations to net primary production and decomposition rates through changes in moisture and temperature, as well as shifts in plant and microbial species composition. Wet tropical soils are more likely to respond to changes in soil moisture extremes (drying, flooding) than to temperature (Cusack and Marín-Spiotta in press). In an experimental study in a high-elevation wet tropical soil, a 29% reduction in soil moisture after 3 months of soil drying led to a 35% increase in soil respiration (Wood et al. 2013). In contrast, Wood and Silver (2012) concluded that decreased rainfall in humid tropical forests may cause a negative feedback to climate through lower soil CO_2 emission and greater methane and nitrous oxide consumption.

Research in the mountains of the Luquillo Experimental Forest suggests that forests along elevation gradients will respond differently to changes in climate. For example, indirect effects of temperature and precipitation (McGroddy and Silver 2000) could explain modeled results of SOC losses (up to 4.5 Mg ha^{-1}) from low to high elevation and small increases (up to 2.3 Mg ha^{-1}) at middle elevations (Wang et al. 2002). In a laboratory incubation, cooler, upper elevation rainforest soils were more sensitive to temperature than a warmer, lower elevation forest, although soil respiration in both forest types responded positively to warming (Cusack et al. 2010). In a field soil translocation experiment, Chen et al. (2017) studied the impacts of decreasing temperature but increasing moisture on SOC and respiration along an elevation gradient in northeastern Puerto Rico. They found that soils translocated from low elevation to high elevation showed an increased respiration rate with decreased SOC content at the end of the experiment, which indicated that the increased soil moisture and altered soil microbes may affect respiration rates. Further, soils translocated from high elevation to low elevation also showed an increased respiration rate with reduced SOC at the end of the experiment, indicating that increased temperature at low elevation enhanced decomposition rates. Thus, these tropical soils at high elevations may be at risk of releasing sequestered C into the atmosphere given a warming climate in the Caribbean (Chen et al. 2017). An ongoing warming experiment, the Tropical Responses to Altered Climate Experiment (TRACE), which began in 2016 in Puerto Rican montane forests on Oxisols and is sponsored by the USDA Forest Service and the Department of Energy, will provide insights into the response of aboveground and belowground ecosystem components to a warming climate (Cavaleri et al. 2015; Kimball et al. 2018).

Nitrogen Deposition

Puerto Rican soils in general have high N content (Lugo-López 1992); hence, N additions are not expected to increase aboveground C but can have contrasting effects on SOC dynamics. Research in wet tropical forest soils indicates that SOC responds positively to N additions through biotic and abiotic mechanisms (Cusack et al. 2016). In an experimental N fertilization study in montane rainforests in Puerto Rico, N fertilization enhanced soil C after 5 years via decreased microbial decomposer activity and an accumulation of C in mineral-associated pools (Cusack et al. 2011). Similarly, continuous N additions in another study enhanced mineral-associated C with a negligible effect on total SOC pool (Li et al. 2006). The effects of N deposition on soil nutrients, which can affect processes that control C accumulation and loss from soils, are variable, with different responses to soil acidification based on soil properties (Cusack and Marín-Spiotta in press). More work quantifying the effects of increasing N deposition on soils with variable nutrient content will improve predictions of the response of tropical ecosystems and their C cycling to multiple global change factors.

Soil Biology and Ecosystem Processes

Given the high rate of forest conversion and persistence of deforestation in the Tropics, it is important to study the diversity of the region's fauna and assess how global changes will affect the links between soil biota and ecosystem function (González and Barberena-Arias 2017). Understanding how environmental variation affects the dynamics of different soil microbial and faunal assemblages, and how variation in the composition of such assemblages controls decomposition processes and nutrient cycling, is critical for long-term sustainability and management of ecosystems that are subject to global change (González and Lodge 2017). Many ecological investigations in Puerto Rico are focused on the characterization of the edaphic fauna, and how they influence ecosystem processes (e.g., see review of literature in González 2016; González and Barberena-Arias 2017; González and Lodge 2017). Results from studies in Puerto Rico indicate soil organisms (and the interactions of soil fauna and microbes) are important regulating factors of litter decomposition. In Puerto Rico, more than half the decay of litter material can be explained by the effects of soil fauna alone (González and Seastedt 2001). Yet there is still a need for comprehensive and manipulative field studies that try to tease apart the distinct effect of fauna and microorganisms. This is not an easy task as the interactions of the abundance, diversity, activity, and functionality of soil organisms are at play (González 2002).

Research in Puerto Rico has revealed soil microbiome sensitivity to changes in soil moisture, which provides insight into how soil function may be altered by climate change. In a reforestation chronosequence, forest floor and surface mineral soil microbial community composition and enzyme activity were more sensitive to seasonal fluctuations in soil moisture than to changes in plant communities with forest succession (Smith et al. 2015). Soil microbial composition varied more among soil organic matter pools (macroaggregates, microaggregates, silt and clay fractions) at the fine scale than between forests of different ages (Smith et al. 2014). A throughfall exclusion study to simulate drought in the Luquillo Experimental Forest found that soil microbial diversity decreased in response to rainfall reduction and that the soil microbiome composition was sensitive even to small changes in soil water potential (Bouskill et al. 2013). Prolonged drought resulted in shifts in functional gene capacity of the microbial community as well as changes in extracellular enzyme activity (Bouskill et al. 2016). Pre-exposure to drought conditions buffered the soil microbiome response.

In the Luquillo Experimental Forest, soil fungal biovolume was found to vary directly with soil moisture (Lodge 1993). Consistent with this earlier work, Li and González (2008) reported significant decreases in total and active fungal and bacterial biomass in the drier season compared to the wetter season. While canopy trimming in the CTE decreased litter moisture, soil moisture increased due to reduction of evapotranspiration (Richardson et al. 2010; Shiels and González 2014; Shiels et al. 2015). It is therefore not surprising that Cantrell et al. (2014) found no effects of canopy trimming and debris deposition treatments in soil microbial communities using fatty acid methyl ester and terminal restriction fragment length polymorphism analyses, but did find differences attributable to drought in the control plots between years.

Conclusions

The land area of the United States Caribbean is small relative to the continental United States. However, it contains higher species diversity than all non-Caribbean national forests combined and is a globally important reservoir of C. Its level of aboveground biological complexity combined with a rich mixture of geology, climate, life zones, and land use practices is reflected in a diverse set of soil-forming factors and soil landscape. The steep gradients in elevation and climate found in Puerto Rico over short distances represent an ideal setting to study the long-term effects of global climate changes on a diverse and dynamic landscape. Most work has focused on the larger island, Puerto Rico. Supporting more soils research in the other islands, which have unique geographic and social histories, will be important for tailoring management to local environments and needs. The United States Caribbean is dynamic in time and space due to its history of natural and anthropogenic disturbances. Within the context of natural disturbance (e.g., droughts and hurricanes), we are still learning how biotic changes and interactions in the detrital food webs affect nutrient and C cycling.

Key Findings

- Identifying controls on soil C storage and turnover across environmental gradients is crucial for improving predictions of feedbacks between the terrestrial biosphere and climate change. Evaluating the long-term effects of prior land use history and management on soils is important for quantifying the C sequestration potential of human-altered landscapes. Despite the importance of land use history, this variable is often absent from regional and global assessments of soil C, although Puerto Rico leads the way in this aspect.
- The availability of historical data (aerial photographs, the Soil Survey Geographic [SSURGO] database, land tenure documents, economic and demographic data, and land cover maps) makes Puerto Rico one of the best places in the Tropics to study land use. The land use history of Puerto Rico illustrates strong feedbacks between social and ecological processes with important implications not only for C sequestration but also for food security and biodiversity conservation.
- Studies along environmental gradients and experimental manipulations in the field, such as those conducted in the Luquillo Experimental Forest, will continue to provide insights into the response of ecological and biogeochemical processes to a changing climate. Urban expansion and a growing need for diversified local agricultural production impose a different set of environmental change factors on tropical soils. Given its dynamic history, the US

Caribbean stands to provide many lessons for other areas of the world.

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Literature Cited

Beinroth FH, Hernández PJ, Esnard AM et al (1992) Organic carbon content of the soils of Puerto Rico. In: Beinroth FH (ed) Organic carbon sequestration in the soils of Puerto Rico: a case study of a tropical environment. University of Puerto Rico Mayagüez Campus and USDA Soil Conservation Service, San Juan, pp 33–56

Beinroth FH, Vázquez MA, Snyder VA et al (1996) Factors controlling carbon sequestration in tropical soils: a case study of Puerto Rico. University of Puerto Rico at Mayaguez, Department of Agronomy and Soils, and USDA Natural Resources Conservation Service World Soil Resources and Caribbean Area Office, San Juan, 35 p

Beinroth FH, Engel RJ, Lugo JL et al (2003) Updated taxonomic classification of the soils of Puerto Rico, 2002. Bull. 303. University of Puerto Rico, Agricultural Experiment Station, Rio Piedras

Bouskill NJ, Lim HC, Borglin S et al (2013) Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. ISME J 7:384–394

Bouskill NJ, Wood TE, Baran R et al (2016) Belowground response to drought in a tropical forest soil. I. Changes in microbial functional potential and metabolism. Front Microbiol 7:525

Brown S, Lugo AE (1990) Effects of forest clearing and succession on the carbon and nitrogen content of soils in Puerto Rico and US Virgin Islands. Plant Soil 124:53–64

Cantrell SA, Molina M, Lodge DJ et al (2014) Effects of a simulated hurricane disturbance on forest floor microbial communities. For Ecol Manag 332:22–31

Cavaleri MA, Reed SC, Smith K, Wood TE (2015) Urgent need for warming experiments in tropical forests. Glob Chang Biol 21:2111–2121

Chakroff M (2010) U.S. Virgin Islands forest resources assessment and strategies: a comprehensive analysis of forest-related conditions, trends, threats and opportunities. Virgin Islands Department of Agriculture, Kingshill, 100 p

Chen AA, Taylor M (2002) Investigating the link between early season Caribbean rainfall and the El Niño + 1 year. Int J Climatol 22:87–106

Chen D, Yu M, González G et al (2017) Climate impacts on soil carbon processes along an elevation gradient in the tropical Luquillo Experimental Forest. Forests 8(3):90

Cusack DF, Torn MS, McDowell WH, Silver WL (2010) The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. Glob Chang Biol 16:2555–2572

Cusack DF, Silver WL, Torn MS, McDowell WH (2011) Effects of nitrogen additions on above- and belowground carbon dynamics in two tropical forests. Biogeochemistry 104:203–225

Cusack DF, Lee J, McCleery T, LeCroy C (2015) Exotic grasses and nitrate enrichment alter soil carbon cycling along an urban-rural tropical forest gradient. Glob Chang Biol 21:4481–4496

Cusack DF, Karpman J, Ashdown D et al (2016) Global change effects on humid tropical forests: evidence for biogeochemical and biodiversity shifts at an ecosystem scale. Rev Geophys 54(3):523–610

Cusack DF, Marín-Spiotta E (In press) Tropical wet forests. In: Page-Dumroese D, Morris D, Giardina C, Busse M (eds) Global change and forest soils: demands and adaptations of a finite resource, Cultivating stewardship, vol 36. Elsevier, New York. Chapter 8

Daley BF (2010) Neotropical dry forests of the Caribbean: secondary forest dynamics and restoration in St. Croix, US Virgin Islands. University of Florida, Gainesville, 107 p. Ph.D. dissertation

Daly C, Helmer EH, Quiñones M (2003) Mapping the climate of Puerto Rico, Vieques and Culebra. Int J Climatol 23:1359–1381

Dialynas YG, Bastola S, Bras RL et al (2016) Impact of hydrologically driven hillslope erosion and landslide occurrence on soil organic carbon dynamics in tropical watersheds. Water Resour Res 52:8895–8919

Dietz JL (1986) Economic history of Puerto Rico: institutional change and capitalist development. Princeton University Press, Princeton

Eswaran H, Van Den Berg E, Reich P (1993) Organic carbon in soils of the world. Soil Sci Soc Am J 57:192–194

Ewel JJ, Whitmore JL (1973) The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Res. Pap. IT-018. U.S. Department of Agriculture, Forest Service, Institute of Tropical Forestry, San Juan

Gao Q, Yu M (2014) Discerning fragmentation dynamics of tropical forest and wetland during reforestation, urban sprawl, and policy shifts. PLoS One 9(11):e113140

Gao Q, Yu M (2017) Reforestation-induced changes of landscape composition and configuration modulate freshwater supply and flooding risk of tropical watersheds. PLoS One 12(7):e0181315
Giannini A, Kushnir Y, Cane MA (2000) Interannual variability of Caribbean rainfall, ENSO, and the Atlantic Ocean. J Clim 13:297–311
González G (2002) Soil organisms and litter decomposition. In: Ambasht RS, Ambasht NK (eds) Modern trends in applied terrestrial ecology. Kluwer Academic/Plenum Publishers, London, pp 315–329
González G (2016) Deadwood, soil biota and nutrient dynamics in tropical forests: a review of case studies from Puerto Rico. In: Proceedings of the 112th Annual Meeting of the American Wood Protection Association. American Wood Protection Association, Birmingham, pp 206–208
González G, Barberena-Arias MF (2017) Ecology of soil arthropod fauna in tropical forests: a review of studies from Puerto Rico. J Agric Univ Puerto Rico 101(2):185–201
González G, Lodge DJ (2017) Soil biology research across latitude, elevation and disturbance gradients: a review of forest studies from Puerto Rico during the past 25 years. Forests 8(6):178
González G, Luce MM (2013) Woody debris characterization along an elevation gradient in northeastern Puerto Rico. Ecol Bull 54:181–194
González G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82(4):955–964
González G, Waide RB, Willig MR (2013a) Advancements in the understanding of spatiotemporal gradients in tropical landscapes: a Luquillo focus and global perspective. Ecol Bull 54:245–250
González G, Willig MR, Waide RB (2013b) Ecological gradient analyses in a tropical landscape: multiple perspectives and emerging themes. Ecol Bull 54:13–20
González G, Lodge DJ, Richardson BA, Richardson MJ (2014) A canopy trimming experiment in Puerto Rico: the response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. For Ecol Manag 332:32–46
Gould WA, González G, Carrero Rivera G (2006) Structure and composition of vegetation along an elevational gradient in Puerto Rico. J Veg Sci 17:653–664
Gutiérrez Del Arroyo O, Silver WL (2018) Disentangling the long-term effects of disturbance on soil biogeochemistry in a wet tropical forest ecosystem. Glob Chang Biol 24:1673–1684
Hall SJ, Silver WL (2013) Iron oxidation stimulates organic matter decomposition in humid tropical forest soils. Glob Chang Biol 19:2804–2813
Hall SJ, Silver WL (2015) Reducing conditions, reactive metals, and their interactions can explain spatial patterns of surface soil carbon in a humid tropical forest. Biogeochemistry 125:149–165
Harmon M, Hua C (1991) Coarse woody debris dynamics in two old-growth ecosystems. Bioscience 41:604–610
Helmer EH (2004) Forest conservation and land development in Puerto Rico. Landsc Ecol 19:29–40
Henareh Khalyani A, Gould WA, Harmsen E et al (2016) Climate change implications for tropical islands: interpolating and interpreting statistically downscaled GCM projections for management and planning. J Appl Meteorol Climatol 55(2):265–282
Hernández-Delgado EA, Ramos-Scharrón CE, Guerrero-Pérez CR (et al) (2012) Long-term impacts of non-sustainable tourisms and urban development in small tropical islands coastal habitats in a changing climate: lessons from Puerto Rico. In: Kasimoglu M (ed) Visions for global tourism industry. IntechOpen, pp 357–398. https://doi.org/10.5772/38140
Houghton RA (2007) Balancing the global carbon budget. Annu Rev Earth Planet Sci 35:313–347
Jenny H (1941) Factors of soil formation: a system of quantitative pedology. McGraw-Hill, New York, 281 p
Johnson MG, Kern JS (2003) Quantifying the organic carbon held in forested soils of the United States and Puerto Rico. In: Kimble JM, Heath LS, Birdsey RA, Lal R (eds) The potential of US forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, Boca Raton, pp 47–72
Johnson KD, Scatena FN, Silver WL (2011) Atypical soil carbon distribution across a tropical steepland forest catena. Catena 87:391–397
Johnson AH, Xing HX, Scatena FN (2015) Controls on soil carbon stocks in El Yunque National Forest, Puerto Rico. Soil Sci Soc Am J 79(1):294–304
Kimball BA, Alonso-Rodríguez AM, Cavaleri MA et al (2018) Infrared heater system for warming tropical forest understory plants and soils. Ecol Evol 8(4):1932–1944
Li Y, González G (2008) Soil fungi and macrofauna in the Neotropics. In: Myster RW (ed) Post-agricultural succession in the Neotropics. Springer, Berlin, pp 93–114
Li Y, Xu M, Zou X (2006) Effects of nutrient additions on ecosystem carbon cycle in a Puerto Rican tropical wet forest. Glob Chang Biol 12:284–293
Liu X, Zeng X, Zou X et al (2018) Litterfall production prior to and during Hurricanes Irma and Maria in four Puerto Rican forests. Forests 9(6):367
Lodge DJ (1993) Nutrient cycling by fungi in wet tropical forests, British Mycological Society Symposium Series 19. Cambridge University Press, Cambridge, pp 37–37

Lodge DJ, Cantrell SA, González G (2014) Effects of canopy opening and debris deposition on fungal connectivity, phosphorus movement between litter cohorts and mass loss. For Ecol Manag 332:11–21

Lodge DJ, Winter D, González G, Clum N (2016) Effects of hurricane-felled tree trunks on soil carbon, nitrogen, microbial biomass, and root length in a wet tropical forest. Forests 7:264

Lugo AE, Sanchez MJ, Brown S (1986) Land use and organic carbon content of some subtropical soils. Plant Soil 96:185–196

Lugo-López MA (1992) Review of soil organic matter research in Puerto Rico. In: Beinroth FH (ed) Organic carbon sequestration in the soils of Puerto Rico: a case study of a tropical environment. University of Puerto Rico Mayagüez Campus and USDA Soil Conservation Service, Puerto Rico, pp 33–56

Marín-Spiotta E, Ostertag R, Silver WL (2007) Long-term patterns in tropical reforestation: plant community changes and aboveground biomass accumulation. Ecol Appl 17:828–839

Marín-Spiotta E, Swanston CW, Torn MS et al (2008) Chemical and mineral control of soil carbon turnover in abandoned tropical pastures. Geoderma 143:49–62

Marín-Spiotta E, Silver WL, Swanston CW, Ostertag R (2009) Soil organic matter dynamics during 80 years of reforestation of tropical pastures. Glob Chang Biol 15:1584–1597

McDonald LH, Anderson DM, Dietrich WE (1997) Paradise threatened: land use and erosion on St. John, US Virgin Islands. Environ Manag 21(6):851–863

McGroddy M, Silver WL (2000) Variations in belowground carbon storage and soil CO_2 flux rates along a wet tropical climate gradient. Biotropica 32(4a):614–624

Miller GL, Lugo AE (2009) Guide to the ecological systems of Puerto Rico. Gen. Tech. Rep. IITF-GTR-35. U.S. Department of Agriculture, Forest Service, and International Institute of Tropical Forestry, San Juan, p 437

Muñoz MA, Lugo WI, Santiago C et al (2018) Taxonomic classification of the soils of Puerto Rico. Bull. 313. University of Puerto Rico Mayagüez Campus, College of Agricultural Sciences, Agricultural Experiment Station, Mayagüez, 73 p

Murphy SF, Stallard RF, Scholl MA et al (2017) Reassessing rainfall in the Luquillo Mountains, Puerto Rico: local and global ecohydrological implications. PLoS One 12(7):e0180987

O'Connell CS, Ruan L, Silver WL (2018) Drought drives rapid shifts in tropical rainfall soil biogeochemistry and greenhouse gas emissions. Nat Commun 9:1348

Ostertag R, Scatena FN, Silver WL (2003) Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. Ecosystems 6:261–273

Ping CL, Michaelson GJ, Stiles CA, González G (2013) Soil characteristics, carbon stores, and nutrient distribution in eight forest types along an elevation gradient, eastern Puerto Rico. Ecol Bull 54:67–86

Powers JS, Marín-Spiotta E (2017) Ecosystem processes and biogeochemical cycles during secondary tropical forest succession. Annu Rev Ecol Evol Syst 48:497–519

Prather CM, Belovsky GE, Cantrell SA, González G (2018) Tropical herbivorous phasmids, but not litter snails, alter decomposition rates by modifying litter bacteria. Ecology 99(4):782–791

Ramos-Scharrón CE (2018) Land disturbance effects of roads in runoff and sediment production on dry-tropical settings. Geoderma 310:107–119

Ramos-Scharrón CE, Figueroa-Sánchez Y (2017) Plot-, farm-, and watershed-scale effects of coffee cultivation in runoff and sediment production in western Puerto Rico. J Environ Manag 202:126–136

Resh SC, Binkley D, Parrotta JA (2002) Greater soil carbon sequestration under nitrogen-fixing trees compared with eucalyptus species. Ecosystems 5:217–231

Richardson BA, Richardson MJ, González G et al (2010) A canopy trimming experiment in Puerto Rico: the response of litter invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. Ecosystems 13:286–301

Rudloff W (1981) World-Climates, with tables of climatic data and practical suggestions. Wissenschaftliche Verlagsgesellschaft, Stuttgart

Scatena F, Moya S, Estrada C, Chinea J (1996) The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28(4a):424–440

Shiels AB, González G (2014) Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. For Ecol Manag 332:1–10

Shiels AB, González G, Willig MR (2014) Responses to canopy loss and biomass deposition in a tropical forest ecosystem: synthesis from an experimental manipulation simulating effects of hurricane disturbance. For Ecol Manag 332:124–133

Shiels AB, González G, Lodge DJ et al (2015) Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. Bioscience 65:871–881

Silver WL (1998) The potential effects of elevated CO_2 and climate change on tropical forest soils and biogeochemical cycling. Clim Chang 39:337–361

Silver WL, Lugo AE, Keller M (1999) Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44(3):301–328

Silver WL, Ostertag R, Lugo AE (2000) The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restor Ecol 8:394–407

Silver WL, Lugo AE, Farmer D (2003) Soil organic carbon in tropical forests of the United States of America. In: Kimble JM, Heath LS, Birdsey RA, Lal R (eds) The potential of U.S. forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, Boca Raton

Smith AP, Marín-Spiotta E, de Graaff MA, Balser TC (2014) Microbial community structure varies across soil organic matter aggregate pools during tropical land cover change. Soil Biol Biochem 77:292–303

Smith AP, Marín-Spiotta E, Balser T (2015) Successional and seasonal variations in soil and litter microbial community structure and function during tropical post-agricultural forest regeneration: a multi-year study. Glob Chang Biol 21(9):3532–3547

Sotomayor-Ramírez D, Espinoza Y, Acosta-Martinez V (2009) Land use effects on microbial biomass C, beta-glucosidase and beta-glucosaminidase activities, and availability, storage, and age of organic C in soil. Biol Fertil Soils 45:487–497

Statsgo (1994) State Soil Geographic (STATSGO) database: Data use information. Vol. 1492. Tech. Rep

Torres JA (1994) Wood decomposition of *Cyrilla racemiflora* in a tropical montane forest. Biotropica 26:124–140

Trumbore S (2009) Radiocarbon and soil carbon dynamics. Annu Rev Earth Planet Sci 37:47–66

USDA Natural Resources Conservation Service [USDA NRCS] (2006) Land resource regions and major land resource areas of the United States, the Caribbean, and the Pacific Basin. USDA Handbook 296. 672 p.

van Straaten O, Corre MD, Wolf K et al (2015) Conversion of lowland tropical forests to tree cash crop plantations loses up to one-half of stored soil organic carbon. Proc Natl Acad Sci 112(32):9956–9960

Vaughan E (2016) Factors controlling soil carbon and nitrogen storage in Puerto Rico and the U.S. Virgin Islands. University of Wisconsin, Madison, Madison, 67 p. Master's thesis

Wang H, Cornell JD, Hall CAS, Marley DP (2002) Spatial and seasonal dynamics of surface soil carbon in the Luquillo Experimental Forest, Puerto Rico. Ecol Model 147(2):105–122

Weaver P (2006) Experimental Forest, St. Croix, U.S. Virgin Islands: research history and potential. Gen. Tech. Rep. IITF–30. U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, San Juan. 62 p

Weaver PL, Gould WA (2013) Forest vegetation along environmental gradients in northeastern Puerto Rico. Ecol Bull 54:43–66

Weaver PL, Birdsey RA, Lugo AE (1987) Soil organic matter in secondary forests of Puerto Rico. Biotropica 19:17–23

Wood TE, Silver WL (2012) Strong spatial variability in trace gas dynamics following experimental drought in a humid tropical forest. Glob Biogeochem Cycles 26:GB3005

Wood TE, Cavaleri MA, Reed SC (2012) Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. Biol Rev 87:912–927

Wood TE, Detto M, Silver WL (2013) Sensitivity of soil respiration to variability in soil moisture and temperature in a humid tropical forest. PLoS One 8(12):e80965

Zalamea M, González G, Ping CL, Michaelson G (2007) Soil organic matter dynamics under decaying wood in a subtropical wet forest: effect of tree species and decay stage. Plant Soil 296:173–185

Zalamea M, González G, Lodge DJ (2016) Physical, chemical, and biological properties of soil under decaying wood in a tropical wet forest in Puerto Rico. Forests 7(8):168

Midwest

Lucas E. Nave and Chris W. Swanston

Introduction

The Midwest is a geographically diverse region. Its eight states (Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, Wisconsin) span wide ranges in climate, vegetation, soil, land use, and history, from the distant geologic past up through early human settlement to the present. From the cold winters and glacial past of the forested north, to the long, humid summers and productive soils of the more agricultural southern Midwest states, the issues relevant to soil health and vulnerability are as varied as the lands in this region. The geographic factors that affect life for Midwesterners do not follow state lines, so any resource assessment—soils included—is more meaningful when based on a map drawn with different boundaries. In this regional summary, we use the USDA Forest Service ECOMAP (Cleland et al. 1997), which divides the United States into ecoregions of similar climate, vegetation, and other geographic factors, as our organizational structure. We highlight key soil health and vulnerability issues for the Midwest's five ecoregional provinces (Fig. A9). Two of these provinces—the Laurentian Mixed Forest Province and the Midwest Broadleaf Forest Province—occur exclusively within the Midwest; the other three extend into adjacent