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Predominant climate control on green leaf decomposition across subtropical rain and dry forests following hurricane disturbances

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ABSTRACT

Hurricanes defoliate canopy and break tree branches and stems, generating large amount of plant debris in forest ecosystems. Forest recovery after hurricane disturbances relies heavily on the decomposition of these plant debris. Here we addressed the "tropical hierarchy of factors" hypothesis that substrate quality replaces climate as the predominant control on plant litter decomposition in tropical forests. We compared leaf decomposition between subtropical rain and dry forests on the island of Puerto Rico by reciprocally transplanting green-leaf litter between rain (*Eugenia borinquensis* leaves with higher C/N) and dry (*Bucida buceras* leaves with lower C/N) forests following hurricanes Irma and Maria. We show that leaf decomposed substantially faster in subtropical rain than dry forests, and for high-than low-quality substrates. Over a period of 536 days of field incubation, loss of leaf ash-free dry mass was 51.8% for *B. buceras* and 26.6% for *E. borinquensis* in the rainforest, 15.7% for *B. buceras* and near zero for *E. borinquensis* in the dry forest. We also found that soil arthropod density was more than 10-folds greater in the rainforest than in the dry forest and was only more than 2-folds greater in the low C/N litterbags than the high C/N litterbags. Analyses of structural equation model revealed that leaf decomposition rate correlated positively with total arthropod abundance in the rainforest and only with Oribatida abundance in the dry forest. The number of effective linkages among leaf C/N, precipitation and arthropods was greater in the subtropical rainforest (19) than in the dry forest (4), but did not vary between *B. buceras* (12) and *E. borinquensis* (11) substrates in the rainforest. We conclude that climate, rather than substrate quality, remains to be the predominant control on leaf decomposition across subtropical rain and dry forests following hurricane disturbances, and the controls of substrate quality on leaf decomposition is inferior and climate dependent.

1. Introduction

Litter decomposition in terrestrial ecosystems is an important process in carbon and nutrient cycling (Austin et al., 2014) and in the recovery of forests after anthropogenic (Grau et al., 2003) and natural disturbances (McDowell et al., 2015). While litter production is primarily controlled by forest productivity, it can drastically be affected by hurricane disturbances. Hurricanes can generate plant debris in amount equivalent to the annual litterfall production (Liu et al., 2018a). Furthermore, hurricanes generate high quality green leaf litter that is rich in nutrients (Lodge et al., 1991; González et al., 2014). The altered temporal pattern of plant litter production and elevated litter quality can impose substantial influence on carbon and nutrient cycling in subtropical and tropical forests following hurricane disturbances (Brokaw el al., 2015). The predicted increases in the frequency and intensity of hurricanes as global climate warms (Tartaglione et al., 2003; Mann and Emanuel, 2006; Donnelly and Woodruff, 2007)) would further enhance the alteration of plant litter production and litter quality in tropical forests.

The decomposition of plant litter is governed by three factors namely: climate, substrate quality and biota (Meentemeyer, 1978; Bradford et al., 2016). While climate is viewed as the predominant factor regulating litter decomposition rates at global and cross-regional scales (the "general hierarchy of factors" hypothesis), litter quality is presumed

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to take precedence as a dominant control of decomposition at local scale within a particular climatic region as the "tropical hierarchy of factors" hypothesis (Aerts, R., 1997; Lavelle et al., 1993). The controls of either climate or substrate quality on decomposition are realized through altering biota and their activity. Soil fauna has been identified as one of the important drivers of litter decomposition, enhancing litter decomposition by 35% at a global scale (García-Palacios et al., 2013). The mean effect size of soil fauna on litter decomposition varies from 13% in temperate coniferous forests to 66% in a tropical wet forest (Wall et al., 2008), suggesting a strong climate control. Several studies have recorded a stronger positive effect of soil fauna on litter decomposition in areas with higher total precipitation and minimum temperature (González and Seastedt, 2001; Wall et al., 2008). Furthermore, there is also considerable variability in the effect sizes of soil fauna on litter decomposition within biomes (Swift et al., 1979), suggesting regulations by substrate quality and edaphic conditions. There are now several strands of evidence showing that high quality litter (e.g. lower litter C/N) promotes faster decomposition when soil fauna were present (Frouz et al., 2015).

Climate and litter quality not only affect faunal abundance, but also drive inner connections of soil faunal community, thus litter decomposition. Temporal and spatial variations in precipitation influenced soil invertebrate activity and community composition by changing soil food web structure (Nielsen and Ball, 2015). The complexity (e.g., the number of links) of food webs increases from the poles toward the equator, supporting the notion that more complex food webs are found in the tropics where decomposition is the fastest (Newth, 2008). Wall et al. (2008) suggested that faunal influence on litter decomposition was hampered in harsh environmental conditions. Furthermore, changing resource quality can cause modifications in the structure, dynamics, and activities of the soil food web (Chauvin et al., 2015) through bottom-up trophic cascades (Hunter and Price, 1992). For example, food web interactions were observed to decrease when litter recalcitrance (e.g., C/N ratio) increased (Sauvadet et al., 2016). Few studies have been carried out to study how complexity of linkages among climate, substrate quality and soil fauna affects litter decomposition (Handa et al., 2014).

Lavelle et al. (1993) and Aerts (1997) hypothesized that climate no longer plays a predominant role in decomposition within a particular climate, especially in humid tropical rainforests and savannas; instead, biological mutualistic interactions and substrate quality are likely to play a more important role in litter decomposition. This "tropical hierarchy of factors" hypothesis has not been explicitly tested across a wide precipitation gradient from tropical dry to rain forests with a controlled experiment in the tropics yet. Under tropical and subtropical climate conditions, temperature is usually not a constraint for biological activity, but precipitation may become a limiting factor, suggesting that climate may remain as a major factor limiting biological activities and litter decomposition. For example, although seasonal mean minimum and maximum temperatures in subtropical forests of Puerto Rico, a small Caribbean Island with a total land area of 9,104 km^2, vary between 16.5 and 32.6 °C (Malmgren and Winter 1999), annual precipitation ranges from less than 1000 mm in a subtropical dry forest (Murphy and Lugo, 1986) to more than 6,000 mm in a subtropical rainforest over a short distance of about 100 km (McDowell et al., 2015). While seasonal variations in microbial biomass (Liu et al., 2018b) and soil arthropod abundance (Heneghan et al., 1998; González and Seastedt, 2000) were subtle in the tabonuco subtropical wet forest of Puerto Rico, these variations were profoundly increased for both soil microbial biomass (Liu and Zou, unpublished data) and arthropod abundance (González and Seastedt, 2000) in a subtropical dry forest in Guánica. Therefore, variation in precipitation within subtropical climate in Puerto Rico may play a dominant role in regulating biological activity thus litter decomposition.

Hurricanes Irma and Maria crossed Puerto Rico in September of 2017 and generated large quantity of plant litter (Liu et al., 2018a) including green leaves with substantial higher nutrient concentrations than brown leaf litter (Lodge et al., 1991; González et al., 2014). We therefore designed this study to compare green leaf decomposition between subtropical rain and dry forests of Puerto Rico by reciprocally transplanting green leaf litter (to resemble the hurricane effect) between rain (higher C/N leaf) and dry (lower C/N leaf) forests following hurricane disturbances. We asked questions: (1) what was the relative importance of climate and leaf C/N in litter decomposition after hurricanes within subtropical forests in Puerto Rico? and (2) how do climate and substrate quality jointly structure the complexity of soil interactions (i.e. corresponding changes among abiotic and biotic factors) in decomposition? We tested the following hypotheses: (H1) climate, rather than C/N, remains as the predominant control on leaf decomposition across subtropical rain and dry forests following hurricane disturbances; and (H2) high precipitation and low leaf C/N enhance the complexity of arthropod community structure and their interactions, and consequently the leaf litter decomposition.

2. Material and methods

2.1. Study sites

Two sites representing wide ranges in subtropical climate as measured by precipitation, relative air humidity and ultraviolet (UV) radiation were chosen in subtropical forests of Puerto Rico: a rainforest and a dry forest (Fig. 1, Fig. S1).

The subtropical rainforest is located in Pico del Este of the Luquillo Experimental Forest (also known as El Yunque National Forest), northeastern Puerto Rico (18°16′38.64" N, 65°45′51.34" W), elevation is 1025 m. Mean annual air temperature is 19.3 °C, mean annual air relative humidity is 98.6%, and mean annual precipitation is 4529 mm distributed more or less evenly throughout the year (Weaver et al., 1986). During the study period between 12 December 2017 and 31 May 2019, the accumulative precipitation was 6516 mm (Fig. 1a), and UV radiation under the canopy of this forest ranged between 0.29 and 1.35 W/m^2. Vegetation at this elevation is described as elfin woodland, dominated by *Eugenia borinquensis*, *Cyathea bryophila*, *Ocotea spathulata*, *Tabebuia rigida, Micropholis garciniifolia, Calyptranthes krugii,* and *Henriettea squamulosum* (Gould et al., 2010). The soils are Ultisols, and the bulk density of soil A layer is 0.5–0.6 g/cm^3 (Ping et al., 2013). Forest floor mass decreased steadily from 670.3 g/m^2 on 6 April 2018 (after hurricanes Irma and Maria in Sept 2017) to 175.0 g/m^2 on 4 June 2019 (Fig. 1d) with forest floor mass C/N ranging from 42.4 to 58.1 (Fig. 1e).

The subtropical dry forest is located in the Guayama Research Area, southeastern Puerto Rico (18°02′18.31'' N, 66°10′08.27'' W) with an elevation of 311 m. Mean annual air temperature is 24.6 °C, mean annual air relative humidity is 78.8% with a mean annual precipitation of 809 mm and a relatively dry period from December to March. During the period of this study, the subtropical dry forest received roughly 20% accumulative precipitation and 75% dose of UV radiation as the subtropical rainforest (Fig. 1c). Water stress in the subtropical dry forest can be further intensified immediately after hurricanes due to the accelerated evaporation (Liu et al., 2018a). The most abundant tree species are *Bucida buceras*, *Casearia guianensis*, *Pictetia aculeate*, *Nectandra coriacea*, *Andira inermis*, *Guapira fragrans*, and *Randia aculeata*. The soils are generally composed of shallow Typic Haplustalfs. Bulk density of the soil A layer is 0.95 g/cm^3. Forest floor mass decreased initially after the hurricanes then peaked again on 5 September 2018 likely due to the delayed litterfall from the hanging branches and fallen trees after hurricanes (Fig. 1d). Forest floor mass of the dry forest was significantly lower than that in the rainforest before July 2018 and was higher after June 2019. Forest floor mass C/N of the dry forest was significantly lower than that of the rainforest over the time period of this experiment (Fig. 1e).

Hurricane Maria made landfall as a strong Category 4 storm with maximum sustained winds of ~250 km h^{-1} near Yabucoa Harbor in far southeast Puerto Rico on 20 September 2017 (Fig. S1, Van Beusekom

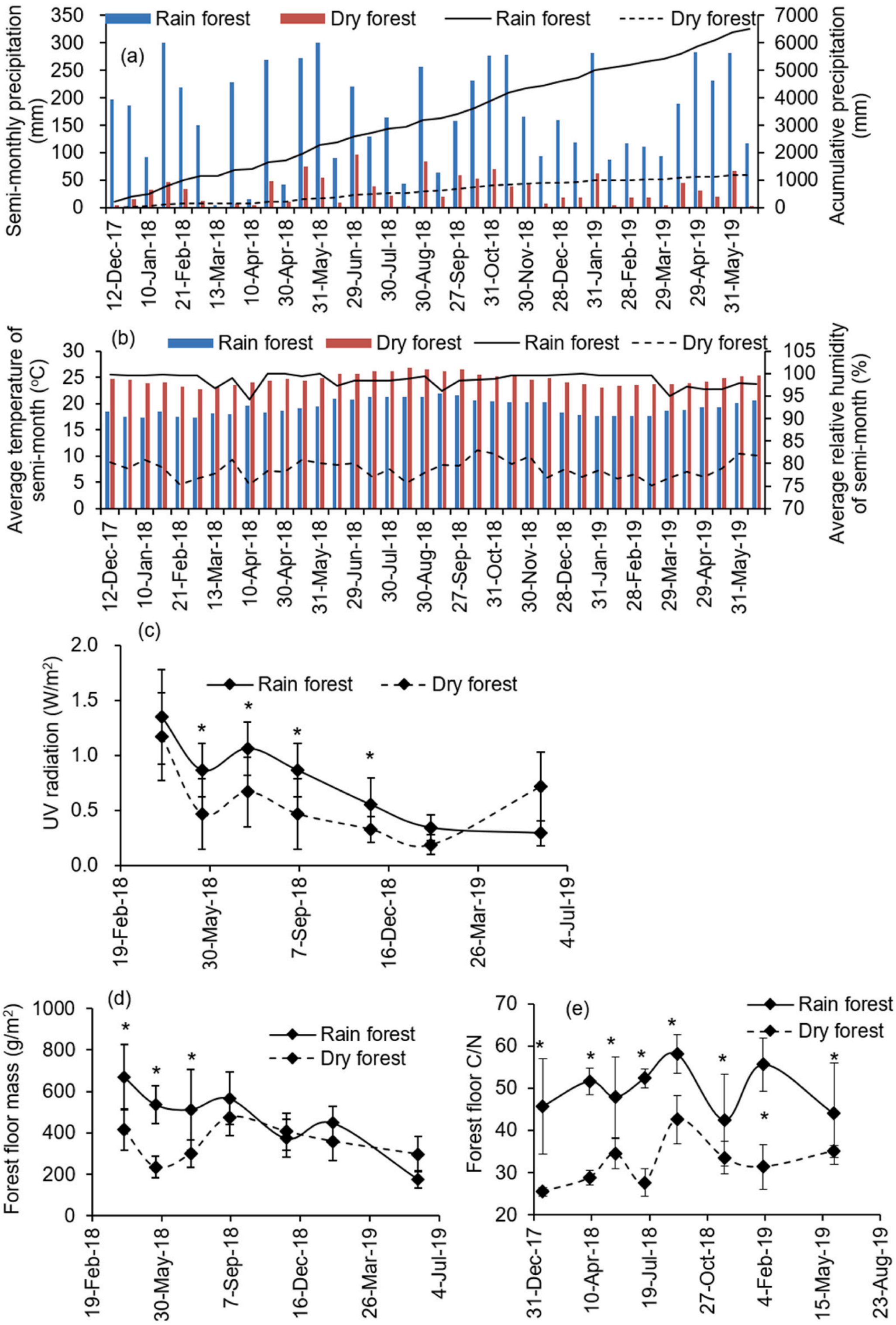

Fig. 1. Climate characteristics (a: semi-monthly precipitation and cumulative precipitation; b: mean air temperature and relative humidity of semi-month), (c) ultraviolet dose, (d) forest floor mass, and (e) forest floor C/N for each forest during the experiment in subtropical rain and dry forests of Puerto Rico. Asterisks indicate a significantly differences between two forests (one-way ANOVA; α = 0.05).

et al., 2018). Hurricane Maria crossed Puerto Rico in a northwest direction, exiting near the city of Arecibo and causing widespread effects across the island (Van Beusekom et al., 2018), including the Luquillo Mountains. Two weeks earlier on September 6th, Category 5 hurricane Irma had passed within ~80 km north of the island, with sustained winds of ~300 km h^{-1}, and affected primarily the northeast region of the island including our rainforest study site at Pico del Este (Van Beusekom et al., 2018). It has been estimated that 23 to 31 million trees were severely damaged or killed in Puerto Rico by hurricane Maria. In the Luquillo Experimental Forest and Guayama Research Area, all plant species were totally defoliated including both canopy tree species and understory shrubs, except for a few understory shrubs and vines with partial defoliation, and the crown of most canopy tree species was severely broken (Liu et al., 2018a; Uriarte et al., 2019). Total hurricane-induced litterfall from hurricanes Irma and Maria amounted to 161% and 125% of the annual litterfall production prior to the hurricanes in the Luquillo Experimental Forest and the Guayama Research Area, respectively (Liu et al., 2018a).

2.2. Litterbags and invertebrate collection

We collected green leaves of *E. borinquensis* and *B. buceras* mostly from the fallen branches and trees in the subtropical rain and dry forests within four weeks after the passage of hurricane Maria in September 2017, respectively. The importance value of *E. borinquensis* was 22.6 in the rainforest, and that of *B. buceras* was 47.9 in the dry forest (Gould et al., 2010; Zeng, 2019). The green leaves were used to simulate the large amounts of green leaf litterfall from the hurricanes, which has higher nutrient concentrations than naturally senesced leaves litter because of not undergoing resorption before falling (Brant and Chen, 2015). Nutrient concentrations in *E. borinquensis* were 0.55 g/kg for P, 8.88 for K, 2.96 for Ca, and 1.60 for Mg, with a C/N of 62 and N/P of 33; and in *B. buceras* were 0.55 g/kg for P, 10.41 for K, 18.8 for Ca, and 2.02 for Mg, with a C/N of 31 and N/P of 50 (Sánchez et al., 2015). We used C/N ratio as a proxy of substrate quality with low C/N as high substrate quality (Krishna and Mohan, 2017). We placed 10 g air-dried *E. borinquensis* or *B. buceras* leaves in each of 15 × 15 cm fiberglass litterbags (1.5 × 1.5 mm mesh size). Leaf C/N of *E. borinquensis* was twice that of *B. buceras* (Fig. 2d). This mesh size allows access by meso- and micro-fauna, and transmission of >73% solar radiation.

We selected 3 sites within an area of approximately 30 × 30 m within each forest to represent micro-site variations from ridge to slope areas. Our leaf mass and soil faunal data did not reveal significant differences among the micro-site topographical variation, thus we eliminated topographical position as a driver in this study. Within each site, we further selected 4 incubation-subsites at least 3 m apart, and each was placed with an aluminum frame of 120 cm × 60 cm × 20 cm (l × w × h). Two frames were randomly assigned to cover with UV-blocking and the other two with UV-passing plastic panels to elucidate the effect of UV radiation from other climate variables on litter decomposition (Huang et al., 2020) after the canopy opening following hurricanes. The UV transparent acrylic (which passes 90% of the solar spectrum, including UV-A and UV-B, Solacryl SUVT, Spartech Polycast, Stamford, Connecticut, USA) or UV non-transparent polycarbonate (hereafter UV block, which blocks 90% of UV-A and UV-B, optically equivalent to Lexan XL-1, GE, Pittsfield, Massachusetts, USA) panels (120 cm × 60 cm) were used because they effectively pass and block, respectively, UV radiation without substantially affecting temperature or photosynthetically active radiation (Brandt et al., 2007). To minimize the UV panel effect on microclimate, we drilled 21 holes (12.5 mm in diameter) in each of the UV panel at a spacing of 15 cm to allow for rainfall input and vertical air exchange. To minimize edge effects, we placed litterbags of both species in the central 45 cm × 90 cm area under each plastic sheet with eight litterbags from each species on 15 December 2017 in the rainforest and on 13 December 2017 in the dry forest. Two 6-inch nails were used to anchor each litterbag to the ground. A total of 192

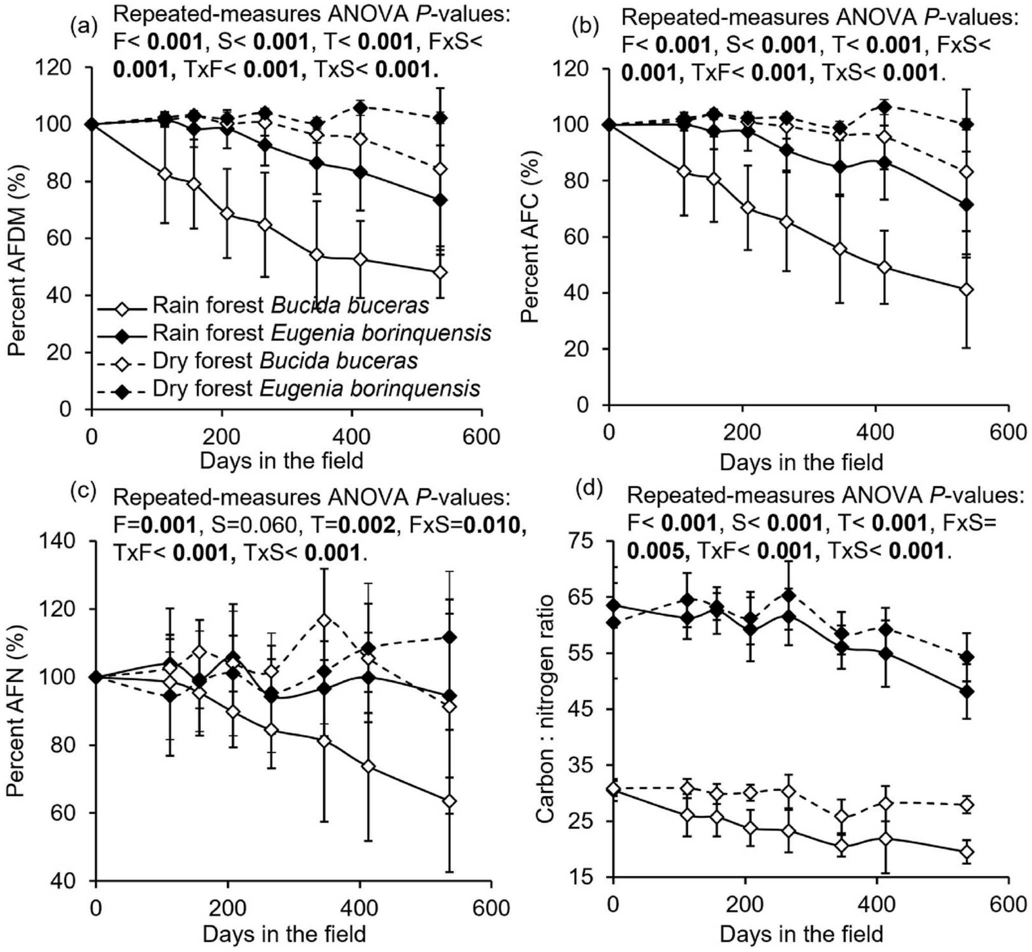

Fig. 2. Change in leaf percent ash-free (a) dry mass, (b) carbon, and (c) nitrogen remaining, and (d) C/N of *Bucida buceras* and *Eugenia borinquensis* leaves in subtropical rain and dry forests of Puerto Rico. Error bars denote standard deviation (n = 12). AFDM – ash-free dry mass remaining, AFC – ass-free carbon remaining, AFN – ash-free nitrogen remaining, F – the effect of forest type, S – the effect of leaf species, T-the effect of time, bold highlights significance level ($P < 0.05$).

litterbags were placed in each forest (2 species × 2 UV treatments × 2 replicates/site/treatment × 3 sites × 8 collections/species). Litterbags were recovered after 0, 112, 157, 208, 226, 346, 431 and 536 days in the field. Floor mass litter was collected at the same time as the litterbags in an 250 × 250 mm area near each of panel structure with a wooden board placed on the ground and a knife to cut around the edges to separate the surrounding floor mass, and then oven-dried to obtain dry weight (González and Seastedt, 2001). The initial set of litterbags was collected and returned to the laboratory immediately after its placement in the field. These bags were oven-dried at 65 °C to establish handling loss (González and Seastedt, 2001). For each of the other 7 sampling dates, arthropods from each bag were first extracted using Tullgren funnels (Bioquip 2845) as described in Huang et al. (2020). After arthropod extractions, the leaf samples were oven-dried then grinded to obtain ash-free mass loss and for chemical analyses (Huang et al., 2020). The collected arthropods were counted, measured for body length, and identified to morphospecies. Arthropod biomass was estimated using arthropod length in equations for estimation of arthropod biomass from previous studies (Schoener, 1980; Hódar, 1996; Richardson et al., 2000; Gruner, 2003). Arthropod densities were standardized to individuals per gram of ash-free leaf dry mass. Arthropod diversity was compared among treatments and over time using Shannon-Weiner index and Simpson's reciprocal index. Because leaf ash-free dry mass remaining, total arthropod density, biomass and biodiversity index were not significantly affected by the UV treatments, we therefore present our results by pooling data from UV-block and UV-pass treatments for all analyses with a total of 12 replicates.

2.3. *Chemical analysis*

Leaf samples were re-dried at 65 °C and ground to pass through an 18-mesh sieve. Total C and N for the leaf samples were determined using the macro dry combustion method by means of the LECO TruSpec CN Analyzer at the USDA IITF Chemistry Laboratory in Río Piedras. Ash content of the leaf litter samples was also determined at 490 °C using the LECO TGA 701 Analyzer. We estimated the litter ash-free dry mass (AFDM) remaining as dry mass minus the ash mass to avoid any soil contamination.

2.4. *Data analysis*

Percent of ash-free dry mass (PAFDM) remaining was calculated by:

$$\text{PAFDM} = \frac{M_t}{M_0} \times 100 \tag{1}$$

where M_t is the ash-free dry mass in a litterbag at time t (here $t = 112$, 157, 208, 226, 346, 431 or 536 days), and M_0 is its ash-free dry mass (g) at time 0.

Percent ash-free carbon (PAFC) or nitrogen (PAFN) remaining was described by:

$$\text{PAFC or PAFN} = \frac{C_t \times M_t}{C_0 \times M_0} \times 100 \tag{2}$$

where C_t is litter C or N concentration (mg/g) in AFDM at time t, C_0 is its C or N concentration (mg/g) in AFDM at time 0.

Relative differences in percent ash free remaining dry mass caused by climate ($\triangle \text{PAFDM}_\text{C}$) between the rain and dry subtropical forests for either Bucida buceras (BB) or *Eugenia borinquensis* (EB), or by substrate quality ($\triangle \text{PAFDM}_\text{SQ}$) between BB and EB in either the rain or dry subtropical forests were calculated as:

$$\Delta PAFDM_{Ci} = \frac{PAFDM_{Di} - \overline{PAFDM_R}}{\overline{PAFDM_R}} \times 100 \tag{3}$$

$$\Delta PAFDM_{SQi} = \frac{PAFDM_{EBi-} - \overline{PAFDM_{BB}}}{\overline{PAFDM_{BB}}} \times 100 \tag{4}$$

where PAFDM_Di represent percent ash free dry mass remaining in the ith replicate (here i = 1, 2, …, 12) at the end of field incubation in the dry forest, $\overline{\text{PAFDM}_\text{R}}$ represent average percent ash free dry mass remaining at the end of field incubation in the rainforest; PAFDM_EBi represent percent ash free dry mass remaining of EB litter in the ith replicate at the end of field incubation, and $\overline{\text{PAFDM}_\text{BB}}$ represent average percent ash free dry mass remaining of BB litter at the end of field incubation.

Similarly, relative differences in percent arthropod density and arthropod Shannon-Weiner index caused by climate or substrate quality were likewise calculated using equations (3) and (4).

One-way analysis of variance (ANOVA) was employed to determine whether differences existed in: (1) initial C/N between the two leaf species; (2) UV doses, forest floor mass and forest floor C/N between the two sites at each litterbag collecting time; (3) mean densities of the main arthropod groups, total arthropod density, arthropod biomass and arthropod diversity indices between the two forests for the same leaf species; (4) mean densities of the main arthropod groups, total arthropod density, arthropod biomass and arthropod diversity indices between two leaf species within a common forest; and (5) the effect of climate on leaf mass remaining and soil biota for *Bucida buceras* and *Eugenia borinquensis*, and the effect of substrate quality on leaf mass remaining and soil biota in the rain and dry forests. A repeated measures ANOVA model was conducted to assess how forest types (rain vs. dry), substrate quality (leaf species) and days in the field influence: (1) the leaf *PAFDM*; (2) *PAFC* and *PAFN*, leaf *C/N* during decomposition; and (3) arthropod density, arthropod biomass, and arthropod diversity indices. The interactions between forest type × leaf species, days in the field × forest type, and days in the field × leaf species were considered. All data were tested for homogeneity of variance using the Levene's test of equality of error variances, and skewness. Log transformations were employed when the data did not meet the assumptions of normality. All ANOVA and Levene's test were conducted using JMP Pro 14.0 (SAS Institute, Cary, USA).

We used structural equation modelling (SEM) to disentangle linkages and relative importance among leaf C/N, precipitation, and arthropod communities as drivers of leaf PAFDM. This technique starts with the development of a priori model that features variables and hypothesized causal relationships among them in a path diagram. Four sets of SEM models were constructed to compare effective linkages and relative importance of different drivers/nodes in the rain and dry forests, and for *E. borinquensis* and *B. buceras* leaves in the rainforest, respectively. The same a priori model was hypothesized for both rain and dry forests, and for both *E. borinquensis* and *B. buceras* species. The influences of microclimate and leaf C/N on leaf PAFDM were evaluated with both direct (mass remaining) and indirect (changes in the composition and abundance of litter arthropods) measures. We tested the fit of the a priori model against the field data. To increase the degrees of freedom and establish effective linkages, any paths with a coefficient <0.10 was removed from the model when not significant. A driver/note is removed when there is a zero effective linkage. The "Modification indices" function of Amos was used to improve the fit of models. A combination of non-significant chi-square (χ^2) test, comparative fit index (GFI) and root mean square error of approximation (RMSEA) were used to find an acceptable structural equation mode with "valid drivers/nodes" and "effective linkages/arrows". All SEM analyses were performed with Amos 24.0 (Amos Development Co., Armonk, NY, USA).

3. Results

There were significant effects of forest type, leaf species, and the interaction between forest type × leaf species, days in the field × forest type, and days in the field × leaf species on leaf PAFDM (Fig. 2a). Leaves decomposed substantially faster in the rainforest than in the dry forest for both leaf species, and *B. buceras* leaves also decomposed faster than *E. borinquensis* leaves in both forests. Leaf PAFDM at 536 days ranged from a low of 42.1 ± 21.2% for *B. buceras* in the rainforest to a high of near 100% for *E. borinquensis* in the dry forest.

There were significant effects of forest type, leaf species, and the interaction between forest type × leaf species, days in the field × forest type, and days in the field × leaf species on leaf PAFC and C/N (Fig. 2b and d). There was also significant effect of forest type, and the interaction between forest type with leaf species on leaf PAFN (Fig. 2c). Leaf PAFC showed a similar variation pattern as leaf PAFDM. There was a significant decrease in PAFN for *B. buceras* leaves, but not for *E. borinquensis* leaves, during the course of decomposition in the rainforest. By the end of field incubation, leaves of *E. borinquensis* and *B. buceras* in the dry forest exhibited greater than the initial amount PAFN, and leaf C/N of *E. borinquensis* was more than twice that of *B. buceras* (Fig. 2d). Leaf C/N of both species was higher in the dry forest than in the rainforest during the entire course of decomposition.

The abundance and diversity of arthropod recovered from litterbags were a magnitude higher in the rainforest than dry forest and were more than twice those in *B. buceras* than *E. borinquensis* litterbags (Tables 1–3). Arthropod community structure differed between the rain and dry forests. In addition to mites, Collembola, Isopoda and Diplopoda were dominant orders in the rainforest, accounted for 44% arthropod density in *B. buceras* litterbags and 23% arthropod density in *E. borinquensis* litterbags; while Araneae, Psocoptera and Hymenoptera were the dominant orders in the dry forest, accounting for 60% arthropod density in *B. buceras* litterbags and 70% arthropod density in *E. borinquensis* litterbags. Isopoda, Diplopoda, Uropygi, Opiliones, Scolopendromorpha, Pseudoscorpiones and Hemiptera were found only in the rainforest, but not in the dry forest. Arthropod community structures differed between *E. borinquensis* and *B. buceras* litterbags in the rainforest. Oribatida was the most abundance group collected from *E. borinquensis* litterbags in the rainforest, which account for 34% of the total arthropod density. Isopoda and Diplopoda accounted only for 3% and 5% of total arthropod density in *E. borinquensis* litterbags in the rainforest, respectively. In comparison, Collembola was the most abundant group collected from *B. buceras* litterbags in the rainforest, accounting for 22% of total arthropod density, and Isopoda and Diplopoda accounted for 10% and 12% of total arthropod density, respectively.

Table 2

Mean arthropod biomass (mg/g leaf ash-free dry mass), Shannon-Weiner Index and Simpson's reciprocal Index for *B. buceras* and *E. borinquensis* litterbags in subtropical rain and dry forests of Puerto Rico.

	Rainforest		Dry forest	
	Bucida buceras	*Eugenia borinquensis*	*Bucida buceras*	*Eugenia borinquensis*
Arthropod biomass	30.27 ± 7.64 a*	10.98 ± 3.62 A	2.83 ± 1.47 b*	0.21 ± 0.06 B
Shannon-Weiner Index	1.79 ± 0.83 a*	1.36 ± 0.85 A	0.47 ± 0.23 b*	0.15 ± 0.03 B
Simpson's reciprocal Index	13.84 ± 1.34 a*	8.80 ± 1.10 A	0.84 ± 0.27 b*	0.15 ± 0.06 B

Values are means ± SD (n = 12). Lowercase letters show statistical difference (at α = 0.05) between the rain and dry forests for *B. buceras* litterbags. Capital letters show statistical differences between the rain and dry forests for *E. borinquensis* litterbags. An asterisk (*) indicates significant difference between the litter species within a forest site.

The relative difference in PAFDM of *B. buceras* leaves between the rain and dry forests (Fig. 3a) was the highest (129.2%), followed by the relative difference in PAFDM between the two leaf species in the rainforest (80.2%), and again followed by the relative difference in PAFDM of *E. borinquensis* leaves between the rain and dry forests (39.3%). The

Table 1

Mean (numbers per 100 g leaf ash-free dry mass) and relative (%) densities of taxonomic groups of arthropods in *B. buceras* and *E. borinquensis* litterbags in subtropical rain and dry forests of Puerto Rico.

	Rainforest				Dry forest			
	Bucida buceras		*Eugenia borinquensis*		*Bucida buceras*		*Eugenia borinquensis*	
	numbers per 100 g leaf ash-free dry mass	%	numbers per 100 g leaf ash-free dry mass	%	numbers per 100 g leaf ash-free dry mass	%	numbers per 100 g leaf ash-free dry mass	%
Oribatida	68.93 ± 42.99a	18.67	48.24 ± 18.84A	34.17	1.81 ± 1.17b*	7.05	0.30 ± 0.06B	2.60
Prostigmata	41.71 ± 6.35a*	11.24	19.02 ± 3.61A	14.23	1.82 ± 0.23b*	7.69	0.60 ± 0.11B	5.19
Mesostigmata	43.77 ± 26.88a*	10.69	13.45 ± 6.30A	9.67	0.63 ± 0.08b*	2.56	0B	0
Collembola	81.12 ± 41.66a*	22.35	20.72 ± 14.67A	15.36	2.19 ± 0.26b*	8.97	0.46 ± 0.11B	3.90
Psocoptera	4.82 ± 0.41*	1.60	1.23 ± 0.18A	0.93	2.87 ± 0.28	13.46	2.86 ± 0.23B	24.68
Coleoptera	6.59 ± 0.69a	1.73	3.46 ± 0.51A	2.65	1.06 ± 0.14b*	4.49	0B	0
Hymenoptera	6.58 ± 1.16a*	1.87	2.63 ± 0.36A	1.19	2.92 ± 0.57b*	12.18	0.47 ± 0.08B	3.90
Araneae	10.51 ± 1.07*	2.71	5.20 ± 0.62	3.58	8.17 ± 5.34*	34.62	4.86 ± 3.98	41.56
Pseudoscorpiones	4.02 ± 0.76a*	1.11	1.02 ± 0.32A	0.66	0b	0	0B	0
Isopoda	42.23 ± 28.37a*	9.92	4.73 ± 1.67A	3.05	0b	0	0B	0
Diptera	3.21 ± 0.34a	0.83	3.00 ± 0.32A	2.12	0.43 ± 0.07b*	1.92	1.36 ± 0.01B	11.69
Thysanoptera	0.20 ± 0.08	0.07	0A	0	0.15 ± 0.05	0.64	0.44 ± 0.07B	3.90
Uropygi	1.98 ± 1.28a*	0.49	0.52 ± 0.08A	0.40	0b	0	0B	0
Orthoptera	0.21 ± 0.09*	0.07	1.26 ± 0.21A	0.93	0.30 ± 0.06	1.28	0B	0
Blattodea	6.43 ± 1.86a	1.73	7.05 ± 1.45A	4.50	0.61 ± 0.11b*	3.21	0.15 ± 0.04B	1.30
Diplopoda	47.35 ± 28.37a*	11.87	7.68 ± 3.79A	5.03	0b	0	0B	0
Homoptera	0	0	0.37 ± 0.08	0.26	0.16 ± 0.04	0.64	0.15 ± 0.05	1.30
Diplura	7.46 ± 2.13a*	1.87	0.72 ± 0.14A	0.53	0b	0	0B	0
Hemiptera	0.27 ± 0.14a	0.07	0.32 ± 0.05A	0.13	0b	0	0B	0
Opiliones	0*	0.83	0.19 ± 0.07A	0.13	0b	0	0B	0
Scolopendromorpha	0.53 ± 0.01a	0.14	0.21 ± 0.07A	0.13	0b	0	0B	0
Microcoryphia	0.36 ± 0.10a	0.07	0	0	0b	0	0	0
Isoptera	0.36 ± 0.10	0.07	0	0	0.16 ± 0.05	0.64	0	0
Total arthropod density	382.30 ± 127.99a*		142.55 ± 50.69A		23.71 ± 8.44b*		11.65 ± 4.81B	

Values are means ± SD (n = 12). Different lowercase letters show statistical differences (at α = 0.05) between the rain and dry forests for arthropods in *B. buceras* litterbags. Different capital letters show statistical differences between the rain and dry forests for arthropods in *E. borinquensis* litterbags. Significance differences between two leaf litter species within a forest site are shown by an asterisk (*).

Table 3
Repeated-measures ANOVA *P*-values for the effects of forest site (F), leaf species (S) and time of sampling (T) on total arthropod density and biomass, diversity indices, recovered from *B. buceras* and *E. borinquensis* litterbags in subtropical rain and dry forests of Puerto Rico.

	F	S	T	F x S	Tx F	T x S
Arthropod density	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.077
Arthropod biomass	**<0.001**	0.170	0.150	0.255	0.182	0.220
Shannon-Weiner Index	**<0.001**	**<0.001**	**<0.001**	0.405	**<0.001**	0.598
Simpson's reciprocal Index	**<0.001**	**0.010**	**<0.001**	**0.047**	**0.003**	0.283

Bold highlights significance level (α = 0.05).

relative difference in PAFDM between the two leaf species in the dry forest was the lowest (21.3%). The relative difference in arthropod density between the rain and dry forests was around 93% for both *B. buceras* and *E. borinquensis* leaves (Fig. 3b), higher than that between the two leaf species in both the rain (64.3%) and dry (53.5%) forests. The relative difference in arthropod Shannon-Weiner index between the rain and dry forests (Fig. 3c) was greatest for *E. borinquensis* leaves (89.0%), followed by that of *B. buceras* leaves (73.7%) which did not differ from that between the two leaf species in the dry forest (67.3%). The relative difference in arthropod Shannon-Weiner index between the two leaf species in the rainforest was the lowest (24.0%).

Our SEM explained 66% of the variance in leaf PAFDM in the rainforest (Fig. 4a), but only 20% of the variance in leaf PAFDM in the dry forest (Fig. 4b). Many more effective linkages among leaf PAFDM, leaf C/N, precipitation and arthropods were found in the rainforest (19) than in the dry forest (4). Within the rainforest, leaf C/N (r = 0.56), precipitation (r = −0.30) and total arthropod densities (r = - 0.22) accounted for most of the variation in leaf PAFDM. Precipitation (r = −0.15) indirectly and negatively affected leaf PAFDM through controlling leaf C/N and total arthropod density (Table 4). Leaf C/N (r = 0.09) also indirectly affected leaf PAFDM through influencing densities of Collembola, Mesostigmata, Diplopoda, Isopoda and Araneae. In the dry forest, leaf C/N (r = 0.26), precipitation (r = −0.22), and Oribatida density (r = 0.32) accounted for most of the variation in leaf PAFDM. Leaf C/N (r = 0.06) also indirectly affected leaf PAFDM through influencing Oribatida density.

Structural equation models explained about 42% of the variance in leaf PAFDM for *B. buceras* leaves (Fig. 4c) and about 59% for *E. borinquensis* leaves (Fig. 4d) in the rainforest. There were apparently no differences between the high and low C/N leaf litter in the effective linkages (12 versus 11) among leaf PAFDM, leaf C/N, precipitation, and arthropods. For *B. buceras* leaves in the rainforest, precipitation (r = −0.55), arthropod density (r = −0.26), Coleoptera density (r = 0.22) accounted for most variation in leaf PAFDM. Leaf C/N (r = 0.03) indirectly and positively affected PAFDM via Diplopoda density (Table 3). Precipitation (r = −0.04) indirectly and negatively influenced leaf PAFDM by affecting leaf C/N and arthropod density. Diplopoda (r = −0.11), Mesostigmata (−0.11), Oribatida (r = -0.09), and Isopoda (r = −0.02) densities indirectly and negatively affected leaf PAFDM. For *E. borinquensis* leaves in the rainforest, precipitation (r = −0.34) total arthropod density (r = −0.44), and Blattodea (r = −0.22) density accounted for most variation in leaf PAFDM. Precipitation (r = −0.25) indirectly and negatively associated with leaf PAFDM through controlling Diplopoda, Oribatid and Blattodea densities. Diplopoda (r = −0.16), Oribatida (r = −0.31), and Isopoda (r = −0.12) density also indirectly and negatively affected leaf PAFDM by influencing total arthropod density. We failed to construct SEMs revealing interactions in leaf decomposition for the high and low C/N ratio leaves in the dry forest.

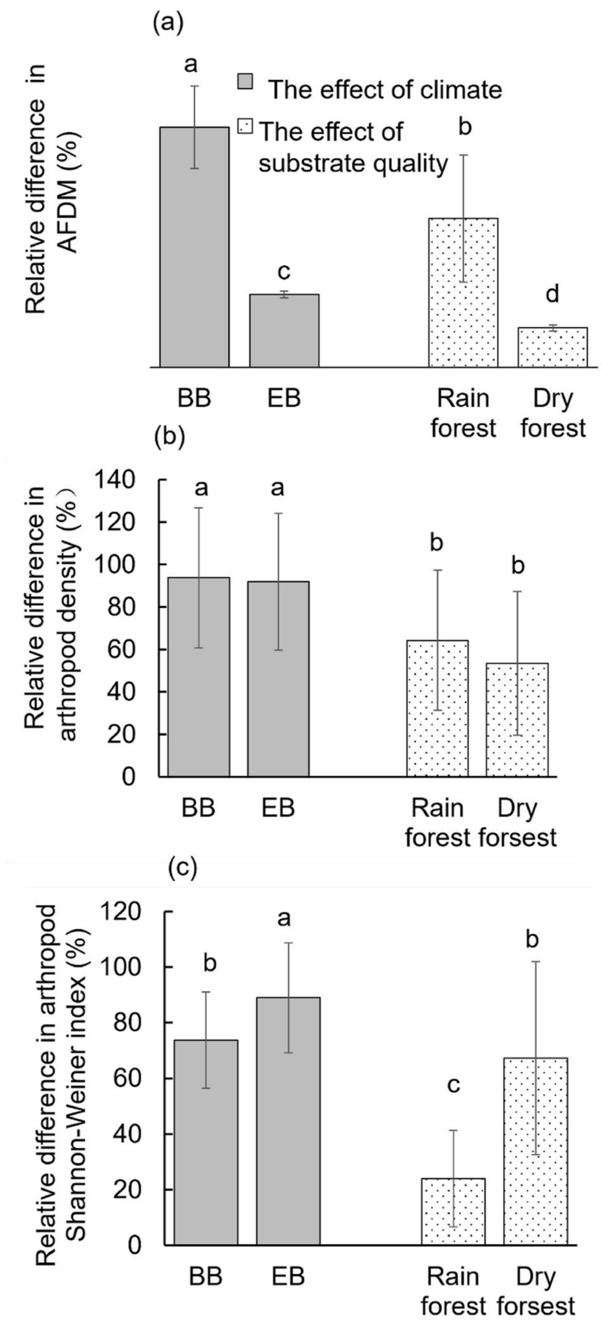

Fig. 3. The relative effect of climate and subtract quality on (a) percent ash free dry mass remaining, (b) arthropod density, and (c) arthropod Shannon-Weiner index. Different lowercase letters indicate a significant difference among the relative effects of climate and substrate quality on *Bucida buceras* and *Eugenia borinquensis* leaf species and in the rain or dry forests of Puerto Rico, respectively.

4. Discussion

Our data supported the hypothesis that climate remains as the predominant control over substrate quality in green leaf decomposition following hurricane disturbances. First, leaves decomposed much faster in the rainforest than in the dry forest and the difference in leaf PAFDM between the rain and dry forests was larger than that between leaf species. After 536 days of field incubation, the ratio of leaf PAFDM in the dry forest to that in the rainforest averaged around 4 whereas the ratio of leaf PAFDM for the high to low C/N litter averaged around 2, suggesting a much stronger control of climate on leaf decomposition than leaf C/N.

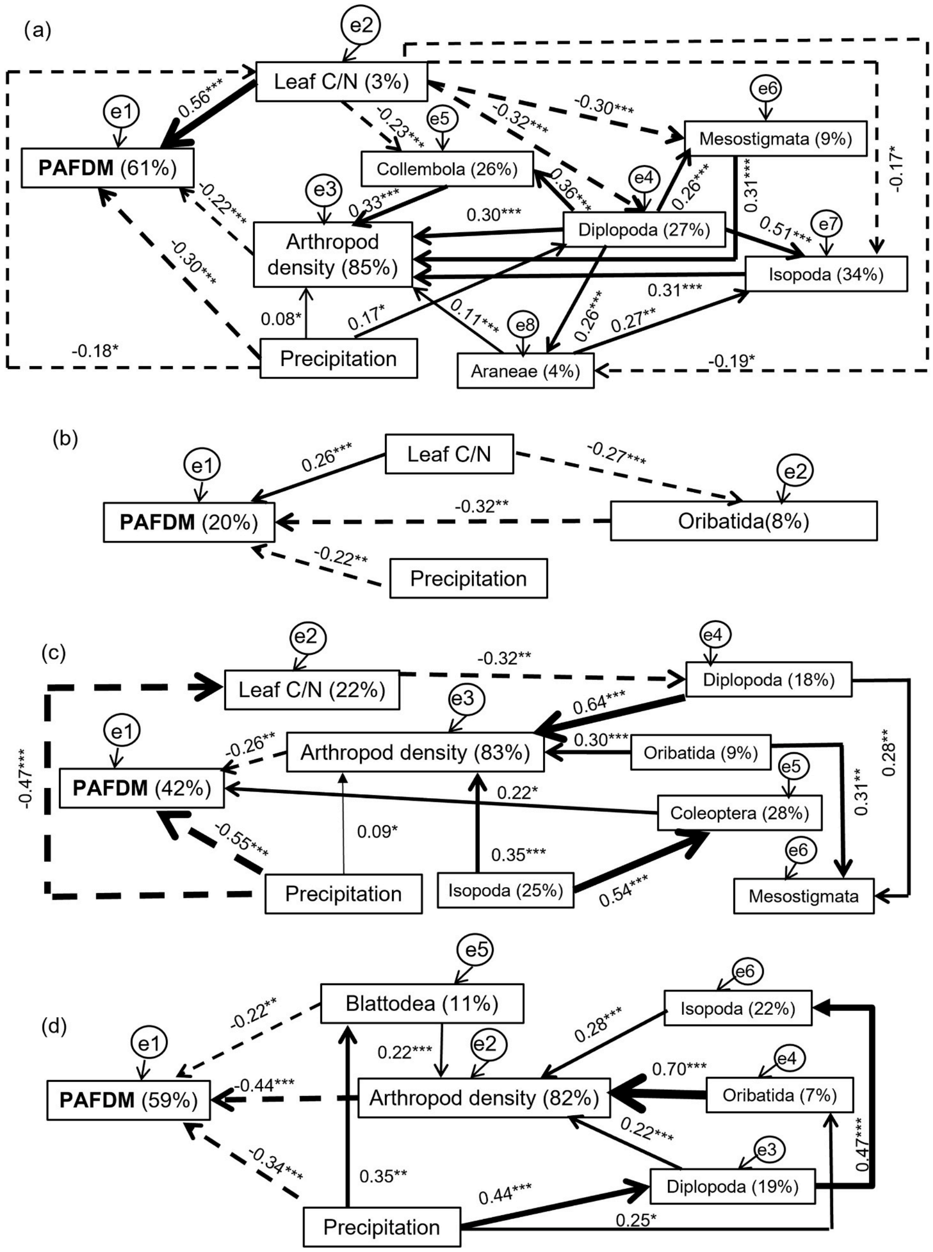

Fig. 4. Structural equation models describing the influences of precipitation, arthropod densities and leaf C/N on leaf percent mass remaining (PMR) in Puerto Rican (a) rainforest (with data from both leaf species), (b) dry forests (with data from both leaf species), (c) *B. buceras* leaves decomposed in the rainforest, and (d) *E. borinquensis* leaves decomposed in the rainforest. Continuous and dashed arrows represent positive and negative relationships, respectively. Boxes indicate measured variables; circles indicate error terms of endogenous variables. The widths of the arrows are proportional to the strengths of the path coefficients. Numbers on the arrows are standardized regression weights. Percentages in parentheses near endogenous variables are the variances explained by the model (R^2). Goodness-of-fit tests are: rainforest ($\chi 2 = 20.97$, $P = 0.23$, CMIN/DF = 1.23, CFI = 0.99, RMSEA = 0.037, n = 168), dry forest ($\chi 2 = 3.79$, $P = 0.15$, CMIN/DF = 1.90, CFI = 0.97, RMSEA = 0.073, n = 168), *B. buceras* leaves in rainforest ($\chi 2 = 23.75$, $P = 0.36$, CMIN/DF = 1.08, CFI = 0.99, RMSEA = 0.031, n = 84), and *E. borinquensis* leaves in dry forest (($\chi 2 = 12.51$, $P = 0.25$, CMIN/DF = 1.25, CFI = 0.99, RMSEA = 0.055, n = 84)). *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$.

Second, ratios of soil arthropod density and diversity index for the rain to dry forests was also greater on average than those for the low to high C/N litter, suggesting greater control on decomposer fauna by climate than by leaf C/N. Third, we successfully constructed SEMs of leaf decomposition for the high- and low-quality leaf species in the rainforest but failed to do that in the dry forest, suggesting that the influence of leaf C/N on decomposition was climate dependent following hurricane disturbances across subtropical forests of Puerto Rico.

Climate was shown to be the foremost driver for leaf litter decomposition across a narrower precipitation gradient (than our gradient) between tropical montane and tropical lowland forests (Ostertag et al., 2021). González and Seastedt (2001) compared litter decomposition between a subtropical wet forest in the Luquillo Mountains and a subtropical dry forest in Guánica of Puerto Rico using a low C/N (36) litter (*Cecropia scheberiana*) from the wet forest and a high C/N (64) litter (*Quercus gambelii*) from Colorado of USA. They also found that difference in decomposition rate between the subtropical wet and dry forests was greater than that between litter types. Data from our study and these other two studies did not support the “tropical hierarchy of factors” hypothesis, instead, supported the “general hierarchy of factors” hypothesis that climate is the foremost overarching driver in litter decomposition across ecosystems including tropical forests.

Our data also support our second hypothesis that high complexity of arthropod community structure and their interactions are associated with high precipitation and low leaf C/N values as well as fast leaf decomposition. Both arthropod abundance and linkages in SEM were higher in the rain than dry forests. Arthropod abundance was higher in the low than high C/N leaf litter, but linkages in SEM did not differ between the two species, suggesting interactions between climate and substrate quality for their influences on arthropod interactions.

Nielsen and Ball (2015) reported that increase in precipitation is associated with increase in microbial biomass and fungal/bacterial ratio, likely causing cascade effect on soil arthropods. Soil arthropods can influence litter decomposition through their direct consumption of detritus materials and indirect mediation of microbial activity (González et al., 2001; Hättenschwiler et al., 2005; Gessner et al., 2010). The

Table 4

Standardized direct and indirect effects derived from the structural equation models describing the influence of precipitation, arthropod densities and leaf C/N ratio on leaf percent ash-free dry mass remaining (AFDM) in subtropical rain and dry forests of Puerto Rico.

		Rainforest			Dry forest
		Combined	*Bucida buceras*	*Eugenia borinquensis*	Combined
Direct effects	Precipitation	−0.30	−0.33	−0.34	−0.34
	Litter C/N	0.52	–	–	0.26
	Total arthropod density	−0.22	−0.26	−0.44	–
	Oribatida density	–	–	–	−0.23
	Coleoptera density	–	0.22	–	–
	Blattodea density	–	–	−0.22	–
Indirect effects	Precipitation	−0.15	−0.04	−0.25	–
	Litter C/N	0.09	0.03	–	0.06
	Collembola density	−0.07	–	–	–
	Mesostigmata density	−0.10	−0.11	–	–
	Oribatida density	–	−0.09	−0.31	–
	Prostigmata density	–	–	–	–
	Diplopoda density	−0.12	−0.11	−0.16	–
	Isopoda density	−0.07	−0.02	−0.12	–
	Araneae density	−0.04	–	–	–
	Blattodea density			−0.10	

indirect effect of soil fauna on litter decomposition is often larger than their direct contribution (Berg et al., 2001). Therefore, the capacity of soil fauna to regulate litter decomposition depends on soil food web interactions, rather than solely on faunal abundance (Moore et al., 1988). It has also been shown that the interaction between microbes and soil fauna (including mites, earthworms, collembolans, enchytraeids and nematodes) stimulated decomposition (González et al., 2001; Nielsen et al., 2011). Litter is notably decomposed more quickly in biomes with complex food webs than with simple food webs in tropical rain and wet forests (Trzcinski et al., 2016).

Regulation of substrate quality on leaf decomposition and arthropod interactions are more pronounced in the subtropical rainforest than in the dry forest. Arthropod density was far lower in the dry forest than in the rainforest. High moisture conditions are reported to be beneficial to arthropod abundance (González and Seastedt, 2000) and are associated with complex food web (Wise and Lensing, 2019). Freshly dissolved organic matter (DOM) can be influenced by both rainfall and litter C/N. The quantity and quality of litter DOM can then alter the activity and interactions of soil biota (Wieder et al., 2008). Low C/N litter and high precipitation are associated with more abundant soil organisms (Curry and Schmidt, 2007; Coq et al., 2010) and likely results in more complex interactions among drivers of decomposition. For example, litter with lower C/N was quickly colonized by soil microbes (Morriën et al., 2018). Enhanced microbial growth can favor microbivore such as Coleoptera or Blattodea.

We found that soil arthropod density had a direct and negative association with leaf PAFDM in the rainforest, suggesting that arthropods play a notable role of accelerating leaf decomposition as expected. Arthropod acceleration of litter decomposition is likely achieved through multiple mechanisms including (1) direct consumption of detritus by detritivores, (2) elevated surface area for microbial activity through arthropod comminution of plant litter, (3) accelerated microbial inoculation to plant litter following movement and soil mixing, and/or (4) stimulated microbial activity through improved physio-chemical soil conditions or priming effect by arthropod body excretions (Frouz et al., 2015; Kitz et al., 2015; Zhang et al., 2015; Lin et al., 2019). In our study, major detritivores in the rainforest include Oribatida, Diplopoda and Isopoda. The ten-folds increase in arthropod abundance in the rainforest as compared to the dry forest not only may elevate the direct consumption of leaf litter, but also enhance microbial inoculation rate. Furthermore, earthworms are abundant in the rainforest but are rare in the dry forest (González et al., 2007), and earthworm abundance is positively associated with litter decomposition in a Puerto Rican wet forest (Liu and Zou, 2002; Dechaine et al., 2005) and at global scale (Huang et al., 2020) and its borrowing are shown to have a priming effect on carbon mineralization (Hoang et al., 2017). In the dry forest, a decrease in precipitation not only reduced the abundance and diversity of arthropods, especially for mainly detritivores (e.g. Diplopoda) and microbivores (e.g. Collembola), but also favored groups that could tolerate drought and heat conditions like Hymenoptera and Araneae. These drought tolerant groups are often main predators or omnivores and may suppress litter decomposition by feeding on micro decomposers. Thus, leaf PAFDM was only associated with Oribatida and not with other groups in the dry forest.

Our results showed that fast rate of leaf decomposition was positively associated with complex linkages among the driving factors of leaf decay. High density of linkage among soil biota was suggested to enhance system stability in a strongly developed food web (Digel et al., 2014). Several studies have recorded high litter decomposition rate given a high soil food web complexity (Coûteaux et al., 1996; Zheng et al., 1997). The slow decomposition processes obtained with simple soil food webs has been explained by the limited availability of nitrogen in N-poor litter to fast growing micro-organisms responsible for decomposition of hemicelluloses and cellulose (Coûteaux et al., 1996). The C/N of *B. bucera* and *E. borinquensis* leaves in the dry forest was higher than that in the rainforest during leaf decomposition, suggesting that nitrogen availability was lower in the dry than in the rain forest. Thus, nitrogen availability might become the limiting factor for diverse linkages among biotic drivers of litter decay, consequently retarding litter decomposition rate in the dry forest.

It was worthy to notice that decomposition in the subtropical dry forest was almost negligible for 1.5 years following hurricane disturbance. We suspect that this slow decomposition was not the norm in the dry forest because there is no massive accumulation of undecomposed litter on forest floor. Decomposition k value for senesced brown leaves was estimated to be 0.24 (Liu et al., 2018a) in this dry forest without hurricane disturbances, which was within the range of leaf litter decomposition k values (0.23–2.49) in tropical and subtropical dry forests (González and Seastedt, 2001; Powers et al., 2009; Rai et al., 2016). The green leaves generated by hurricanes shall have decomposed faster than brown leaves because of higher nutrient concentration and higher substrate quality (Lodge et al., 1991). There were several speculations to explain the observed abnormal slow decomposition of the green leaves following hurricanes in the dry forest. First, hurricane disturbance can slow down litter decomposition. Slower litter decomposition rate after hurricanes has been documented in a tropical dry forest of Mexico (Gavito et al., 2018). Nutrient immobilization several weeks after hurricane in leaf litter (Lodge et al., 1991; Sanford et al., 1991) and later in woody tissue (Zimmerman et al., 1995) as well as reduction in detritivores activity (Richardson et al., 2010) may explain the reduction in litter decomposition post-hurricanes. However, the pulse of leached litterfall N and P around 3–6 months after hurricanes and in the early-rainy seasons may benefit microbe activity (Anaya et al., 2007; Ostertag et al., 2013), likely leading to the clear loss of forest floor mass in the dry forest in early rain season 2018. This acceleration of leaf litter decomposition did not occur in our study because we placed our litterbags in the field 3 month after Hurricane Maria. Second, both *E. borinquensis* and *B. buceras* leaves are leathery in texture (Weaver al., 1973), and were likely resistant to water for many months in the field. This might explain the observed apparent litter mass loss on forest floor (with many non-leathery leaves) while negligible ash-free dry mass loss in litterbags of *E. borinquensis* and *B. buceras* in the dry forest after hurricane disturbances. Third, the installation of UV exclusion and transparent panels might have altered the microclimate by intercepting some precipitation and increasing soil temperature through greenhouse effect, resulting in reduced leaf decomposition in the dry forest. We strongly suggest a new decomposition study to compare: (1) green versus brown leaf litter, (2) with multiple leathery versus non-leathery leaf species, and (3) with wood versus without wood to elucidate these possible causes for the observed slow litter decomposition in the subtropical dry forest following hurricanes. Furthermore, the "home-court" effect in decomposition shall also be examined because it was shown to play an important role in decomposition in a subtropical wet forest of Puerto Rico (Santana et al., 2005).

We initially designed our experiment also to include UV radiation as a driver in decomposition because the hurricane defoliated the forest canopy and allows for additional UV radiation reaching forest floor. Our study in a pasture land adjacent to the Guayama dry forest indicated that UV can significantly affect litter decomposition after prescribed burning (Huang et al., 2020). However, we found insignificant difference in PAFDM and all arthropod groups except Collembola between UV exposed and excluded treatments. This lack of UV effect was likely due to the presence of thick layer of plant litter on forest floor and fast recovery of forest canopy after hurricane disturbances.

We showed that climate remains to be the overarching control on litter decomposition across subtropical rain and dry forests of Puerto Rico. Regulation of substrate quality on decomposition is climate dependent and occurs when climate constraints on biological activities are relaxed. The influence of climate and substrate quality on leaf decomposition is noticeably linked to changes in arthropod community and their interactions. The abundance of total arthropods showed a positive effect to accelerate leaf decomposition in subtropical rainforest of Puerto Rico, while only Oribatida was linked with leaf decomposition in subtropical dry forest of Puerto Rico following hurricane disturbances. This positive effect of soil arthropods on leaf decomposition was stronger for high C/N leaves than for low C/N litter in this subtropical rainforest. Drivers for this variation in decomposition can be attributed to a hierarchy order of controls by which climate plays the overarching role and substrate quality further modifies arthropod's influence on leaf decomposition across subtropical rain and dry forests.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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