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Cover Photographs: Study stand of *Tabebuia heterophylla* (Roble Blanco) at Palmer, Luquillo, Puerto Rico. Left: on 22 November 2017, after hurricanes Irma and María. Right: on 14 March 2020, over 2 years after the passage of both hurricanes and 5 years after the completion of this study. Photographs © Ariel E. Lugo.

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A Stoichiometric Comparison of Primary and Secondary Forest Stands on Acid Soils

Ariel E. Lugo[1,*], Mary Jean Sánchez[1], Luz S. Betancourt[2], Olga M. Ramos González[1], and Iván Vicens[1]

Abstract - A basic tenant of ecological stoichiometric theory applied to plant nutrition is that, in the absence of metabolic selection of elements, plants should reflect their soil environment. We used ecological and stoichiometric data to gain insight into how stoichiometry might influence the productivity of primary and secondary forest stands dominated by native tree species. The study involved 2 sets of measurements of soil and litter stoichiometry 26 years apart plus results from long-term ecological research in similar forest types and watersheds in the vicinity of our study area within the Luquillo Experimental Forest. We asked the following questions: What are the differences, if any, in the stoichiometry of vegetation and soil in the 2 study sites? How does soil pH influence the stoichiometry of the study sites? What are the net balances for element storage in soil and vegetation mass over the 26 years of study, and how do they compare across sites? We found that carbon molar ratios (C:N, C:P, C:S) were higher in the secondary forest and the nitrogen molar ratios (N:Ca, N:K, N:Mg, N:P) were higher in the mature forest. The secondary forest also had the highest molar ratios with phosphorus in the denominator (Ca:P, K:P, Mg:P, S:P). Soil stoichiometry separated the sites by their effective cation exchange capacity, Ca:Al ratio, and phosphorus availability. The mature forest with higher soil acidity was under greater physiological stress due to potential aluminum toxicity and a lower soil quality index than the secondary forest (45% vs. 70%). High soil acidity imposed metabolic costs to trees when concentrating, storing, and recycling elements. In spite of the above, both sites were carbon sinks. The secondary forest had a faster aboveground carbon sink as biomass and over 26 years lost calcium, magnesium, and potassium in the soil. The mature forest had a faster belowground carbon and elements sink. The contrasting stoichiometric characteristics of the dominant tree species at the 2 sites reflect the different biogeochemical niche that they occupy, which appear adaptive to prevailing site conditions.

Introduction

Crop expansion and agricultural activities in the Neotropics account for over 50 percent of deforestation (FAO 2022). Deforestation for agricultural use can be followed by land abandonment and secondary forest regrowth. Chazdon (2014) estimates that most of the tropical forest cover is secondary growth. This common pattern of land-use change, when conducted at low intensity and with sufficiently long periods of recovery, is viable in the high rainfall and nutrient-limited soils of many tropical regions (Nye and Greenland 1960). However, agricultural land-use abandonment and secondary-forest regrowth has many alternative pathways of

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forest succession (Ewel 1980) depending on land-use intensity, length of recovery, rainfall, and soil fertility. In certain cases, deforestation followed by decades, if not centuries, of agricultural use, can lead to environmental changes in soil conditions that result in either arrested or drastically altered secondary forest succession. In the arrested-succession pathway, the land cover usually remains as pastures for extended time periods. In the secondary-forest succession pathway, forest establishment follows the pasture stage.

Over the past century, Puerto Rico has experienced a forest transition (Grau et al. 2003) driven by a decrease in pastoral and agricultural land uses that result in secondary forests with altered species composition (Lugo and Helmer 2004). The species combinations in these successional pathways do not always resemble the species combinations of forest successions after non-anthropogenic disturbances (Aide et al. 1995, 1996, 2000). This change in species composition, a footprint of human activity on the landscape, remains measurable for decades and cannot be erased by non-anthropogenic disturbances such as hurricanes (Thompson et al. 2002).

Nye and Greenland (1960) identified processes of oxidation, leaching, and erosion as the causes of degradation when soils are denuded and exposed to the effects of rainfall. They focused their analysis of the effects of soil degradation on land productivity and losses of phosphorus and nitrogen content. Unfertilized Puerto Rican soils that have been exposed to continued agricultural use or pasture cover have lower concentrations of phosphorus and nitrogen than soils covered by forests (Roberts 1942, Soil Conservation Service 1967, Weaver et al. 1987). Moreover, at the peak of agricultural activity, about half of the agricultural soils in Puerto Rico had lost over 75 percent of their topsoil (Picó 1969). These data are consistent with the notion that depletion in the supply of essential chemical nutrients, and/or the accumulation of toxic ones, may be involved in the selective regeneration and growth of tree species after the abandonment of lands used intensively and extensively for agricultural purposes. However, we do not know what the long-term effects of deforestation and agricultural activities are on the stoichiometry of recovering secondary forests, although island-wide surveys of forests have shown significant differences in the element molar ratios of litter between mature and successional vegetation (Erickson et al. 2014, Lugo and Erickson 2017). Greater understanding of this phenomena can result from a comparison of forest stands growing on contrasting environmental conditions over the long-term.

In this paper we compare the stoichiometry of vegetation and soil on a site that was farmed and abandoned with that of a site in the same watershed that has maintained mature tree cover for hundreds of years. We address the following questions: What are the differences, if any, in the stoichiometry of vegetation and soil in the 2 study sites? How does soil pH influence the stoichiometry of the study sites? What are the net balances for element storage in soil and vegetation mass over the 26 years of study, and how do they compare across sites? Ultimately, we are seeking an explanation for the differences in the outcomes of succession in terms of species composition in altered vs. non-altered soils in a region where the outcomes should be similar.

Methods

Study sites

The 2 study sites were located in the Mameyes watershed within the Luquillo Experimental Forest (LEF; Fig. 1). The watershed provides vegetation cover to the Mameyes River, a wild and scenic river. One site is a primary forest (from now on TR-1) dominated by *Dacryodes excelsa* Vahl (Tabonuco; Burceraceae), (from now on *Dacryodes*), and the other is a secondary forest (from now on Palmer) dominated by *Tabebuia heterophylla* (DC) Britton (Pink Trumpet Tree; Bignoniaceae), from now on *Tabebuia*. These 2 stands represent the opposite ends of the successional pathways in wet and rainy volcanic environments in the LEF. The age differential of the 2 forest stands is large, with TR-1 having an estimated age of over 400 yr for its oldest trees (Weaver 1994), while Palmer was 34 years old when studied in 2015. There is no record of any anthropogenic alteration of vegetation or land use at TR-1 (Fig. 2). In contrast, the Palmer site has been affected by anthropogenic activities, including deforestation, farming, and cattle grazing. Upon abandonment of agricultural activity, a secondary forest of *Tabebuia* developed through succession.

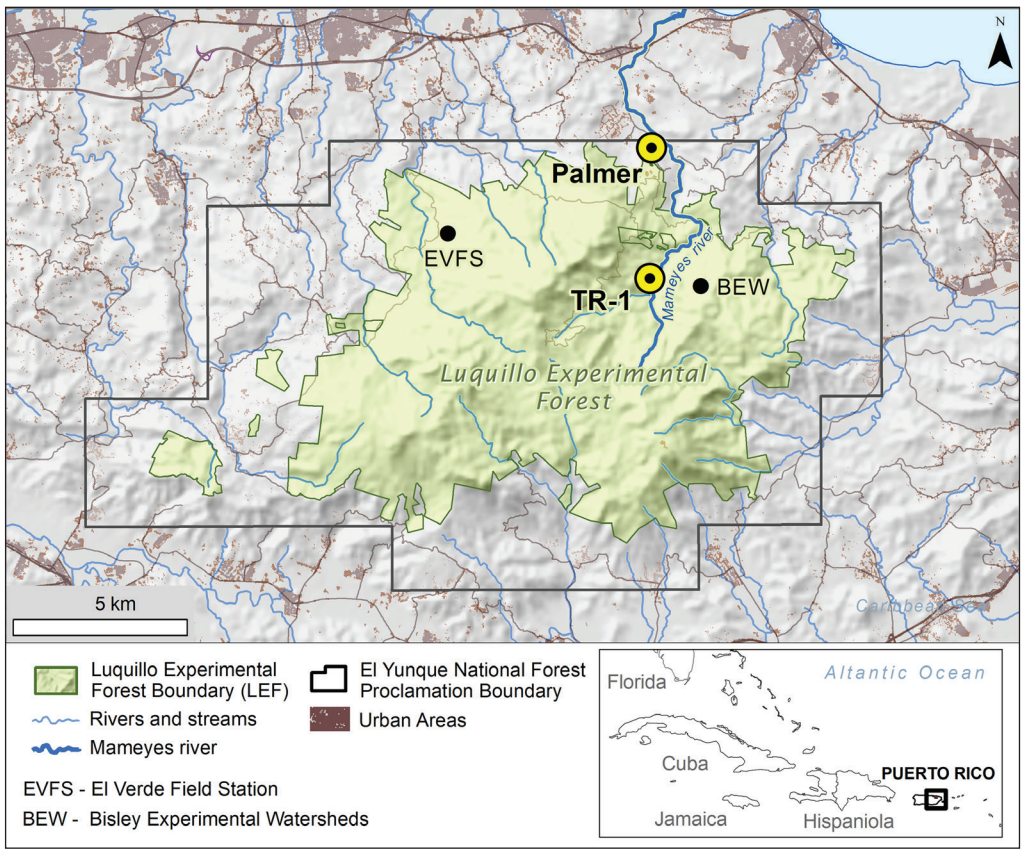

Figure 1. Map of the Luquillo Experimental Forest with the location of the 2 study sites and other sites mentioned in the text. This map was prepared by O.M. Ramos González.

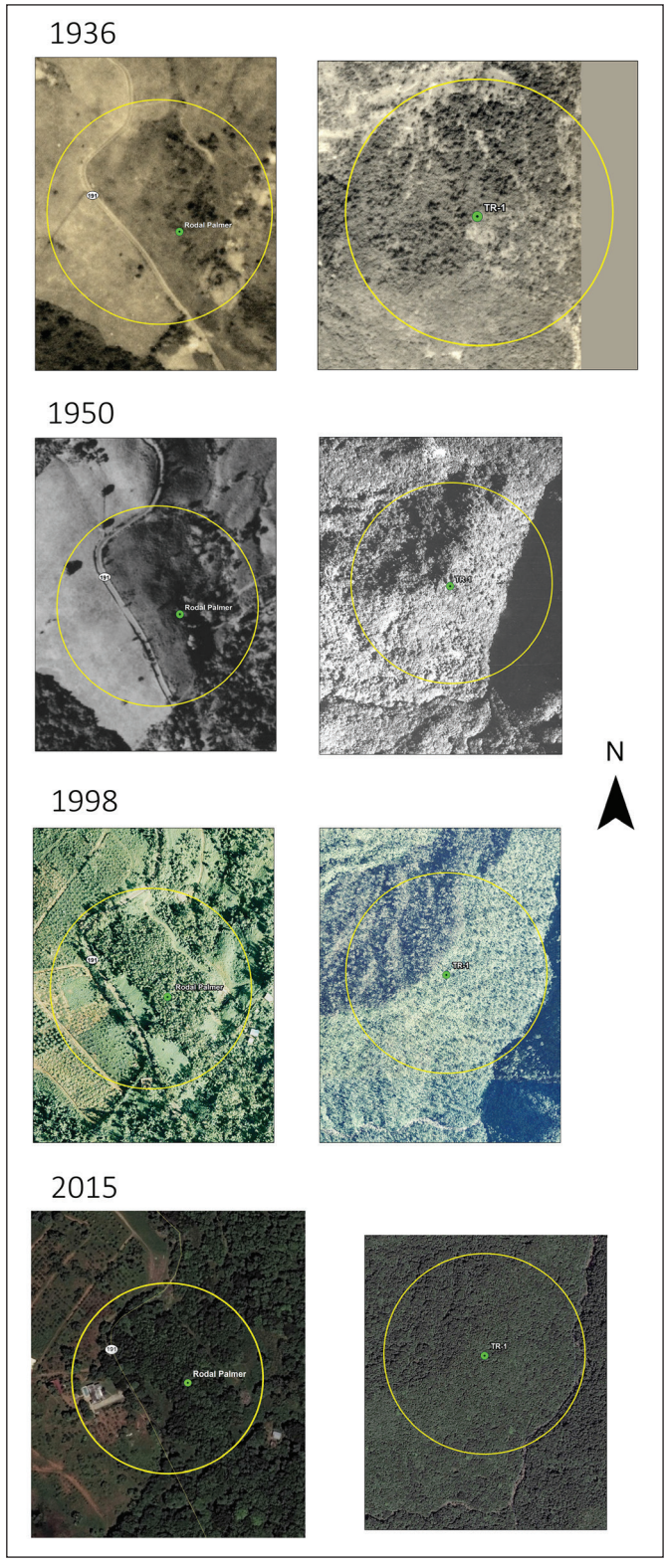

Figure 2. Time series (1936, 1950, 1998, and 2015) of land cover for the vicinity of the Palmer (left column of aerial photographs) and Tabonuco Ridge (TR-1; right column of aerial photographs) study sites. In each image, the study site is shown inside of a wider circle that helps with visualizing the immediate surroundings of the plot.

We inferred historical land-use since 1936 for the 2 sites from aerial photographs (Fig. 2). In 1936, extensive agriculture was present in Palmer whereas TR-1 was forested. In 1936, the forest at TR-1 reflected the effects of 1932 hurricane San Ciprián. By 1950, air photographs showed increased vegetation cover east of the Palmer site and continuous forest cover at TR-1. Then, aerial photographs from 1998 showed a developing canopy at Palmer with no evidence of the effects of hurricane Georges, which passed south and west of the LEF in 1997. Palmer was on the leeward side of hurricane Georges winds, protected by the northwestern elevation of the Luquillo Mountains. Wind aspect and exposure are known to be responsible for the differential effects of hurricane Georges in the LEF (Lugo and Frangi 2016, Lugo et al. 2017). In contrast, TR-1 was located at a higher and more exposed elevation and did experience hurricane wind effects as reflected in its canopy in the 1998 aerial photograph. In the 2015 satellite image derived from Google Earth timeline, both stands appear as closed-canopy forests.

Soils at TR-1 are not suitable for farming while those at Palmer are arable when managed (Table 1). Soils at TR-1 are classified in the Zarzal-Cristal complex, 20–60 percent slopes, while those at Palmer are a complex of soils including 2 predominant soil series: Humatas clay, 20–40 percent slopes, and Caguabo clay loam, 20–60 percent slopes (NRCS 2022). Soils at both sites have a well-drained dominant condition. Those at TR-1 were sandier (see Fig. S-1 in Supplemental File 1, available online at https://www.eaglehill.us/CANAonline/suppl-files/C230-Lugo-s1) and heavier with similar average bulk densities (0.68 to 0.88 g/cm^3) that were not statistically different within and among sites in 1989 and within Palmer in 2015 compared to 1989. In 2015, TR-1 averaged 1.16 g/cm^3, which was statistically different from the others. The soil taxonomic classes are: very-fine, kaolinitic, isohyperthermic Typic Kandiudox (TR-1); and very-fine, parasesquic, isohyperthermic Typic Haplohumults and loamy-skeletal, mixed, active, isohyperthermic, shallow Typic Eutrudepts (Palmer) (NRCS 2022).

We selected the TR-1 and Palmer sites because of their contrast in land-use history, and for the following additional reasons that align with our objectives. First, they are both located in a region of the watershed where succession pathways led to the same forest type, the *Dacryodes* forest. Second, the TR-1 site provides the best example of the conditions at the end of succession. Third, current forest communities at both sites exhibit high dominance by 2 native tree species whose ecological and stoichiometric characteristics are known. For example, the distribution of both species within the watershed spans the climatic, elevational, and edaphic range represented by the Palmer and TR-1 sites. While *Tabebuia* grows with *Dacryodes* at various locations such as TR-1 and El Verde (Fig. 1) and in successions following non-anthropogenic disturbances, *Dacryodes* does not appear at Palmer or in regenerating stands following anthropogenic disturbances where *Tabebuia* can dominate.

Fieldwork

The intensity of sampling varied with time and the sampled parameter (see Table S-1 in Supplemental File 1). We sampled litter and soil from both sites in 1989 and

2015. We sampled litter and soil at TR-1 on 16 September 1989 and visited the Palmer site for litter and soil sampling on 7 October 1989. Hurricane Hugo passed east of the LEF on 18 September 1989. We also sampled litter and soil on 23 July 2015 at Palmer and on 23 September 2015 at TR-1. We studied the vegetation at Palmer on 23 July 2015. For TR-1, we used the vegetation data for 1976 (Weaver 1983, 1994) for comparison with Palmer data.

Vegetation. On 23 July 2015, we established 3 circular plots at Palmer, each with a diameter of 22 m. These plots were distributed perpendicularly to road PR 191 following a west–east azimuth. We located, identified to species, and measured the diameter and height of trees inside the circular plot with a diameter at breast height (dbh at 1.4 m) ≥4.5 cm. Based on the amount of light exposure, we sorted trees into 4 crown classes: suppressed (no direct light from the top or sides of the crown and located below the level of dominant and co-dominant crowns), intermediate

Table 1. Environmental and vegetation structure descriptors and coordinates for the sites where the 2 study areas are located in the Mameyes watershed, Luquillo Experimental Forest. TR-1 is a *Dacryodes excelsa* primary forest and Palmer is a *Tabebuia heterophylla* secondary forest[A]. Life zone is sensu Holdridge (1967). Structural data correspond to 23 July 2015 for the secondary forest at Palmer and 1976 for TR-1 (Weaver 1983, 1994). The sampled area was 0.1 ha. Standard error for mean tree diameter is in parenthesis (n = 211). Empty cells mean data are not available (TR-1). Values were rounded.

Descriptor	TR-1	Palmer
Coordinates	18.31°N, 65.76°W	18.35°N, 65.76°W
Elevation (m)	350	74–116
Life zone (subtropical)	Rain forest	Wet forest
Geology	Volcanic	Volcanic
Soil order	Oxisol[B]	Ultisol (85%)[C] and Inceptisol (80%)[C]
Sub order, great group, and subgroup	Udox, Kandiudox, Typic Kandiudox	Humults, Haplohumults, Typic Haplohumults and Udepts, Eutrudepts, Typic Eutrudepts
Texture[D]	Sandy loam	Silty clay loam
Importance value of dominant species (%)	32	63
Mean tree diameter (cm)		13 (1)
Tree density per ha	1188	1831
Basal area (m^2/ha)	51	33
Number of tree species[E]	17	15
Aboveground biomass (Mg/ha)	226[F]	188
Woody biomass (Mg/ha)	210[F]	108
Tallest 3 trees (m)	28	24
Complexity index for 0.1 ha	288	218

[A]The age of the largest trees at TR-1 are about 420 yr (Tropical Forest Experiment Station 1953), while we estimate those at Palmer at 34 yr in 2015 based on conversations with the landowner in 1989.
[B]Soils in this location have Inceptisol qualities.
[C]Refers to the percent of Ultisol or Inceptisol soils at the site without qualities of other soil types.
[D]See Figure s-1 in Supplemental File 1.
[E]On 0.11 ha for secondary and 0.10 ha for primary forest.
[F]Mature *Dacryodes* forest in the Bisley sector of the Mameyes river watershed (Scatena et al. 1993).

(crowns occupy a subordinate position, are exposed to strong lateral competition, and receive some light from above through canopy openings but no side light), co-dominant (crowns receive full light from the top but little light from the sides), and dominant (crowns receive full light from the top and partly from the sides).

Litter. On 16 September (at TR-1) and 7 October (at Palmer) 1989, we used a 0.25-m^2 frame placed on the forest floor to collect loose litter. We collected 10 replicate samples along a 100-m transect (i.e, at 10-m intervals), placed each sample in a paper bag, and transported them to the laboratory for sorting and chemical analysis. On 23 July (at Palmer) and 23 September (at TR-1) 2015, we sampled the litter layer by stratifying the collection into 3 categories representing a temporal gradient within the litter compartment. We used the appearance of the litter material to define the categories as follows: (1) recently fallen—the litter material is intact and loosely arranged on the top layer of the litter compartment, (2) older materials—located immediately below recently fallen with obvious signs of degradation and fragmentation, and (3) bottom layer—material is pressed against the humus or mineral soil layer. We herein identify these litter layers by their vertical position: top, middle, and bottom.

Soil. On 16 September 1989, we dug 3 soil pits at the TR-1 site and sampled soils at depths of 0–10, 30–35, and 50–65 (or in 1 pit, 60–75) cm. On 7 October 1989, we dug 2 soil pits at Palmer and sampled at 3 depths: 0–15, 15–30, and 30–50 cm. All soil samples in the study were placed in cloth bags and taken to the laboratory for processing and analysis. On 23 July 2015, we dug 5 soil pits at Palmer and sampled at depths of 0–15, 15–30, and 30–60 cm. We also collected a soil sample every 10 m along a 100-m transect at 0–5 cm depth. On 22 September 2015, we dug 3 soil pits at TR-1 and sampled at depths of 0–10, 10–30, 30–35, 35–50, and 50–75 cm. In addition, we collected a soil sample (0–5 cm depth) every 10 m along a 100-m transect.

Every time we sampled a soil depth, we also collected a known volume of soil from each depth using a bulk density sampler. We transported these samples to the laboratory for processing and estimating the bulk density of each soil layer.

Laboratory work

Litter. We sorted all loose-litter samples into leaves, fine wood, and miscellaneous. For the litter that was separated by vertical stratification in 2015, we sorted flowers and fruits as a separate category. After sorting, we oven dried the materials at 65 °C to constant weight, recorded their dry weight, and then homogenized them using a Wiley mill (in 1989; Arthur H. Thomas Company, Philadelphia, PA, USA) or a Foss Tecator 1093 Cyclotec mill (in 2015; Foss, Hilleroed, Denmark).

Soil. We air-dried soil samples before sieving through a 20-mesh (0.85 mm) or 10-mesh (2 mm) when used for chemical or texture analysis, respectively. Sieved samples were transported to the laboratory for analysis. We dried those soils used for bulk-density determinations at 105 °C to constant weight and recorded their weight. We translated soil elemental concentrations (below), averaged across collection depths, to per area estimates (kg/ha or Mg/ha) using the corresponding bulk density.

Chemical analysis

Litter. We digested homogenized loose-litter samples using an open block digester and performed the elemental analysis with a Spectro Ciros ICP-OES (Kleve, Germany) for the 1989 collection and a Spectro SpectroBlue ICP-OES for the 2015 collection. We followed the method recommended by Luh Huang and Schulte (1985) for digesting samples with concentrated HNO_3, 30 percent H_2O_2, and concentrated HCl. The analysis included aluminum, calcium, iron, potassium, magnesium, manganese, phosphorus, sodium, and sulphur. For the analyses for total carbon and total nitrogen of the 1989 litter samples, we used a CNS-2000 elemental analyzer (LECO Corp. 2003a). For the analysis of total carbon, total nitrogen, and total sulphur of 2015 litter, we used a LECO TruSpec CN analyzer (LECO-Corp 2003b). We combusted samples at 950 °C in a stream of 99.99% oxygen. We did not analyze the 1989 litter samples from TR-1 because a power failure associated with the passage of hurricane Hugo resulted in the loss of samples to fungal growth while they were in the drying oven. Thus, loose-litter chemistry data for 1989 are not compared.

Soil. We extracted for total elements as with litter (strong extractions), and also used weak acids to extract available elements (weak extractions). The available elemental analyses of the soils in the 1989 collection were based on 2 types of extractions. We obtained available phosphorus, exchangeable potassium, extractable manganese, and extractable iron using the modified Olsen-EDTA extraction and exchangeable calcium, magnesium, sodium, and exchangeable acidity (Al^{+3}-H^{+}) using a KCl (1N) extraction. We determined the available elements utilizing the Spectro Ciros ICP, except for exchangeable acidity, which we obtained by titration with 0.01N NaOH to a phenolphthalein endpoint. These weak extractions are comparable to the chemical soil extraction methods in the Kellogg Soil Survey Laboratory (2014) and reported in the Soil Conservation Survey (1967).

We used sub-samples from all soil depths (both 1989 and 2015) and both locations for the determination of soil pH (1:1 water and 1:1 KCl 1N). We treated with 30% H_2O_2 the soils from the 1989 collection used for texture analysis with the Bouyoucos method. We estimated loss on ignition by raising the temperature to 490 °C and used a modified Walkley Black method to estimate soil organic matter in the 1989 soil collection. Aluminum was not analyzed in 1989 samples used for total extractions. No available elements, soil texture analysis, or organic matter content were performed on the soils of the 2015 collection.

Our laboratory chemical analysis procedures corrected for sample moisture, precision, and element recovery as described in Lugo and Abelleira Martínez (2018). Analyzing duplicate samples every 10 determinations assessed precision. To assess elemental recovery after extraction, we analyzed reference materials with known chemical composition in every batch of 40 samples. These materials were obtained from the National Institute of Standards and Technology in Gaithersburg, MD and the LECO Corporation, St Joseph, MI.

Data analysis

Vegetation. We estimated species stem densities, basal areas, and importance values using standard procedures (Lugo et al. 2017), and used these to calculate the Holdridge (1967) complexity index (= h * BA * D * S * 10^{-3}, where h is the mean height in m of the 3 tallest trees, BA is basal area, D is tree density, and S is the number of species). The parameters BA, D, and S, but not tree height, are expressed on a 0.1-ha basis. We estimated the total biomass and aboveground woody biomass for Palmer using the allometric equations of Weaver and Gillespie (1992) and Lugo (1992), respectively. Scatena et al. (1993) used a similar approach to estimate the biomass of a mature *Dacryodes* forest at the Bisley Experimental Watersheds located between the Palmer and TR-1 sites in the Mameyes watershed (Fig. 1).

We based element molar ratios (hereafter element ratios) on molar concentrations determined by dividing the concentration of the element (mg/g or percent) by its molar weight (g/mole) and expressing the result in mmol/kg. We based the estimate of soil mass and its element storage on measurements from depths of 0 to 50 cm.

Statistical analysis. We statistically analyzed data using Excel spreadsheets for basic statistics (Microsoft, Redmond, WA, USA) and StatPlus:mac Pro version 7.3.3.0 (AnalystSoft, Inc., Walnut, CA, USA) for testing the differences between mean values. First, we tested the data for normality with a variety of tests including the Shapiro–Wilk W test. If the data were normal, we used one-way ANOVA and post hoc comparison of means at $P \leq 0.05$. We used the Scheffe test to determine significance between means. We analyzed data that were not normal with the non-parametric ANOVA test Kruskal–Wallis at $P \leq 0.05$. For the analysis of stoichiometric element ratios, we verified that the log transformation of data yielded the same results as non-transformed data as suggested by Isles (2020), who recommended log-transforming large metadata datasets that are much more heterogeneous than ours.

Results

Vegetation

In 1989 the forest stand at Palmer was ~8 years old and was almost a monoculture dominated by *Tabebuia heterophylla*. This stand had recently emerged after the abandonment of a pasture used for cattle grazing (Fig. 2a). Visits to the TR-1 forest in 1989 and through our study, confirmed it to be a mature undisturbed forest as reported by the Tropical Forest Experiment Station (1953). By 2015, the basal area at Palmer was 33 m^2/ha, still lower than at TR-1 in 1976, i.e., basal area at TR-1 was 1.6 times higher than the basal area at Palmer (Table 1). The average aboveground and wood biomass at Palmer was 83% and 51%, respectively, of the corresponding values estimated for a mature *Dacryodes* stand nearby (Table 1). Despite the differences in basal area and aboveground and woody biomass, the overall structure of TR-1 and Palmer forests were remarkably similar in terms of height, tree density, and number of tree species at the 0.1-ha scale. The overall vegetation complexity was higher at TR-1 (Table 1). The stands also differed in the presence of large

trees. The largest diameter tree was 43.8 cm dbh at Palmer and 1 m dbh at TR-1. At Palmer, 15% of the trees occupied the largest diameter class of ≥20 cm dbh. At TR-1, trees ≥20 cm dbh represented 29% of the stems, and the largest diameter class, with 4% of the stems, was the >40-cm dbh class (Wadsworth 1951).

The vertical structure of the forests, as reflected in the distribution of crowns relative to accessibility to light, had a similar percentage of trees with intermediate crowns (24%) but differed in the percent of trees in the other crown categories. Palmer had a greater proportion of trees in the dominant and co-dominant crowns (13% and 21%, respectively) than TR-1 (3% and 8%, respectively), while TR-1 had a greater proportion of suppressed crowns (65%). The mean tree diameter and mean tree height (SE, *n*) at Palmer decreased from trees with dominant crowns to those with suppressed crowns from 23.9 cm (1.9, 25) and 17.5 m (9.4, 25), respectively, in dominant crowns to 8.5 cm (0.5, 94) and 9.5 m (0.3, 91), respectively, in suppressed crowns.

While the top-ranked species of both forest communities had a high importance value, the importance value of *Tabebuia* at Palmer was almost twice as high as that of *Dacryodes* at TR-1 (Table 2). Only *Tabebuia* grew at both sites.

Litter

Chemistry. Element concentrations of forest-floor loose litter varied according to the element, the litter component, and the vertical position of the litter component in the litter layer (see Tables S-2, S-3 in Supplemental File 1). Leaf litter, flowers and fruits litter, and miscellaneous litter at Palmer had higher concentrations of most elements that those litters at TR-1 (Fig. 3 a, c, d). In contrast, fine wood litter at TR-1 had higher concentrations of most elements than fine wood litter at Palmer (Fig. 3b). Carbon, nitrogen, phosphorus, and sulfur concentrations in leaf litter were higher at TR-1 than at Palmer (Fig. 3a). Fine wood litter at Palmer had higher concentrations of aluminum, iron, potassium, manganese and sodium than fine wood litter at TR-1 (Fig. 3b).

Ash and element concentrations of loose litter at both locations tended to increase from the top of the litter layer to the bottom as illustrated for phosphorus in Palmer leaf litter (see Table S-3 in Supplemental File 1). In other instances, loose-litter element concentrations remained unchanged with depth as illustrated by phosphorus in the leaf litter of TR-1. In leaf and fine wood litter, carbon, nitrogen, sulphur, and ash concentrations increased with depth at Palmer but did not change at TR-1.

Soil

Both sites had acid soils at all depths (Table 3). Soils at TR-1 were significantly more acid than those at Palmer and were below 4.0 (KCl extractions) in 1989 and 2015. However, soil pH was not significantly different between 1989 and 2015 at each of the 2 study sites. The pH values measured at TR-1 classifies the soils as extremely acid based on KCl extractions (between 3.5 and 4.4) or as strongly acid based on H_2O extraction (between 4.5 and 5.0). Soils at Palmer were strongly acid based on KCl extractions. The ratio of pH in H_2O to pH in KCl was not different among and within sites, except for 2015 at Palmer, when it was lower than all other values.

Mean available concentrations of phosphorus, potassium, calcium, magnesium, manganese, and sodium to 50-cm depth at Palmer in 1989 were significantly higher than those at TR-1 (Table 4; for data by depth, see Table

Table 2. Importance values (IV) in percent of the top 15 species in a primary and a secondary forest in the Mameyes watershed, Luquillo Experimental Forest, Puerto Rico. Data correspond to 1976 for the primary forest (Weaver 1983) and 2015 for the secondary forest. Species are arranged in order of IV in the respective forest. * indicates non-native species.

Species	Authority	Common name	Primary forest	Secondary forest
Dacryodes excelsa	Vahl	Tabonuco	31.76	
Prestoea montana	(Graham) G. Nicholson	Palma De Sierra	10.92	
Micropholis garciniaefolia	Pierre	Caimitillo Verde	6.84	
Melastomataceae spp.			5.47	
Schefflera morototoni	(Aubl.) Maguire, Steyerm, & Frodin	Yagrumo Macho	4.37	
Cyrilla racemiflora	L.	Palo Colorado	3.50	
Hirtella rugosa	Pers.	Icaquillo	3.29	
Ocotea moschata	(meisn.) Mez	Nuez Moscadn	3.15	
Magnolia splendens	Urb.	Laurel Sabino	3.09	
Buchenavia tetraphylla	(Aubl.) R.A. Howard	Granadillo	2.87	
Calycogonium squamulosum	Cogn.	Jusillo	2.71	
Sloanea berteroana	Choisy ex DC.	Cacao Motillo	2.5	
Meliosma herbertii	Rolfe	Aguacatillo	2.07	
Rheedia portoricensis	Urban	Palo de Cruz	1.71	
Matayba domingensis	(DC.) Radlk	Negra Lora	1.52	
Tabebuia heterophylla	(DC.) Britton	Roble Blanco	0.64	63.29
Others				9.42
Eugenia biflora				5.55
Calophyllum calaba	Jacq.	María		5.14
*Swietenia macrophylla**	King	Caoba Hondureña		4.07
Guarea guidonia	(L.) Sleumer	Guaraguau		3.69
Ocotea leucoxylon	(Sw.) Mez	Laurel Geo		2.18
Alchorneopsis portoricensis	Urban	Palo de Gallina		2.09
Casearia sylvestris	Sw.	Cafeillo		1.73
Hura crepitans	L.	Molinillo		1.03
Dendropanax arboreus	(L.) Decne. & Planch	Pollo		0.59
Coccoloba diversifolia	Jacq.	Uvilla		0.34
Cinnamomum elongatum	(Vahl) Kosterm	Laurel Avispillo		0.33
Miconia prasina	(Sw.) DC.	Camasey		0.28
Casearia guianensis	(Aubl.) Urban	Palo Blanco		0.26

Figure 3 (following page). Ratio of ash and element concentration in leaf (upper left), fine wood (upper right), flowers and fruits (lower left), and miscellaneous (lower right) litter at different litter depths in a secondary forest dominated by *Tabebuia heterophylla* (Palmer) to the corresponding element concentration in litter in a primary forest dominated by *Dacryodes excelsa* (TR-1). Sites were in the Mameyes watershed within the Luquillo Experimental Forest. Note the logarithmic scale. Asterisks above columns identify the molar ratios that were statistically significant at $P \leq 0.05$. Missing bars mean insufficient or no sample for that depth.

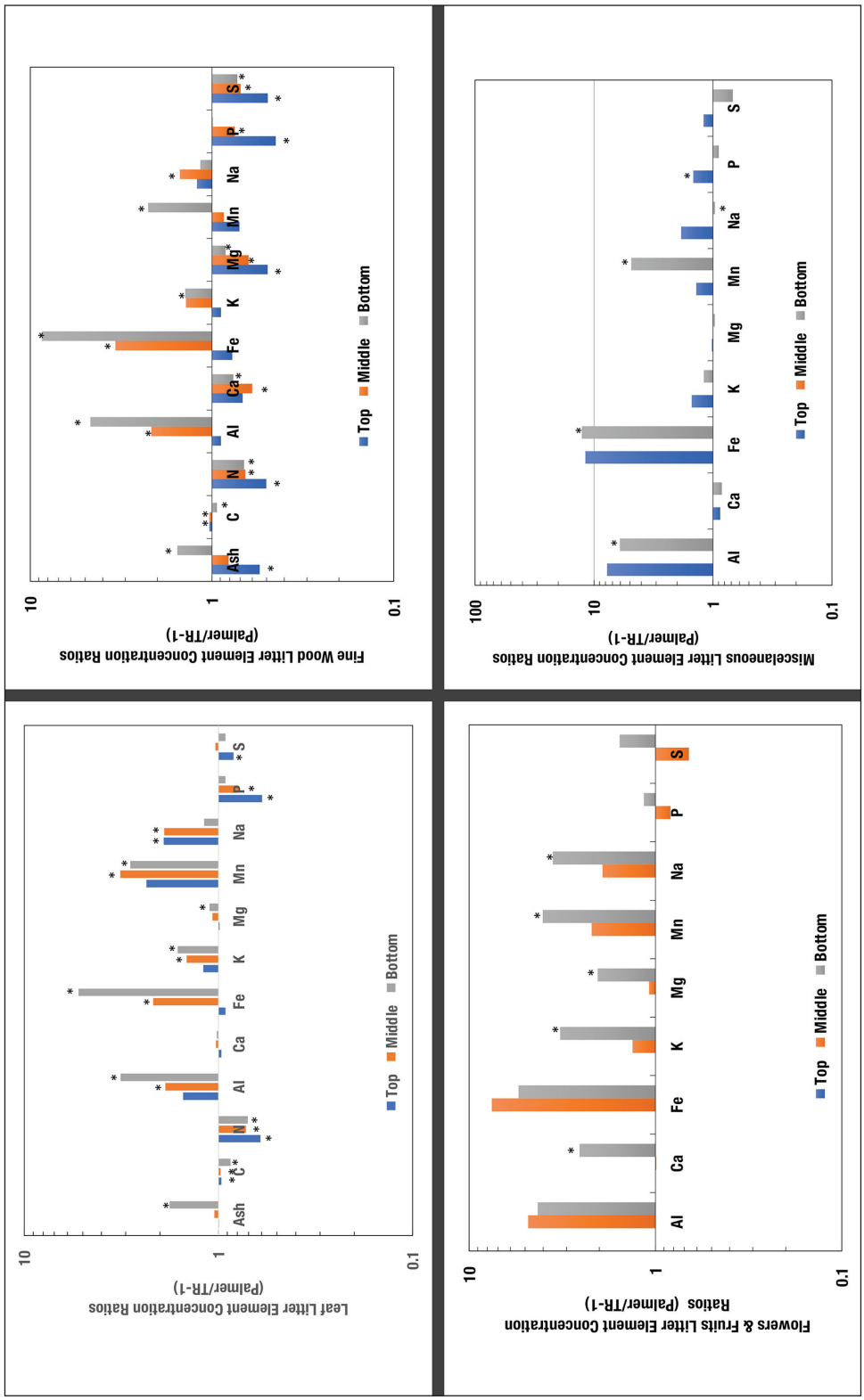

Figure 3. [See previous page for caption.]

S-4 in Supplemental File 1). The mean concentration of other elements listed in Table 4, including carbon and nitrogen, and soil organic matter, were not significantly different between sites.

The mean total element concentration of phosphorus, potassium, calcium, magnesium, manganese, iron, and sodium of Palmer soils to 50-cm depth in 1989 were significantly higher than those at TR-1 (see Table S-5 in Supplemental File 1). The loss on ignition to 50-cm depth of Palmer soils was also significantly higher than that at TR-1.

In 2015, Palmer soils had significantly higher total concentration of phosphorus, manganese, iron, and sulphur than TR-1 soils, but lower mean concentration of total potassium, magnesium, aluminum, and sodium (Table 4; for data by depth, see Table S-5 in Supplemental File 1). The difference in mean total calcium concentration was not significantly different between the 2 sites.

Between 1989 and 2015, the total concentration of elements in soils at TR-1 increased (Fig. 4) except calcium (at depths of 10–35 and 35–50 cm) and manganese (at 35–50 cm depth), which did not change. Those at Palmer either decreased (potassium, calcium, and magnesium) or increased (phosphorus and sulfur). While most differences in the mean total concentration of soil elements at Palmer between

Table 3. Arithmetic mean soil pH at various depths and for all depths combined in a *Tabebuia heterophylla* secondary forest and a *Dacryodes excelsa* primary forest in the Mameyes watershed, Luquillo Experimental Forest. The standard error is in parenthesis. For the 0–5 cm depth data, the *n* was 10; for other depths in the secondary forest, *n* is 5 for 2015, 3 for September 1989, and 2 for October 1989; and for the primary forest it is 3. Rows with the same letter are not statistically different at $P < 0.05$.

	Primary forest		Secondary forest	
Depth (cm)	pH (H_2O)	pH (KCl)	pH (H_2O)	pH (KCl)
1989				
0–5	4.83 (0.04)	3.95 (0.04)	5.80 (0.13)	5.07 (0.16)
0–10	5.02 (0.06)	3.91 (0.04)		
10–15			5.03 (0.07)	4.25 (0.07)
10–30	5.22 (0.08)	3.99 (0.00)		
15–30			5.11 (0.05)	4.22 (0.03)
30–35	5.13 (0.00)	3.89 (0.01)		
30–50			5.43 (0.08)	4.47 (0.04)
35–50	5.08 (0.10)	3.85 (0.02)		
50–75	5.09 (0.10)	3.82 (0.03)		
2015				
0–10	4.8 (0.1)	3.8 (0.1)		
0–15			5.3 (0.3)	4.5 (0.3)
15–30			5.5 (0.3)	4.2 (0.4)
30–35	4.8 (0.1)	3.9 (0.1)		
30–50			5.7 (0.0)	4.2 (0.4)
50–75	5.0 (0.1)	3.9 (0.0)		
All depths combined	2015		1989	
pH in H_2O	4.9^{B}	5.0^{B}	5.5^{A}	5.4^{A}
pH in KCl	3.9^{B}	3.9^{B}	4.3^{AB}	4.6^{A}
pH H_2O/pH KCl	1.27^{A}	1.28^{A}	1.30^{A}	1.18^{B}

1989 and 2015 were significant (see Table S-5 in Supplemental File 1), the concentrations of manganese, iron, carbon, and nitrogen did not change.

The 2 sites had significant differences in the storage of elements in the soil to 50-cm depth (Table 5; for data by depth, see Table S-6 in Supplemental File 1). Palmer had higher storage of available elements than TR-1. The exceptions were aluminum, phosphorus, and iron, which were not significantly different between sites. In 1989, the predominant pattern in the comparison of total element storage between the sites was their non-significant differences in most elements. The exceptions were manganese, carbon, and nitrogen, which had higher storages at Palmer compared to TR-1. In the 2015 sampling, TR-1 had higher storages of potassium, calcium, magnesium, aluminum, and sodium, while Palmer had a higher

Table 4. Comparison of the mean available and total soil element concentrations to 50 cm depth in 1989 and 2015 for a primary *Dacryodes excelsa* forest (TR-1) and a secondary *Tabebuia heterophylla* forest in the Mameyes river watershed, Luquillo Experimental Forest. Data are in mg/g unless otherwise indicated. NS means the difference between forest means is not significant at $P \leq 0.05$. Empty cells mean the analysis was not done. LOI = loss on ignition, SOM = soil organic matter, and values were rounded. Original data by soil depth for 1989 available and total concentration data are provided in Tables S-3 and S-4, respectively, in Supplemental File 1, and data by soil depth for 2015 total concentration are provided in Table S-5 in Supplemental File 1. * indicates the medians were significantly different at $P = 0.03$.

	Available			Total		
Parameter	TR-1	Palmer	*P*	TR-1	Palmer	*P*
1989						
Phosphorus	0.01	0.03	0.05	0.14	0.40	0.0014
Potassium	0.03	0.32	0.01	0.12	1.57	8.3E-04
Calcium	0.11	1.10	8.44E-04	0.32	1.97	1.3E-06
Magnesium	0.06	0.81	0.0034	0.56	7.71	2.7E-05
Manganese	0.01	0.09	0.00897	0.30	2.77	5.5E-05
Iron	0.59	0.58	NS*	33.14	95.83	3.2E-06
Sodium	0.03	0.12	2.42E-08	0.05	0.24	2.0E-08
Sulphur %				0.02	0.04	NS*
Carbon %				0.84	2.15	NS*
Nitrogen %				0.06	0.22	NS*
LOI %				5.89	12.51	0.0013
SOM %				1.72	3.23	NS*
2015						
Phosphorus				0.42	0.57	1.2E-06
Potassium				2.12	0.64	4.6E-09
Calcium				0.76	0.96	NS*
Magnesium				4.56	1.20	3.4E-08
Manganese				0.42	3.42	4.6E-09
Aluminum				89.47	66.18	2.8E-06
Iron				61.14	81.61	6.7E-09
Sodium				0.22	0.18	0.02
Sulphur				0.47	0.68	2.5E-05
Carbon %				3.11	4.46	0.05
Nitrogen %				0.34	0.38	NS*
LOI %				18.67	19.95	NS*

storage of manganese. For the other elements, the differences in storage were not significantly different. The top 5 cm of mineral soil at Palmer had a greater proportion of total element storage than did TR-1, except for aluminum; it stored a larger amount of potassium, magnesium, manganese, and sodium (Table 6).

Discussion

We first discuss those forest structural parameters that are relevant to addressing the 3 questions that are the focus of this study. We then address the questions posed in the introduction and end with a discussion of stand stoichiometry in relation to the successional position and the fitness to site conditions of dominant tree species.

Differences in structure

Our results reveal a similar overall structural edifice among sites (tree height, density, and species richness), but a more robust structure at TR-1 compared to Palmer. The differences in robustness among sites were reflected in basal area and biomass, which were both significantly larger at TR-1 compared to Palmer (Table 1). The higher number of tree canopies in the suppressed position at TR-1

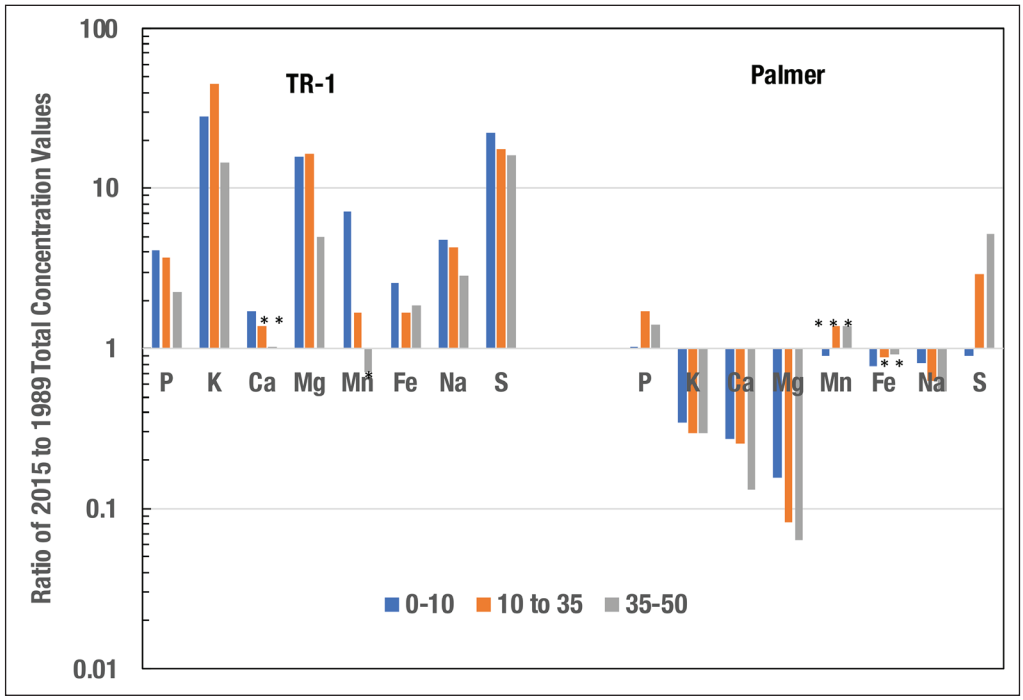

Figure 4. Ratio of total concentration of elements in 2015 to total concentration of elements in 1989 at different soil depths (cm) in 2 forests stands in the Mameyes watershed. All element ratios are significant at $P \leq 0.05$ except those with asterisks (*). The data grouping on the left corresponds to a primary forest dominated by *Dacryodes excelsa* (TR-1), and the data grouping to the right corresponds to a secondary forest dominated by *Tabebuia heterophylla* (Palmer). A ratio of 1.0 means that both times the concentrations were the same. Note the logarithmic scale.

Table 5. Comparison of mean storage to 50-cm depth of total and available extractions of elements and loss on ignition (LOI) in soils of a primary forest dominated by *Dacryodes excelsa* (TR-1) and a secondary forest dominated by *Tabebuia heterophylla* (Palmer) in the Luquillo Experimental Forest. Two independent soil collections and extractions for available elements were conducted in 1989. Values are given in kilograms per hectare and have been rounded. Table S-6 in Supplemental File 1 contains element data by depth at both sites. Empty cells mean that the analysis was not done and NS that the means were not significantly different at $P \leq 0.05$. * indicates medians were significantly different at $P = 0.03$.

	Total in 2015			Total in 1989			Available in 1989					
Element	TR-1	Palmer	*P*	TR-1	Palmer	*P*	TR-1	Palmer	*P*	TR-1	Palmer	*P*
Phosphorus	2531	1852	NS	483	1043	NS*	24	86	NS*			
Potassium	15,100	1727	5.5E-4	383	5792	NS*	127	933	0.0027	66	891	0.0043
Calcium	3015	1486	0.02	1361	6233	NS*	435	3425	0.0056	309	3911	1.5E-4
Magnesium	34,367	2450	2.5E-4	25,033	25,291	NS	258	2559	8.6E-4	185	2970	0.0017
Manganese	2664	11,179	0.0077	1088	6944	0.0029	34	279	0.0063			
Aluminum	565,434	229,380	0.01							462	334	NS
Iron	404,704	291,570	NS	137,687	243,370	NS*	2542	1659	NS			
Sodium	1204	561	0.0034	184	717	NS*	137	414	0.0031	95	410	0.0021
Sulphur	2219	2255	NS	845	902	NS						
Carbon	123,993	107,513	NS	39,763	56,747	0.05						
Nitrogen	8343	9415	NS	3334	5822	0.05						
LOI	899,265	664,001	0.0033	244,453	333,739	NS						

compared to Palmer increases the occupation of the vertical volume of the forest. This difference in structural volume affects the growth of trees due to the access to solar energy for photosynthesis. *Tabebuia*, with a greater fraction of its canopies in dominant or co-dominant positions produces more mass per unit area and time than *Dacryodes* (Table 7). In contrast, the metabolic cost of maintaining the forest volume should be higher at TR-1 compared to Palmer due to the larger amount of biomass at TR-1.

The structural difference among stands also affects the interception of rainfall, which affects the potential for soil erosion. We do not have rainfall-interception data for the *Tabebuia* forest but expect that rainfall interception is lower than in mature stands of *Dacryodes*. The rainfall interception of a *Dacryodes* forest at Bisley with a wet forest climate is 40–50% compared to <20% in most montane forests (Scatena 1990). Less rainfall interception in the secondary forest means that more rainwater reaches the forest floor and with higher velocity, particularly during the period when *Tabebuia*, a deciduous species (Little and Wadsworth 1964), is leafless. *Dacryodes* is an evergreen primary forest species with a continuous closed-canopy cover (Smith 1970).

Differences in stoichiometry

The differences in loose-litter and soil element concentration between sites (Figs. 3, 4; Table 4; see Tables S-2 to S-5 in Supplemental File 1) affected the element ratios that we estimated (Tables 8, 9; see Tables S-7, S-8 in Supplemental File 1). Three stoichiometric patterns differentiated the leaf loose litter of the 2 study sites (Table 8). First, carbon molar ratios (C:N, C:P, C:S) were higher at Palmer compared to TR-1. Second, the nitrogen molar ratios (N:Ca, N:K, N:Mg, N:P) were higher at TR-1 than at Palmer. Third, element ratios with phosphorus in

Table 6. Comparison of the 2015 mean total soil element content to 5-cm depth and the percent it represents relative to the mean total storage to 50-cm depth between a primary *Dacryodes excelsa* forest (TR-1) and a secondary *Tabebuia heterophylla* forest (Palmer) in the Mameyes river watershed, Luquillo Experimental Forest. The means of total storage of elements and loss on ignition to 50 cm are given in Table 5. NS = not significant. Values were rounded. Original concentration data are available in Table S-5 in Supplemental File 1.

	Total (kg/ha)			Percent of total to 50 cm	
Parameter	TR-1	Palmer	*P*	TR-1	Palmer
Phosphorus	268	230	NS	10.6	12.4
Potassium	392	915	2.12E-4	2.6	53.0
Calcium	506	680	NS	16.8	45.9
Magnesium	836	1781	3.47E-4	2.4	72.7
Manganese	213	1502	2.39E-5	8.0	13.4
Aluminum	42,122	25,524	0.00967	7.4	11.1
Iron	29,836	31,524	NS	7.4	10.8
Sodium	127	104	0.01000	10.5	18.5
Sulphur	320	358	NS	14.4	15.9
Carbon	27,600	26,800	NS	22.3	24.9
Nitrogen	2210	2210	NS	26.5	23.5
LOI	107,010	97,140	NS	11.9	14.7

the denominator (Ca:P, K:P, Mg:P, S:P) were higher at Palmer than at TR-1, which reflects the lower phosphorus concentration of loose litter at Palmer. The calcium molar ratios (Ca:Mg, Ca:Al, Ca:P) of loose litter, particularly Ca:Mg, tended not to be different among sites and had the highest values in the top litter layer. Element ratios in flowers and fruits and miscellaneous litter had few consistent patterns, the most notable being the difference between sites in the bottom miscellaneous-litter element ratios (Table 8). Nine element ratios were higher at TR-1 than Palmer with only the K:P molar ratio being higher at Palmer. We now discuss each of the 3 patterns observed adding information from the literature.

Carbon molar ratios. The higher carbon molar ratios of loose litter at Palmer compared to TR-1 (flowers and fruits litter excepted; Table 8) indicates that the secondary forest is concentrating more carbon per unit of nitrogen, phosphorus, and sulfur stored. This result was surprising as a fast-growing and rapid turnover

Table 7. Net change in soil elements and soil loss of ignition, and net aboveground biomass increment for a secondary forest of *Tabebuia heterophylla* and a primary and a cutover forest of *Dacryodes excelsa* in the Mameyes watershed of the Luquillo Experimental Forest. Estimates are between 1989 and 2015 for soils, between 1981 and 2015 for aboveground biomass of *T. heterophylla*, and between 1946 to 1956 and 1956 to 1966 for aboveground biomass in *D. excelsa* (Briscoe and Wadsworth 1970). Negative signs mean a net loss of elements. The 2 soil sulphur values are from different samples and methods of analysis. Numbers in parenthesis represent the rainfall input of elements in the same units for lower montane forests (Medina et al. 2013) and Bisley Experimental Watersheds (carbon, nitrogen, and phosphorus; Heartsill Scalley et al. 2007). Data were rounded and soil values correspond to 0–50-cm depth.

Parameter	TR-1 (primary forest)	Palmer (secondary forest)
Soil elements (kg/ha•yr)		
Phosphorus (1.1[A])	79	31
Potassium (30)	566	-156
Calcium (10)	64	-183
Magnesium (10)	359	-879
Manganese	61	163
Aluminum	21,747	8822
Iron	10,270	1854
Sodium (70)	39	-6
Sulphur (41[B])	53	52
Carbon (132[C])	3240	1953
Nitrogen	193	138
Loss on ignition (kg/ha•yr)		
Loss on Ignition	25,185	12,702
Aboveground mass (kg/ha•yr)		
Primary *D. excelsa* 1946–1956	760	
Primary *D. excelsa* 1956–1966	1710	
Cutover *D. excelsa* 1946–1956	1770	
Cutover *D. excelsa* 1956–1966	3160	
Secondary *T. heterophylla*		5500

[A]As PO_4.
[B]As SO_4.
[C]Dissolved organic carbon.

Table 8. Comparison of the mean element molar ratios of loose-litter compartments along a vertical gradient (top, middle, bottom) between the litter layer of a primary (TR-1) and secondary (Palmer) forest in the Luquillo Experimental Forest. Means in paired columns with the same letter superscript are not different at $P \leq 0.05$. Empty cells = data unavailable. [Table continued on following page.]

	Top		Middle		Bottom	
Element ratio	TR-1	Palmer	TR-1	Palmer	TR-1	Palmer
Leaf litter						
C:N	28.6^{B}	45.9^{A}	25.5^{B}	35.0^{A}	23.8^{B}	29.4^{A}
C:P	1687^{B}	2746^{A}	1555^{B}	1928^{A}	1512^{A}	1434^{A}
C:S	612^{B}	722^{A}	581^{A}	556^{A}	557^{A}	530^{A}
N:CA	4.20^{B}	2.72^{A}	4.27^{B}	3.04^{A}	4.83^{B}	3.43^{A}
N:K	31.1^{B}	15.7^{A}	43.9^{B}	21.4^{A}	55.7^{B}	24.4^{A}
N:Mg	11.8^{B}	7.2^{A}	12.8^{B}	8.4^{A}	13.9^{B}	8.8^{A}
N:P	59.24^{A}	60.8^{A}	61.4^{B}	55.5^{A}	63.8^{B}	48.8^{A}
N:S	21.5^{B}	15.9^{A}	22.9^{B}	15.9^{A}	23.5^{B}	18.0^{A}
CA:Mg	2.80^{A}	2.71^{A}	3.00^{A}	2.83^{A}	2.89^{A}	2.67^{A}
CA:Al	30.3^{A}	22.3^{A}	13.54^{B}	5.96^{A}	7.94^{B}	1.28^{A}
CA:P	14.2^{B}	23.3^{A}	14.5^{B}	18.6^{A}	13.3^{A}	14.7^{A}
K:P	2.04^{B}	4.09^{A}	1.43^{B}	2.65^{A}	1.16^{B}	2.06^{A}
Mg:P	5.13^{B}	8.64^{A}	4.85^{B}	6.63^{A}	4.61^{B}	5.63^{A}
S:P	2.77^{B}	3.87^{A}	2.69^{B}	3.52^{A}	2.72^{A}	2.72^{A}
Fine wood litter						
C:N	33.0^{B}	71.1^{A}	32.3^{B}	51.0^{A}	30.2^{B}	43.3^{A}
C:P	1868^{B}	4954^{A}	1851^{B}	2515^{A}	2079^{A}	2070^{A}
C:S	714^{B}	1726^{A}	670^{B}	1023^{A}	694^{B}	903^{A}
N:CA	4.54^{B}	3.33^{A}	2.91^{A}	3.23^{A}	3.61^{A}	3.18^{A}
N:K	21.0^{A}	17.4^{A}	31.5^{B}	16.5^{A}	45.4^{B}	20.9^{A}
N:Mg	9.78^{A}	10.32^{A}	8.27^{A}	8.91^{A}	10.80^{B}	8.50^{A}
N:P	55.1^{B}	63.3^{A}	55.6^{B}	49.0^{A}	68.7^{B}	47.8^{A}
N:S	21.0^{A}	21.9^{A}	20.3^{A}	19.9^{A}	23.0^{A}	20.8^{A}
CA:Mg	2.28^{A}	3.12^{A}	3.02^{A}	2.84^{A}	3.13^{A}	2.73^{A}
CA:Al	24.49^{A}	26.55^{A}	27.52^{B}	5.39^{A}	16.81^{B}	2.62^{A}
CA:P	12.6^{B}	19.7^{A}	20.9^{A}	16.0^{A}	20.1^{A}	16.1^{A}
K:P	3.44^{A}	7.88^{A}	1.89^{B}	3.34^{A}	1.56^{B}	2.45^{A}
Mg:P	5.92^{A}	6.57^{A}	6.92^{B}	5.64^{A}	6.49^{A}	5.73^{A}
S:P	2.64^{A}	2.93^{A}	2.76^{A}	2.51^{A}	2.98^{B}	2.32^{A}
Flowers and fruits litter						
C:N	57.8^{B}	32.8^{A}	37.9^{A}	39.1^{A}	46.5^{B}	31.3^{A}
C:P			1212^{A}	1906^{A}	1856^{A}	1505^{A}
C:S			780^{A}	966^{A}	993^{A}	635^{A}
N:CA			7.73^{A}	8.82^{A}	9.8^{B}	4.1^{A}
N:K			10.9^{A}	10.3^{A}	29.1^{A}	5.9^{A}
N:Mg			13.4^{A}	11.4^{A}	17.4^{B}	9.1^{A}
N:P			38.7^{A}	47.5^{A}	41.9^{A}	35.9^{A}
N:S			19.3^{A}	26.0^{A}	21.8^{B}	15.1^{A}
CA:Mg			1.63^{A}	1.58^{A}	1.8^{A}	2.2^{A}
CA:Al			35.1^{B}	6.25^{A}	11.1^{A}	5.2^{A}
CA:P			4.8^{A}	7.5^{A}	4.6^{A}	8.8^{A}
K:P			3.52^{A}	5.52^{A}	1.99^{B}	6.28^{A}
Mg:P			2.97^{A}	4.37^{A}	2.47^{A}	3.96^{A}
S:P			2.02^{A}	1.95^{A}	1.93^{A}	2.38^{A}

secondary forest is expected to be less carbon dense than a primary forest. This finding raises the question of whether this difference in C:N alone regulates the leaf-decomposition rate. We believe not, as other element ratios such as the N:P, come into play in regulating litter decomposition.

Leaf litter at TR-1 had a higher concentration of nitrogen than leaf litter at Palmer. The high concentration of nitrogen at TR-1, coupled with a small change with depth in the carbon concentration of those leaves, results in low C:N, but high N:P. The higher reduction with depth in carbon concentration in Palmer litter

Table 8, continued.

	Top		Middle		Bottom	
Element ratio	TR-1	Palmer	TR-1	Palmer	TR-1	Palmer
Miscellaneous litter						
C:N			23.3^{B}	19.9^{A}	22.2^{A}	20.6^{A}
C:P					1280^{B}	811^{A}
C:S					510^{B}	428^{A}
N:CA					5.62^{B}	4.27^{A}
N:K					53.8^{B}	28.5^{A}
N:Mg					14.2^{B}	9.2^{A}
N:P					57.4^{B}	38.8^{A}
N:S					22.9^{B}	20.5^{A}
CA:Mg					2.55^{A}	2.25^{A}
CA:Al					3.87^{B}	0.41^{A}
CA:P					10.3^{A}	9.6^{A}
K:P					1.08^{B}	1.44^{A}
Mg:P					4.06^{A}	4.42^{A}
S:P					2.51^{B}	1.89^{A}

Table 9. Molar ratios for soil elements based on total mass-weighted element concentrations to 50-cm depth in Table 5. Data are for 2015 and 1989 in a primary forest dominated by *Dacryodes excelsa* (TR-1) and a secondary forest dominated by *Tabebuia heterophylla* (Palmer) in the Mameyes river basin, Luquillo Experimental Forest. Values have been rounded. Empty cells are due to lack of information on aluminum concentration.

	2015		1989	
Ratios	TR-1	Palmer	TR-1	Palmer
C:N	17.3	13.3	13.9	11.4
C:P	126	150	212	140
C:S	149	127	126	168
N:Ca	7.9	18.1	7.0	2.7
N:K	1.5	15.2	24.3	2.8
N:Mg	0.42	6.7	0.23	0.40
N:P	7.3	11.2	15.3	12.3
N:S	8.6	9.6	9.0	14.8
Ca:Mg	0.05	0.37	0.03	0.15
Ca:Al	0.0036	0.0044		
Ca:P	0.92	0.62	2.2	4.6
K:P	4.7	0.74	0.63	4.4
Mg:P	17.3	1.7	66.0	30.9
S:P	0.85	1.2	1.7	0.84

compared to TR-1 litter, suggests that leaf-litter decomposition in this forest is faster at Palmer than at TR-1, despite its higher initial C:N molar ratios. These data suggest that the N:P ratio might be a better indicator of the speed of decomposition in these 2 forests. The expectation of slower litter-decomposition rate at TR-1 with higher nitrogen concentration is consistent with the notion that nitrogen may induce abiotic formation of compounds that resist microbial attack and slow down decomposition rates (Hobbie 2015).

Nitrogen molar ratios. When the N:P molar ratios of biomass and necromass from Palmer and TR-1 are plotted against their C:P ratios, the sites separate into nearly 2 parallel trend lines where TR-1 materials show both higher N:P and C:P element ratios than Palmer materials (Fig. 5). Those ratios decrease from wood, fine wood litter, and leaf fall towards miscellaneous litter. Fine roots from *Tabebuia*, which had a higher C:N than fine roots from *Dacryodes*, had lower N:P and C:P than *Dacryodes* fine roots. We believe that the C:N:P stoichiometry of materials from Palmer and *Tabebuia* define these materials as being more labile and prone for quicker recycling than those from TR-1 and *Dacryodes*. High N:P molar ratios typical of *Dacryodes* and TR-1 are associated with slower material turnover and lower biomass-production rates (Güsewell 2004). This comparison does not imply that decomposition rates in *Dacryodes* litter are slow. In fact, they are rapid

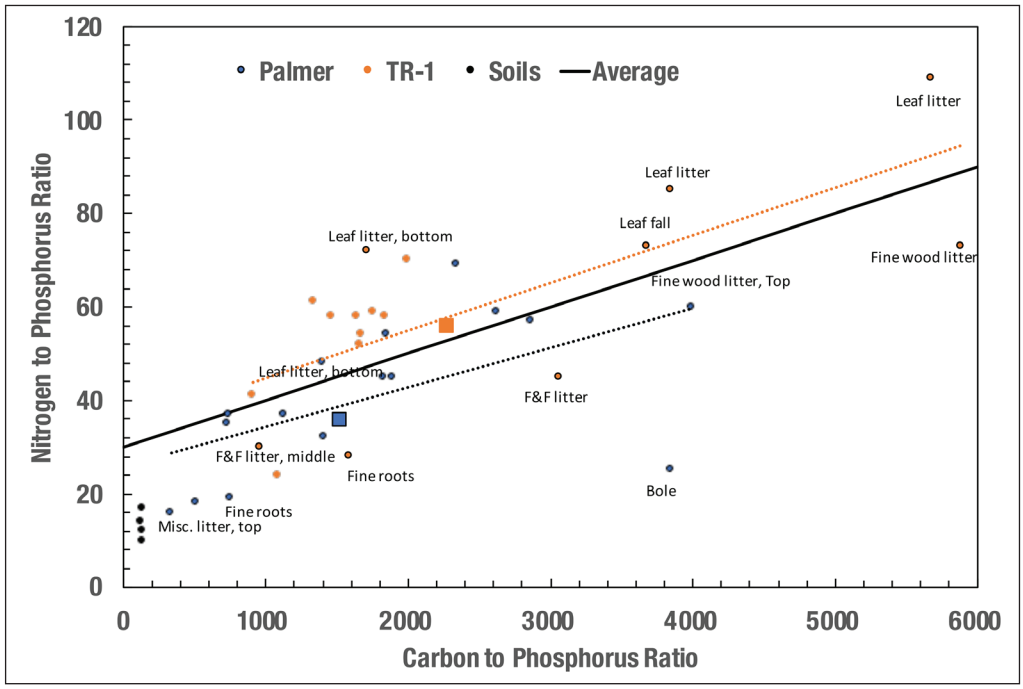

Figure 5. Relationship between the N:P ratio to the C:P ratio in plant compartments of 2 forest types: a secondary forest at Palmer dominated by *Tabebuia heterophylla* and a primary forest (TR-1) dominated by *Dacryodes excelsa*. The square points represent the ratio for leaves of the dominant species. The black line is an average between sites. A black border on data points identify labeled points. Soil data for the 2 sites are included for comparison. The sites are in the Mameyes watershed, Luquillo Experimental Forest.

(Bloomfield et al. 1993, La Caro and Rudd 1985, Wiegert 1970), it's just that the chemical changes suggest that the rates are faster (decomposition constant >>1) in the secondary forest at Palmer.

Phosphorus molar ratios. Phosphorus concentration at Palmer increased significantly from the top litter layer where recently fallen leaves are located to the bottom, where leaves have been exposed to the decomposition process for a longer time. As phosphorus appears more limiting than nitrogen to trees in Puerto Rico (Medina 2015), the capacity of Palmer to concentrate more phosphorus through the litter-decomposition process than TR-1 gives it a competitive edge in the recycling of its necromass. Necromass at Palmer is more labile to microbial organisms than the necromass at TR-1. The different behavior of phosphorus and nitrogen in the study forests was reflected in the N:P ratio of loose litter, which had the opposite pattern of change at TR-1, where it increased with depth, compared to Palmer. Fine wood litter at Palmer maintained the differences in element ratios between the top and bottom of the litter layer in contrast with TR-1, which did not.

Patterns of stoichiometric changes in the litter layer. The stoichiometry of the liter layer is controlled by 2 processes. The initial conditions at the top of the litter layer are the result of litter fall and the chemistry of the falling material, which are both controlled by the vegetation, particularly by the ecophysiological traits of dominant species. Once the litter is exposed to the conditions of the forest floor, its chemistry is controlled by the decomposer community and the process of decomposition, whose outcome is the litter in the bottom of the litter layer. At Palmer, leaf-litter element ratios involving carbon (C:N, C:P, C:S) and phosphorus (Ca:P, K:P, Mg:P, S:P) significantly decreased with litter depth as did Ca:Al. At TR-1, the changes in element ratios with litter depth were mostly not significant, and those that were significant followed the same pattern observed at Palmer (C:N, N:Ca, N:Mg, Ca:Al, Mg:P).

Influence of soil pH

Soil pH was one of the 19 measures of soil structure and chemistry used by Amacher et al. (2007) to develop a soil quality index to assess forest soil health. Based on 13 soil parameters for our sites, we calculated a soil quality index of 45% and 70% for TR-1 and Palmer, respectively. The TR-1 value is below, and the Palmer value is above, the mean for soils in the United States of America (Amacher et al. 2007). The parameters that most deviated from the norm in our study were pH and the concentrations of potassium, aluminum, and phosphorus for TR-1, and the concentrations of aluminum and manganese for Palmer. Manganese is an essential plant element that can become toxic at certain pH conditions (Millaleo et al. 2010).

Low soil pH affects the availability of limiting nutrients such as phosphorus and calcium and also affects the concentration of aluminum, which is potentially toxic to plants at certain levels. The low pH of TR-1 soils resulted in lower concentrations of available elements than in Palmer soils, which were less acid (Table 4). While in 2015 the concentration of calcium was not different in the soils at Palmer and TR-1, soil calcium concentration values at both locations were low (well below 60 mmol/kg; see Table S-9 in Supplemental File 1).

The aluminum concentration in soils increased with depth and was variable in part because it is exponentially related to soil pH; a small variations in pH result in large variation in aluminum concentration (Fig. 6). The total aluminum concentration in soils varied from 2400 to 3300 mmol/kg, and available aluminum varied from 7.0 to 8.1 mmol/kg (Table S-9). Moreover, the concentration of elements in the soil were not in the same rank-order as for loose litter. For example, Palmer had higher soil nitrogen concentration than TR-1, but TR-1 loose litter had higher nitrogen concentration than Palmer litter (see Table S-2 in Supplemental File 1). In 1989, soils at Palmer consistently had higher concentrations of elements than soils at TR-1, including available and total element concentrations (Table 4). However, TR-1 leaf litter had higher nitrogen and phosphorus concentrations than Palmer leaf litter (Fig. 3a).

By influencing element concentration, soil pH also affects element ratios. Element ratios in soils were lower in magnitude than element ratios in loose litter (compare Tables 8 and 9), the difference reflecting the differential concentration of elements by vegetation. The Ca:Al molar ratios of Palmer's soils are 1–2 orders of magnitude higher than those of soils at TR-1 (Fig. 7). At TR-1, the Ca:Al molar ratio is 1 or below, while at Palmer it is >1. The TR-1 site was among the lowest ranked sites in terms of Ca:Al molar ratios reported by Cronan and Grigal (1995).

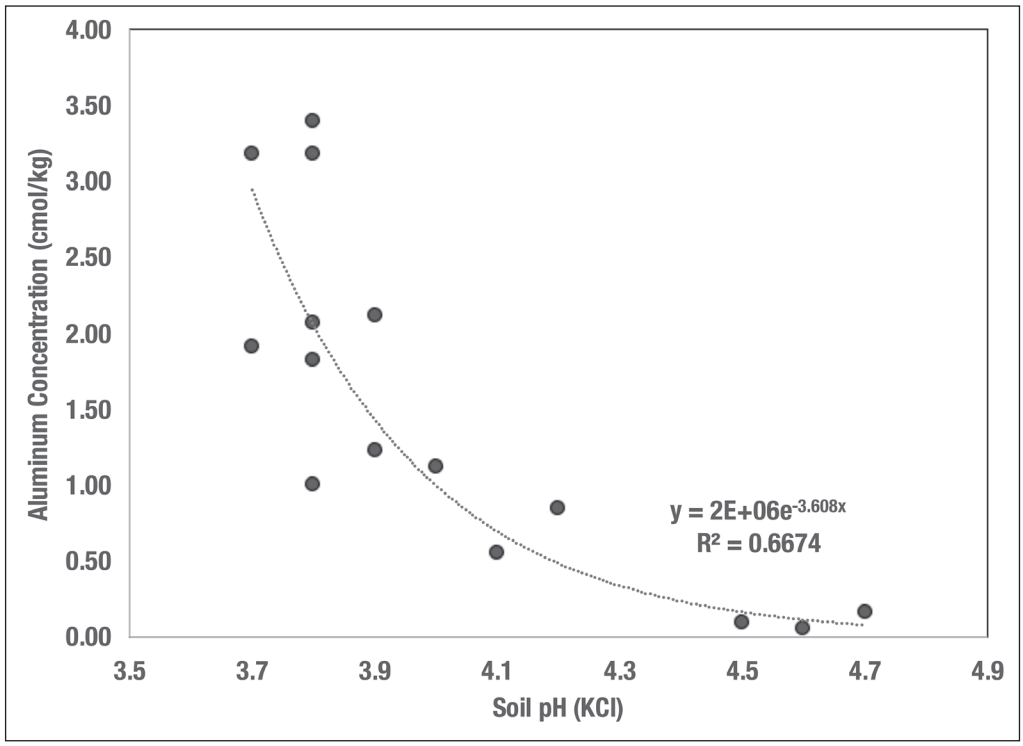

Figure 6. Relationship between the concentration of aluminum in soil and soil pH in soils of 2 forest types: a secondary forest at Palmer dominated by *Tabebuia heterophylla* and a primary forest (TR-1) dominated by *Dacryodes excelsa*. Each point is a paired pH and concentration value analyzed in this study. The relationship is statistically significant at $P < 0.001$.

This finding raises the question of how these forests can function so productively despite the stress imposed by the Ca:Al molar ratio of their soils. It appears that acid soil conditions can stress the physiology of plants, much as salinity stresses the physiology of mangroves and influences their productivity (Tomlinson 1986). However, as discussed below, low soil-pH stress, like salinity stress in mangroves, can also be overcome through metabolic adjustments by trees.

Significance of calcium:aluminum molar ratios. The concentration of calcium on the exchange complex of soils affects the Ca:Al molar ratio of roots (Khanna and Ulrich 1984). High concentrations of calcium in the exchange complexes lead to favorable Ca:Al molar ratios in soils and roots (values above 1). Aluminum toxicity is the primary factor limiting crop productivity in acid soils with the root apex acting as the site of aluminum toxicity (Kochian 1995). The presence of aluminum can prevent cell division and root development (Lambers et al. 1998). However, plants have 2 mechanisms that account for their resistance to potentially toxic levels of aluminum: exclusion from the root apex, and aluminum tolerance.

Trees must actively invest energy in the production of a variety of substances that either help exclude aluminum from the root or overcome its toxic effects (Kochian 1995, Lambers et al. 1998). These include humic acid, fluvic acid, concentrating

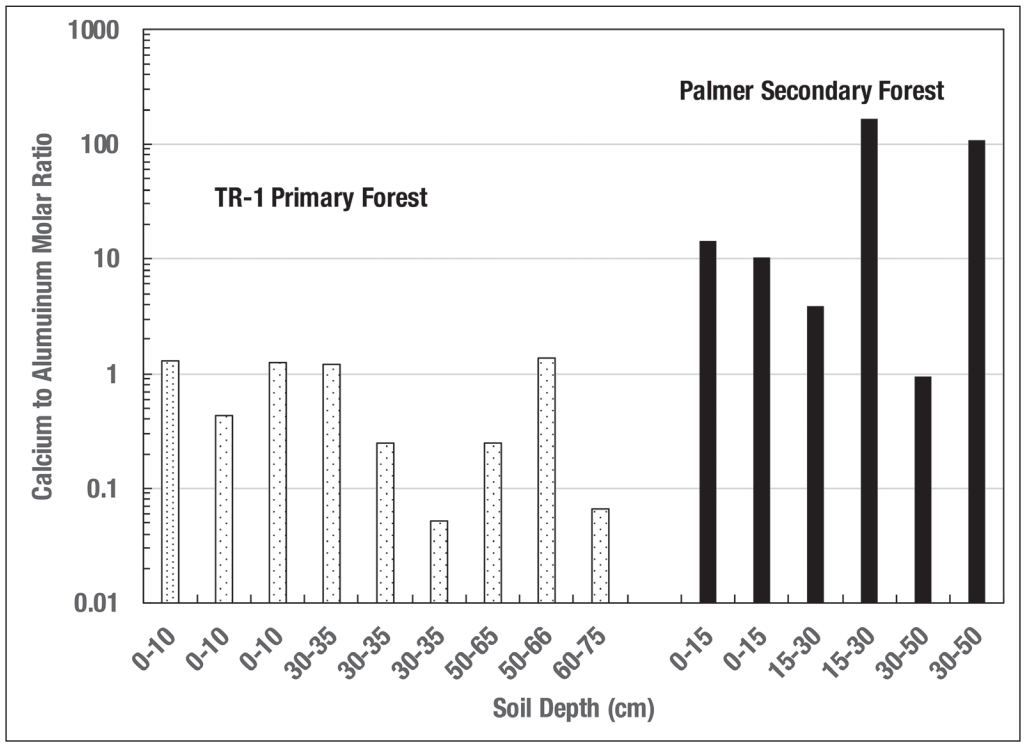

Figure 7. The Ca:Al molar ratio with soil depth at a secondary forest at Palmer dominated by *Tabebuia heterophylla* and a primary forest (TR-1) dominated by *Dacryodes excelsa*. The forests are in the Mameyes watershed, Luquillo Experimental Forest. Bars are arranged by depth and represent 3 soil pits at TR-1 and 2 at Palmer in 1989. Notice the vertical scale is logarithmic.

calcium or magnesium, root-induced increases in rhizosphere pH, release of aluminum-chelating ligands, malate release, cell-wall low cation exchange capacity, and others, including potential genetic resistance in some species. The tree must invest energy in the production and release of materials that influence the interaction with aluminum. This metabolic cost is a chronic investment of energy required for survival. Thus, we interpret the effects of chronic high aluminum concentration on trees as an energy tax on tree metabolism, whose cost depends on the level of toxicity and the metabolic capability of the species.

Response of the vegetation. Vegetation responds to low soil Ca:Al molar ratio by developing biomass with Ca:Al ratios well above 1. We found these values higher at TR-1 than at Palmer for loose-litter biomass (Table 8; see Table S-7 in Supplemental File 1). Leaf and fine wood litter materials had lower concentration of aluminum at TR-1 compared to at Palmer in bottom litter layers (Table S-2). These differences result in higher Ca:Al molar ratios at TR-1 than at Palmer (Table 8). The TR-1 vegetation concentrates more calcium in its biotic components and against a steeper concentration gradient of soil availability than vegetation at Palmer. This is the opposite trend observed in the soil chemistry with lower Ca:Al molar ratios at TR-1 compared to Palmer (Fig. 7). Higher Ca:Al molar ratios are more favorable to plant growth given the lower relative aluminum concentration but require energy to overcome the low soil calcium concentration. *Dacryodes* roots were shown to operate at a Ca:Al molar ratio of 3, a ratio much lower than that of leaves (Ca:Al = 15) in the same study (Bloomfield et al. 1993). The lower root Ca:Al ratio is still >1 and reflects the exposure to acid soils with low Ca:Al molar ratio.

Changes in mass and element storage

As expected, the secondary forest had rates of aboveground biomass accumulation (5.5 Mg/ha•yr; Table 7) that varied from 3 to 7 times faster than the primary forest and 2 to 3 times faster than a cutover *Dacryodes* stand (Briscoe and Wadsworth 1970). The min–max values of aboveground biomass accumulation rate for a cutover and a primary *Dacryodes* forest in the LEF between 1946 and 1966 were, respectively: 1.77 to 0.76 (1946–1956) and 3.16 to 1.71 (1956–1966) (Briscoe and Wadsworth 1970). Less expected was our finding of a combinded above- and belowgorund carbon sink of up to 4.8 Mg/ha•yr in the mature forest due to a larger soil carbon sink at TR-1 compared to Palmer (Table 7).

Soils at both sites behaved as carbon and chemical element sinks over the 26-year span of the study (Table 7). The soil sink levels were higher at TR-1 than at Palmer and reached 3.2 Mg/ha•yr for carbon and 0.19 Mg/ha•yr for nitrogen. In fact, over the period of study, soils in the primary forest increased the storage of all the elements that we measured. The TR-1 site maintained a net accumulation of elements at a rate that exceeded the annual elemental inputs except sodium in rainfall (Table 7) and the annual accretion rates measured in 3 watersheds at El Verde (McDowell and Asbury 1994). In contrast, soils in the secondary forest stored elements at a slower rate and had a net loss of calcium, magnesium, potassium, and sodium.

The net change (positive or negative) of soil elements reflect site conditions over the span of observation, and those balances can tilt either towards gains or losses

as has been observed in other forests. For example, over a span of 37 years, soils in northeastern Scotland lost bases (calcium, magnesium, potassium, and sodium) but gained aluminum because of atmospheric acidification, ecological demand, and soil pedogenic processes (Billett et al. 1990). In contrast, boreal forests in Canada fluctuated between gains, losses, and steady state over a 209-year span that involved fire at the beginning of the chronosequence (Hume et al. 2016). Over the first 3 decades post fire, the C:N:P dynamics in litter and soil showed rapid gains, like those we observed at Palmer following deforestation. However, in our case, we also lost bases, not to acid rain, but probably to greater leaching by rainfall due to low canopy interception as discussed above. Experiments show that rainwater alone can leach and erode potassium, calcium, and magnesium from soils (Barrows and Kilmer 1963).

Our comparative results provide insight into the mechanisms of carbon sequestration of mature systems. The aboveground biomass production in young forests is high as measured here in Palmer and decreases to low levels at maturity as measured at El Verde. However, reaching steady state carbon storage at the level of the biota is not inconsistent with continued net accumulation of carbon and elements in the soil, where necromass is decomposed. While most of the necromass is converted to carbon dioxide and water through decomposition, a fraction is recalcitrant mass that accumulates in the soil profile or is exported by runoff. Soil carbon accumulation in the soil profile of a *Dacryodes* forest down to 60-cm depth was confirmed experimentally by adding organic debris to the forest floor (Gutiérrez del Arroyo and Silver 2017). The soil functions as a long-term sink of carbon and other elements as shown here and discussed for the tropics by Lugo and Brown (1986).

Synthesis: The big picture

Biogeochemical niche. Peñuelas et al. (2019) suggested that each species has its own biogeochemical niche. This biogeochemical niche is a response to the chemical challenges posed by soil. Stoichiometry information revealed that the 2 study stands, while growing under similar environmental conditions, had significant differences in soil fertility measured by the ECEC (15.8 meq/100 g for Palmer vs 3.1 meq/100 g for TR-1; $P = 0.00086$) and concentrations of essential elements such as phosphorus. Stoichiometry also revealed that trees in one of the sites (TR-1) were growing under low soil pH, which caused the stress of low molar Ca:Al, high aluminum concentrations, and low phosphorus and potassium concentrations. Acid soils impose an energy tax on trees because the concentration of essential elements takes place against steep gradients of availability and because they must overcome the toxic effects of elements such as aluminum found in high concentrations in these soils.

In support of the biogeochemical niche of species, stoichiometry data discussed above revealed differences between sites in their molar element ratios of forest-floor loose litter. For leaf litter, for example, even though canopy leaves of *Tabebuia* and *Dacryodes* had the same C:N molar ratio (see Table S-8 in Supplemental File 1), their stoichiometry contrasted sharply after leaf fall and through the process of decomposition. The differences that occurred as recently fallen leaves fragmented and

decomposed over time, suggested different rates of mass decomposition and levels of storage and recycling of elements through this compartment.

Comparing species strategies. Growing on soils that are relatively less acid and more fertile, *Tabebuia* can concentrate essential elements to a higher degree and at a lesser metabolic cost than *Dacryodes*. High phosphorus, potassium, and calcium concentrations in *Tabebuia* correlate with faster tree growth in acidic tropical soils (Baribault et al. 2012), which helps the species dominate through early succession (Wadsworth 1943) and even share the canopy with *Dacryodes* later in succession (Ovington and Olson 1970). However, *Tabebuia* has no adaptation for growing under low light intensity and thus cannot regenerate under the closed canopy of a *Dacryodes* forest. High light energy is required to optimize its energy capture for maintaining stoichiometric element ratios and growth in acid soils.

Dacryodes was exposed at TR-1 to extremely acid soil, and responded by concentrating nitrogen and calcium against a steeper soil–plant gradient than *Tabebuia*. The chronic energy tax on its metabolism reduces the amount of potential energy available for growth. However, *Dacryodes* has low-light adaptation, its seedlings can grow under shade, and when hurricanes create intermediate light conditions in understories, *Dacryodes* saplings and poles can grow rapidly. Nevertheless, *Dacryodes* seeds and seedlings cannot germinate and grow under the open-pasture conditions that *Tabebuia* prefers. The failure of *Dacryodes* to grow in pastures has a stoichiometric explanation because *Dacryodes* seeds normally germinate, and seedlings grow, in humus with high levels of organic matter at low light intensity and high humidity. The low Ca:Al ratio of eroded soil coupled with lower organic matter and humidity and higher temperature in pastures is unfavorable for the ecesis of *Dacryodes*. Therefore, *Dacryodes* is absent in these environments. *Tabebuia* can grow under both conditions but loses dominance in later stages of succession when light limits its regeneration. Soil pH, by controlling nutrient availability and soil toxicity, tilts the balance of species success through the cost it imposes on their stoichiometric strategies.

Long-term strategies. On the long-term, mature stands of *Dacryodes* form tree unions (Basnet et al. 1993), which allow for the exchange of materials among trees (Bormann 1966) and develop an organic bench that promotes better aeration of root substrates and the concentration of essential elements, and results in greater resistance to hurricane winds (Basnet et al. 1993:figure 4). While concentrating essential elements is a significant response to dilute nutrient availability, we add that avoidance of the effects of aluminum toxicity and low Ca:Al ratios are also adaptive advantages of an organic bench.

The ultimate strategy for dealing with acid soils appears to be the isolation to the extent possible of biotic activity from the mineral soil by accumulating and recycling nutrients within trees or tree unions, and by elevating the forest floor through the accumulation of organic matter in the organic bench or tree mounds. The accumulation of soil organic matter also reduces the potential of aluminum toxicity (Khanna and Ulrich 1984) and allows for the cycling of essential elements under biotic control while reducing dependence on mineral soils. This strategy is supported by the findings of Zederer et al. (2017) in temperate *Fagus sylvatica* L.

(European Beech) and spruce *Picea abies* (L.) H. Karst. (Norway Spruce) forests on acidic soils. They found that microbial biomass (mostly fungi) in forest litter was higher than microbial biomass in mineral horizons and that this concentration of decomposers in litter could supply 16–47% of the annual phosphorus demand of the stands. They also found strict homeostatic regulation of microbial biomass C:N:P stoichiometry within the litter compartment, a decline in litter carbon to microbial biomass phosphorus ratio with litter depth, and abrupt change in the ratio in mineral soil where pH, aluminum, and iron factors came into play.

Potential linkage to evolution. Natural selection acts on alternative solutions to situations that affect the performance of populations or systems of greater complexity. In the case of stoichiometric situations, McGroddy et al. (2004) found alternative solutions at the leaf-metabolism and ecosystem levels, responding respectively to local and global constrains on nutrient cycles. They argued that "to the degree that variations in physiological strategies are shaped by differences in nutrient availability, they offered evidence for ecosystem- or biome-scale selection for plant nutrient-use strategies at the individual plant level" (McGroddy et al. 2004:2399). The response can also occur with species-composition changes over time and space. McGroddy and colleagues saw this as ecosystem-scale selection on local biodiversity. More recently, Leal et al. (2017) outlined the mechanisms by which stoichiometric phenotypes could bridge the fields of ecology and evolution at the ecosystem level. Our study contributes to this narrative by highlighting soil conditions, specifically acidity, as a strong selective force on whole-ecosystem stoichiometric response. Soil acidity constrains nutrient availability and imposes chemical stress on trees by its effects on phosphorus availability and aluminum toxicity, among others.

The contrasting stoichiometric responses of *Dacryodes* and *Tabebuia* represent alternative solutions to the environmental challenge of concentrating, storing, and recycling elements in support of harnessing solar energy for growing and maintaining forest structure. However, the environmental challenge is more severe at TR-1 than at Palmer given the greater acidity of its soil. The contrasting stoichiometric strategies involve different element ratios, particularly N:P and C:P, that lead to faster mass turnover and net productivity at Palmer compared to TR-1, where higher soil-element storage and lower net productivity prevail. The selective pressure on the system would be the cost associated with overcoming the limitations imposed by acidity; the greater the acidity, the higher the cost of buffering it. The feedback from the functional outcome of the response to evolutionary change would be the level of net energy remaining in each system for growth and maintenance. Selection will benefit stoichiometric solutions that maximize the solar power conversion of the system, as all ecological systems depend on solar energy to maintain their ecological processes.

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