PLANT FUNCTIONAL DIVERSITY ACROSS TWO ELEVATIONAL GRADIENTS IN SERPENTINE AND VOLCANIC SOILS OF PUERTO RICO

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ABSTRACT

Mountains are model systems for understanding the mechanisms that underlie patterns of biodiversity and ecosystem function. This study disentangles the effects of climatic and edaphic properties on patterns of trait variation across two mountains, tests foundational assumptions of trait-based approaches, and tests the stress dominance hypothesis of decreasing trait variation with increasing environmental stress. The results suggest that elevation as a proxy of abiotic conditions is not enough to generalize the variability of plant strategies across mountains. The ability to distinguish trait variation in different environments depends on the type of trait used, due to variable strength of trait-environment relationships. These results suggest that trait-environment relationships may vary in predictable ways across environmental gradients. Even though serpentine plant communities were more functionally dispersed compared to volcanic communities (contrary to the stress dominance hypothesis), this can be explained by complex interactions between climatic and edaphic properties.

RESUMEN

Las montañas son sistemas modelo para comprender los patrones de biodiversidad y función del ecosistema. Este estudio aclara el efecto de las propiedades climáticas y edáficas en la variación de los rasgos a través de montañas, probando supuestos fundamentales del enfoque funcional y la hipótesis de estrés-dominancia (SDH). Los resultados sugieren que la elevación no es un predictor suficiente de las condiciones abióticas, lo cual impide generalizar estrategias de plantas en sistemas montañosos. La variación de los rasgos disminuye al aumentar el estrés ambiental, debido a la fuerza variable de relaciones rasgo~ambiente. Distinguir la variación de los rasgos en diferentes entornos depende del tipo de rasgo utilizado. Ambas relaciones parecen ser idiosincráticas. El análisis por categorías de rasgo (PCA) va acorde a la SDH. Sin embargo, un enfoque multirasgo (FDis) sugiere mayor dispersión de las comunidades en serpentina, contrario a la SDH, demostrando complejas interacciones entre propiedades climáticas y edáficas.

DEDICATION

I dedicate this work to my family, especially my parents Patricia Díaz and Gustavo Garnica, my sister Patricia Garnica, and my nephew Gabriel Siqueira. I am grateful for all their support even from afar, for helping me when I felt alone and far away from my country, and for their constant encouragement to follow my dreams. Also, I dedicate this to my graduate student peers who helped me during my time in the Master's program. Finally, to all the coincidences of my life that led me to study tropical ecology, and to all the forest ecosystems around the world.

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TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1. Literature Review

No figures

Chapter 2: Effect of climatic and edaphic properties on plant functional trait variation across elevation

LIST OF TABLES

LIST OF APPENDIXES

LIST OF ABBREVIATIONS

Plant functional traits

Bwd: Basic Wood Density
LDMC: Leaf Dry Matter Content
LT: Leaf thickness
PoreDens: Pore Density
PoreDiam: Pore Diameter
SLA: Specific Leaf Area

Functional Diversity Concepts

CWM: Community Weighted Mean
FD: Functional Diversity
FDis: Functional Dispersion

Measurement units

°C: Celsius degrees
$cm^2.g^{-1}$: Square centimeters by gram. Use for SLA measurement
cm^3: Cubic centimeters (volume)
DBH: Tree diameter at breast height in cm
$g.cm^3$: Grams by cubic centimeter. Use for basic wood density measurement
g: Grams
km: Kilometers
m: Meters
$mg.g^{-1}$: Milligram by gram. Use for nutrient content measurement
mm: Millimeter
$\#pores.mm^{-2}$: Pore quantity by square millimeter
$\mu g.g^{-1}$: Micrograms by gram
µm: Micra

Others

IITF: International Institute of Tropical Forestry
PCA: Principal Components Analysis
PC1: First principal component
PC2: Second principal component
S1: Forest communities on the serpentine gradient, located in the Susua State Forest, at 253 m.
S2: Forest communities on the serpentine gradient, located in the Susua State Forest, at 296 m.
S3: Forest communities on the serpentine gradient, located in the Susua State Forest, at 347 m.
S4: Forest communities on the serpentine gradient, located in the Maricao State Forest, at 421 m.

S5: Forest communities on the serpentine gradient, located in the Maricao State Forest, at 786 m.
S6: Forest communities on the serpentine gradient, located in the Maricao State Forest, at 875 m.
V5: Forest communities on the volcanic gradient, located in El Yunque National Forest, at 380 m.
V6: Forest communities on the volcanic gradient, located in El Yunque National Forest, at 751 m.
V7: Forest communities on the volcanic gradient, located in El Yunque National Forest, at 835 m.
V8: Forest communities on the volcanic gradient located in El Yunque National Forest at 1010 m.

CHAPTER 1: LITERATURE REVIEW

MOUNTAINS AS MODEL SYSTEMS

Mountains are model systems for understanding plant distributions at different scales (Niu, Classen, & Luo, 2018). Dramatic changes in abiotic factors occur over relatively short geographic distances. For example, changes in temperature, rainfall, cloud interception, soil, and wind exposure can lead to differences in species tolerances at physiological and evolutionary levels (González, Willig, & Waide, 2013). Tropical elevational gradients, in particular, contain many of the world's life zones across short distances (10s of kilometers). Indeed, almost all biodiversity hotspots around the world encompass tropical mountains (Körner, 2000; Lomolino, 2001). Tropical elevational gradients harbor rare and endemic species (Kessler & Kluge, 2008), poorly studied soil processes and communities (like serpentine soils) (e.g., Reeves et al., 1996; Querejeta et al., 2007), large stocks of soil organic reservoirs (Ross, 1993; Leuschner & Moser, 2008), a large influence of cloud cover on transpiration rates (Laurance et al., 2011), and aseasonal climates (Grubb, 1977). Also, provides an important stage for understanding the effects of both climatic and edaphic factors on ecosystem function and biodiversity (Malhi et al., 2010).

Climate is a major determinant of plant diversity and distributions globally (Willdenow, 1805; O'Brien, 1998; Walther, 2003; Kreft & Jetz, 2007) as well as across elevation (Candolle, 1855; Wallace, 1878; Whittaker, 1967; Lomolino, 2001). It drives processes like photosynthesis which influences plant growth and reproduction (O'Brien, 1993). However, which climatic variable is most important is highly variable (van de Pol et al., 2016). Temperate ecosystems, for example, are most limited by energy availability, as evidenced by a strong correlation between photosynthesis and temperature in North America and South Africa (Currie, 1991; O'Brien, 1993). Meanwhile, in the tropics, water availability is more important in determining plant performance and function and species richness increases with increasing precipitation along elevational gradients (Holdridge, 1971; Gentry, 1982). For ecosystem carbon cycling, however, temperature is most important rather than water availability (Malhi et al., 2010). Climatic changes across elevation may also modify plant structure, and therefore the quality and quantity of organic carbon entering the soil (Bardgett et al., 2013). In short, interacting climatic factors affect ecosystem

properties and patterns of species diversity across elevation. Further, changes in climate can have cascading effects on edaphic properties across elevation.

Edaphic properties have major effects on the distribution and diversity of plants (Gentry, 1988). The idea that edaphic factors control species distributions is not new (e.g, Bardgett et al., 2013). There is growing evidence that edaphic factors play a larger role in diversity gradients than previously considered (Muenchow et al., 2013). For example, changes in temperature, precipitation and evapotranspiration may promote soil disturbances and enhance erosion, and influence soil structure, stability, and water holding capacity (Karmakar et al., 2016). Soil properties generate changes in plant structure and composition at local scales (Blundo et al., 2012), in montane forests (e.g., Nadkarni et al., 2002), tropical rain forests (e.g., Tuomisto et al., 2003), tropical dry forests (e.g., Becknell & Powers, 2014), as well as savannas (e.g., Bucini & Hanan, 2007). Pedogenic processes that affect the chemical, physical and biological properties of soil also change across elevation (Muenchow et al., 2013). For example, total nitrogen and soil organic matter increase with increasing elevation, while soil bulk density and soil pH change irregularly with increasing elevation, possibly due to changes in climate, geology, and/or net primary productivity across elevation (Yüksek et al., 2013). While soil texture and salinity are more important for plant communities in arid environments, soil nutrients determine patterns of species diversity in tropical montane forests (Soethe, Lehmann & Enquist, 2008; Muenchow et al., 2013). Even microbial biogeography is controlled by edaphic variables (Fierer & Jackson, 2006) which, in turn, may have cascading effects on plant diversity and productivity (Van der Heijden, Bardgett, & van Straalen, 2008; Bever et al., 2010).

Understanding these complex interactions across elevational gradients requires an integrative approach. The stress dominance hypothesis (SDH) posits that tradeoffs between environmental filtering and competition occur across gradients of environmental stress (Grime, 1977), without defining what constitutes environmental stress. Thus, high elevation sites may impose high environmental stress in some systems (for example, where excessive wind limits plant height) whereas other high elevation regions may present more favorable conditions owing to increased precipitation. This hypothesis is consistent with the theory that abiotic changes generate fitness differences which may influence plant community assembly across elevation (Kraft and Ackerly, 2009; HilleRisLambers et al., 2012). And, community composition changes may also affects

ecosystem processes as litter decomposition and nutrient cycling due to differences on litter quality (Cornwell et al., 2008). Yet, the effects of climatic and edaphic properties on plant diversity may counter each other along elevation, such as when water availability increases but soil nutrient availability decreases, questioning whether the stress dominance hypothesis would be manifest. In general, the stress dominance hypothesis can be used to understand and generalize the changing role of environmental filtering on plant communites (Coyle et al., 2014).

APPROACHES FOR STUDYING ELEVATIONAL GRADIENTS THROUGHOUT THE HISTORY OF ECOLOGY

The study of mountain biodiversity has a rich history and resulted in the development of major theories in ecology and evolution (King et al., 2013; MacArthur, 1972). Until recently, mountain research (and ecology in general) was characterized by a taxonomic approach, arguably contributing to the debate of whether community ecology would ever produce predictive and generalizable laws (Lawton,1999). Some of the earliest work on plant diversity across mountains noted the influence of climate. Willdenow (1805) noted the similarity of plant structure and life forms in similar climates separated by thousands of kilometers. This work inspired von Humboldt's expedition across Mt. Chimborazo in Ecuador (Humboldt & Bonpland, 1807) in which he set an important precedent for the study of the climatic influence on plant distributions and plant forms. Yet, this "Humboldtian science", and the work that followed was, by today's standard, quasi-scientific in the sense that no formal methodology was used (Egerton, 2016). This can be seen in von Humboldt's well-known depiction of plant distributions across Mt. Chimborazo (Humboldt & Bonpland, 1807) in which species elevational ranges were based on rudimentary observations (Egerton, 2009). This poorly developed methodology was replicated by scientists around the world who were fascinated by patterns of species turnover across mountains.

Later, Darwin (1859) and Wallace (1878), both inspired by Humboldt's work, emphasized the role of climatic, edaphic, and biotic factors for determining the distribution of plant species, particularly across mountains. Shreve's (1915) work across the Santa Catalina Mountains of Arizona and the Blue Mountains of Jamaica further demonstrated the increasing challenge of generalizing findings between studies based on species identities. It wouldn't be until 50 years later that Whittaker (1960) began developing a more quantitative approach to the study of plant distributions across elevational gradients, later termed "gradient analyses". Whittaker (1960)

studied plant distributions along the Catalina Mountains in Arizona (following Shreve), the Siskiyou Mountains in Oregon, and the Great Smoky Mountains in the eastern United States, including soil analyses and the evaluation of different vegetation transect techniques as a way to enable generalizations about the factors driving patterns of species diversity across very different mountain systems.

This new quantitative aproach was adopted by other scientists as ecology became increasingly quantitative to rival the 'hard' sciences of physics and chemistry (Lawton, 1999). In an attempt to describe broad generalities in the distribution of species across elevation, Janzen (1967), for example, focused on the effects of climatic variables on species elevational ranges and physiological tolerances. He argued that temperate organisms, which experience high climatic variation, should have high tolerance to temperature fluctuations; whereas tropical organisms, evolving in relatively aseasonal climates, should have low tolerance to temperature fluctuations. He used this logic to explain why species elevational ranges were narrower in the tropics relative to temperate forests. Although working with small mammals, Brown (1971) argued that temperature was a determinant factor for species richness patterns across elevation. Later, Rahbek (1995, 2005) highlighted the importance of sampling area and effort to explain the peak in species diversity increasingly reported at mid-elevations. Additional meta-analyses for mammals, birds, and other taxa (McGain, 2007; McCain, 2009; McGain & Grytnes, 2010; Willig & Presley, 2015, Peters et al., 2016, Muenchow et al., 2018, among many others) provided overwhelming evidence of general patterns of species richness across elevation with a peak in species diversity ocurring at mid-elevations.

Whittaker and those who followed were focused on species identities, or taxonomic diversity. Today, Whittaker's gradient analyses across mountains can be improved using a functional trait-based approach, which was developed in response to the need for a more predictive ecology. A functional trait is one that influences an organisms' growth, reproduction or survival and provides a common metric that can be measured in any ecosystem around the world (McGill et al., 2006). Early forms of the trait-based approach for understanding species distribution, can be seen in (at the time) a new definition of ecological communities, one based on how species use resources by classifying life forms based on ecological strategies (Raunkiaer, 1934). Later, this approach was quickly adopted after it became evident that species functional traits were influenced by abiotic

and biotic factors in predictable ways (Knight, 1965; Cummins, 1974; Grime, 1977). It wasn't until the 1980s that a formal definition of "functional trait" appeared (Bradshaw, 1987; Calow, 1987), and, later, incorporated into diversity studies across environmental gradients (Westoby, 1998), including those across elevation.

A TRAIT-BASED APPROACH TO UNDERSTANDING ELEVATIONAL GRADIENTS

Until recently, understanding patterns of diversity across elevation has been studied using a species-centered approach. However, species composition alone cannot be used to generate projections of how plant communities and entire ecosystems may respond to future disturbances or climate change scenarios (Díaz & Cabido, 1997). The challenge of linking species distributions to environmental properties for predicting future changes can be solved by applying a functional trait-based approach. Functional diversity is defined as the relative type, range, and abundance of functional traits present in a community (Díaz et al., 2007). Functional traits are any morphological, physiological, or phenological characteristics that can be measured in an organism (Violle et al., 2007; Hevia et al., 2017). In addition, functional traits are an integrated measure of organismal responses to the environment (Díaz et al., 2013) and provide important linkages to ecosystem-level processes (Díaz et al., 2007) in a way that species abundances and species composition cannot. For example, the functional diversity of tropical woody assemblages is higher than expected based on species richness alone (Swenson et al., 2011a), pointing to important community assembly processes that select species based on their functional traits.

Trait-based approaches in community ecology have seen enormous growth in the past two decades. Relationships between plant functional traits and environmental conditions on a global scale demonstrate that functional diversity decreases with increasing latitude and elevation, with temperature and water vapor pressure as the strongest predictors of those changes (Wieczynski et al., 2019). Further, most traits that influence plant performance (e.g., specific leaf area, leaf carbon, wood density, and tree height) shift toward more conservative growth strategies with increasing latitude and elevation (Reich, 2014; Díaz et al., 2015). However, community trait values are highly influenced by local environmental conditions which can increase trait variation, thus obscuring patterns at large scales. For example, similar abiotic conditions can support communities with very different mean trait values, and, likewise, differing climates can support similar mean trait values

at the community level (Bruelheide et al., 2018). Research efforts have focused on patterns of trait variation across environmental gradients like elevation (e.g., Lambrecht & Dawson, 2006; Cornwell & Ackerly, 2009), or on larger scale biodiversity gradients like latitude (e.g., Swenson & Enquist, 2007; Kunstler et al., 2016, allowing predictions under climate change scenarios (e.g., Elser et al., 2010; Gallagher, Hughes & Leishman, 2013). Nevertheless, a trait-based approach to gradient analyses may help explain why similar trait values occur in divergent climates.

In Puerto Rico, trait-based approaches have primarily focused on elevational gradients within the Luquillo Experimental Forest (LEF) (e.g., Swenson, Anglada-Cordero, & Barone, 2011b; Umaña & Swenson, 2019a) or within tropical dry forests of Guánica Biosphere Reserve (e.g., Salazar, 2015; Lasky, Uriarte, & Muscarella, 2016). Others have compared plant functional traits across precipitation gradients, including Cambalache, Guajataca, Guánica and Río Abajo State Forests (e.g., Muscarella et al., 2015; Muscarella & Uriarte, 2016). In general, community functional similarity across mountain sistems decreases with increasing elevation (Swenson, Anglada-Cordero, & Barone, 2011b), as shown at global scales (Wieczynski et al., 2019). To reflect the multidimensional functionality in different plant responses to elevation across species it is important to use multiple traits and multivariate analyses such as Principal Ccomponent Analysis (Kraft, Godoy, & Levine, 2015; Umaña & Swenson, 2019b). Capturing multidimensionality of trait variation will require the addition of traits beyond commonly measured foliar traits (such as in Umaña & Swenson, 2019a), specially in communities under environmental stress, where it may result in the convergence of species onto an optimal trait value (Coyle et al., 2014). **In line with the stress dominance hypothesis, I argue that the direction of increasing environmental stress is likely to differ across mountains thus modifying the relationship between traits (trait-trait covariation), and between traits and the environment (trait-environment relationships), possibly explaining why these relationships appear idiosyncratic.**

Despite a growing number of studies quantifying trait variation across elevation and/or soil variation, most of these studies emphasize what are known as 'soft' traits (e.g., Reich, Ellsworth & Walters, 1998; Tardieu, Granier & Muller, 1999; Wilson, Thompson & Hodgson, 1999; Evans & Poorter, 2001; Ackerly et al., 2002; Hodgson et al., 2011). 'Soft' traits include leaf area which are only loosely correlated to physiological or demographic processes (Belluau & Shipley, 2018).

Arguably, a more complete understanding of trait variation across elevation requires a thorough sampling of 'hard' traits, like wood anatomy and conduit element length, which better define the efficiency of plant water transport and have a stronger physiological basis (Rosas et al., 2019). 'Hard' traits should be evaluated on at least two different levels: at the species level where traits depend on trade-offs based on different ecological strategies, and at the community level where traits may be decoupled from trade-offs generating different strategies for coexistence within communities and higher efficiency in resource use (Bruelheide, et al., 2018).

Relationships between leaf traits, climate and soil characteristics, demonstrate that on a global scale soil nutrient content explains foliar trait variation, whereas climate more strongly explains variation in growth form (Ordóñez et al., 2009). In general, the emphasis on plant functional trait variation across environmental gradients (e.g., elevation, precipitation, or temperature) does not include soil properties as a primary factor influencing plant community assembly (e.g., Díaz et al., 2015; Wieczinski et al., 2019). Within Puerto Rico, trait variation was more strongly predicted by water availability compared to soil nutrient availability when using ‘soft’ traits like specific leaf area and leaf nitrogen to phosphorus ratio (N:P) in tropical dry forests (Salazar, 2015). In the same tropical dry forest, climate was a stronger predictor of plant function compared to edaphic properties (Lasky et al., 2016). However, both studies were limited to one of the driest regions in Puerto Rico and other studies including both climatic and edaphic properties are lacking. Given the importance of both climate and soil in determining diversity patterns, the lack of studies including both (climatic and edaphic properties) creates a significant gap in knowledge regarding how plant functional diversity varies across elevation. In short, there are still too few studies of trait variation across elevation at global or local scales to generalize relationships between trait variation and edaphic properties (e.g., Wieczynski et al., 2019). In a recent review, Shipley et al. (2016) described major short-comings of trait-based ecology. They argued that patterns of trait variation are still poorly known and encourage research linking trait variation to environmental factors. Additionally, Bruelheide et al. (2018) emphasize the importance of including local environmental variables in trait-based studies because a growing number of studies reveal a limited role of large-scale climate on trait-environment relationships. Finally, Rosas (2019) identified weak correlations between ‘soft’ and ‘hard’ traits, demonstrating the need to include ‘hard’ traits (such as physiological or hydraulic traits) in trait-based studies.

Functional ecology is still evolving and there are specific gaps in our knowledge. Of the recommendations outlined in McGill et al. (2006) for advancing functional trait-based community ecology, understanding functional trait variation across environmental gradients was a key priority which will enable predictions of species and ecosystem responses to climate change. Additionally, Shipley et al. (2016) recognized the need to quantify trait-trait covariation (between 'soft' and 'hard' traits) and trait-environment relationships because these form two foundational assumptions of trait-based ecology: that traits reflect plant function and that the environment selects for different trait optima. The need to test key assumptions in trait-based community ecology and to include both climatic and edaphic properties in tests of community assembly across elevation form the basis of the present research.

CHAPTER 2: EFFECT OF CLIMATIC AND EDAPHIC PROPERTIES ON PLANT FUNCTIONAL TRAIT VARIATION ACROSS ELEVATION

INTRODUCTION

Mountains are hotspots of biodiversity, are priority regions for conservation (Myers, 1988; Myers et al., 2000), and have been studied to understand mechanisms that shape biodiversity patterns and ecosystem function (Grinnell, 1917; Whittaker, 1960; Brown, 1971; Lomolino, 2001; Nogués-Bravo et al., 2008). Today, montane gradients remain central to the study of ecology and evolution (Spasojevic et al., 2014). However, most studies across environmental gradients (e.g., Gentry, 1988; Pan et al., 2013) use elevation as a proxy for changes in abiotic factors and focus solely on taxonomic diversity ignoring other aspects of diversity like functional diversity. Functional diversity reflects individual species' competitive abilities and physiological tolerances which scale up to larger ecosystem processes (Díaz & Cabido, 2001), a linkage not possible using a purely taxonomic approach.

The use of elevation as a proxy of abiotic conditions is not enough to generalize the variability of species richness patterns across mountains. The variation of abiotic conditions across mountains likely explains diversity changes across elevation where climate and soil properties interact (Fortunel et al. 2013; González et al., 2013; Niu et al., 2018). Although some studies consider changes in environmental variables like precipitation and temperature across elevation (e.g., Körner, 2000; Soliveres & Maestre, 2014), many ignore edaphic properties as a determining factor of species diversity patterns. Strong linkages between plant functional traits and soil properties have been demonstrated recently (e.g., Faucon, Houben, & Lambers, 2017). Leaf traits, for example, vary across soil gradients regardless of elevation (Molina-Venegas et al., 2018). However, changes in soil properties across elevation appear highly variable. Soil carbon, nitrogen, and phosphorus increased with elevation in tropical ecosystems dominated by *Pinus* (Birk & Vitousek, 1986) but, in general, soil nutrient availability may vary as a function of climate, soil fertility, successional status, and microbial activity across elevation (Vitousek et al. 1988). In other mountain systems, soil organic matter and nutrient accumulation were higher at lower elevations due to higher rates of productivity, nutrient turnover, and decomposition in warmer environments

(Post et al. 1982, 1985). Climatic and edaphic properties need to be studied with more detail in order to understand how changes across elevation and how these influence patterns of community assembly (e.g., Gould et al. 2006).

A trait-based approach studies can help us better understand the mechanisms that shape assembly patterns across elevation (Whittaker, 1967; Díaz, Cabido, & Casanoves, 1998; Kerkhoff & Enquist, 2006; Ordóñez et al., 2009; Garnier, Navas, & Grigulis, 2015; Yang et al., 2015). Variable abiotic conditions across elevation influence plant growth and survival (and ultimately select for different plant traits), thus influencing community assembly patterns. The stress dominance hypothesis (Grime, 1977) argues that a clustering of trait values (i.e., low trait variation among species) indicates environmental selection for an optimal trait. In contrast, a high dispersion of trait values (i.e., high trait variation among species) indicates more favorable environments and thus the partitioning of resources determines community composition (Weiher & Keddy, 1995; Swenson & Enquist, 2007; Laliberte & Legendre, 2010). Although the stress dominance hypothesis in combination with a trait-based approach to community ecology can be used to inform the underlying processes driving community assembly patterns.

Most studies relating trait diversity across elevation are limited to the temperate zone (e.g., de Bello, Lepš, & Sebastià, 2006; Kraft and Ackerly, 2009; Chun & Lee, 2018; Minden & Venterink, 2019) and cannot be generalized to the tropics. However, a few studies provide direct evidence of how tropical tree communities are influenced by abiotic and biotic drivers. For example, Swenson et al. (2011b) showed that functional trait similarity increases with increasing elevation, suggesting that environmental filtering is higher at higher elevations in line with predictions based on the stress dominance hypothesis. Similarly, Hulshof et al. (2013) found evidence that higher environmental heterogeneity, common at low elevations, generates greater trait variation. Low elevations were characterized by tropical dry forests which are more water limited than higher elevation rain forests, calling into question a key generalization of the stress dominance hypothesis of increasing stress with increasing elevation.

The characterization of plant trait diversity across elevation is additionally limited in scope because of the choice of traits measured. Even though precipitation (and thus water availability) is a primary factor varying with elevation, few studies quantify the variation of traits most directly related to plant water use and physiological processes (i.e., hydraulic traits). These traits are often

referred to as ‘hard’ traits because they are less readily measured (e.g., Weiher et al., 1999; Fichot et al., 2009). Instead, most studies emphasize easily measured, ‘soft’ traits which are, in general, poor predictors of physiological processes like water use efficiency (WUE) or hydraulic capacity (Lavorel & Garnier, 2002; Rosas et al., 2019). Thus, 'hard' traits can provide better insight into how plants respond to abiotic changes across elevation and to the increased drought conditions predicted for many montane areas (Lachenbruch & McCulloh, 2014).

Briefly, changes in temperature, precipitation, and soil nutrient availability (and their interactions) can have direct and indirect effects on functional diversity across elevation. To address the current shortcomings in the application of trait-based ecology to the study of elevational diversity gradients, this study will: (1) test whether the use of elevation as a proxy of abiotic conditions can be used to generalize patterns of trait variation across mountains; (2) test two key assumptions of the trait-based approach (trait covariation and trait-environment relationships); and, finally, (3) test the stress dominance hypothesis and disentangle the effects of climatic and edaphic properties on functional trait variation and community assembly across elevation. To test whether abiotic factors better predict trait variation (rather than using elevation as a proxy), plant traits were measured across two mountains differing in precipitation and soil nutrient content. This study emphasized hydraulic traits because water availability strongly differs across study sites and future predictions for the region, in general, include more frequent and prolonged drought periods (Angeles et al., 2007; Jennings et al., 2014; Van Beusekom, González, & Rivera, 2015).

METHODS

Study site

Puerto Rico is located in the Subtropical Latitudinal Region of the Caribbean and harbors six life zones ranging from subtropical dry to rain and cloud forests (Ewel & Whitmore, 1973). The island is characterized by the Cordillera Central and the Sierra de Cayey mountain ranges distributed from east to west, creating a prominent rain shadow (Gómez-Gómez, Rodríguez-Rodríguez, & Santiago, 2014). Existing vegetation plots across the island were identified using published literature and the USDA Forest Inventory and Analysis National Program online database (FIA; O´Connell et al., 2014). Plots with contrasting soil types were selected for the study. Across the island, there were two distinct mountains which were relatively well-sampled across elevation and which encompassed unique soil types: an elevational gradient on volcanic soils in northeastern Puerto Rico in El Yunque National Forest (Gould, González, & Carrero-Rivera, 2006) and an elevational gradient on serpentine soils in southwestern Puerto Rico within Susúa and Maricao State Forests (FIA) (Figure 1).

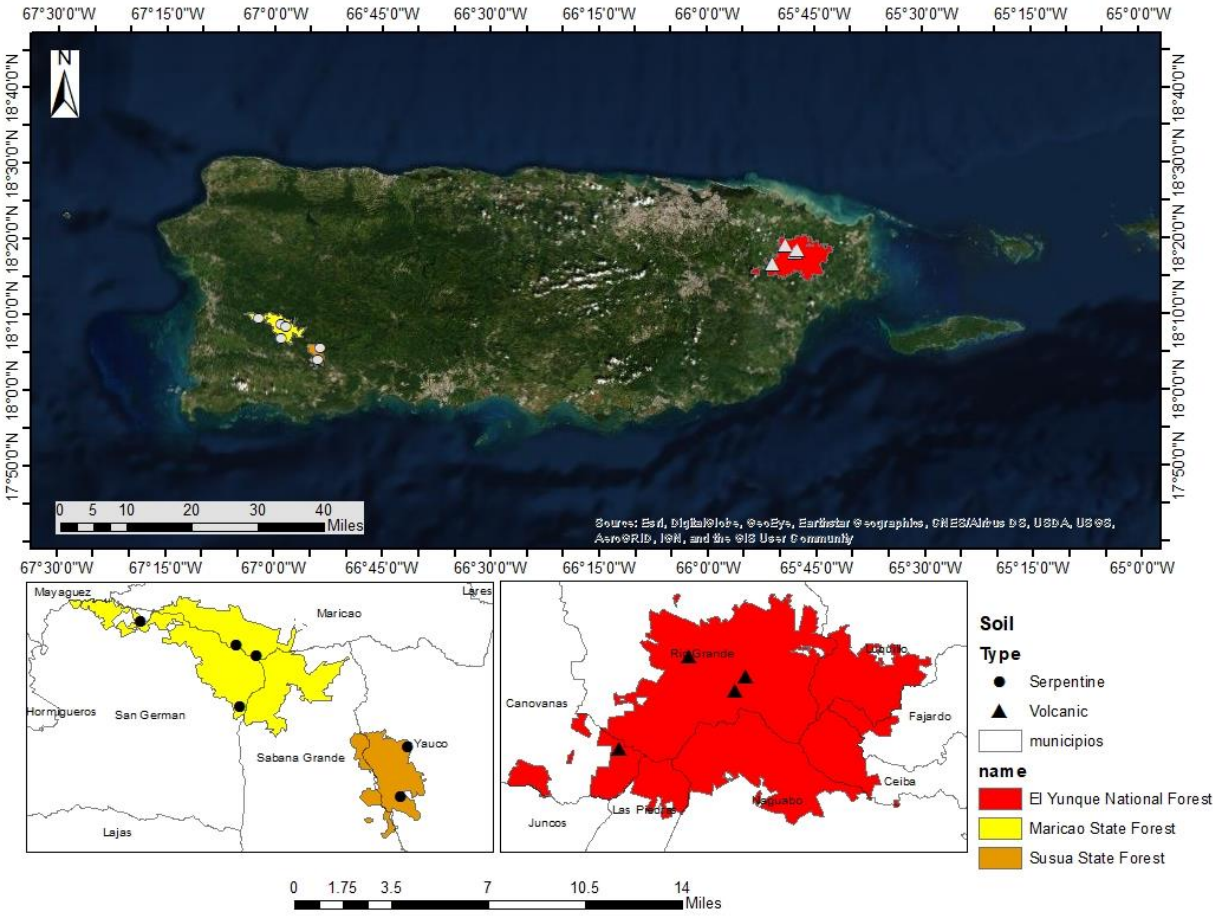

Figure 1. Location of plots selected for the present study. On serpentine soils, two sampling sites were located within Susúa State Forest and four sampling sites were located within Maricao State Forest. On volcanic soils, four sampling sites were in El Yunque National Forest. Protected areas including Susua, Maricao, and El Yunque are shown as green (serpentine) and red (volcanic) polygons.

Study design

From the FIA database, all plots located on serpentine (more generally, ultramafic) soils inside protected areas, were selected. A total of six plots were located within Susúa and Maricao State Forests, ranging from 253 to 875 meters above sea level (Figure 2a and 2b). Each FIA plot had a total area of 672 m^2. Species and abundance data for the most recent inventory was used to generate species lists for trait collection. Additionally, on volcanic soils, plot data from Gould et al. (2006) was used. Plots were in four mature forests (> 60 years) with three plots per forest type. Each plot measured 100 m^2. Although these plots were significantly smaller than those used by FIA, the triplicate sampling of the volcanic gradient was designed to capture the variation in forest types

and species distributions (Gould et al., 2006). Traits were sampled from each of the four forest types located within EYNF (also known as Luquillo Experimental Forest): elfin woodland, sierra palm, palo colorado, and tabonuco forests, ranging from 380 to 1010 m. (Figure 2c and 2d).

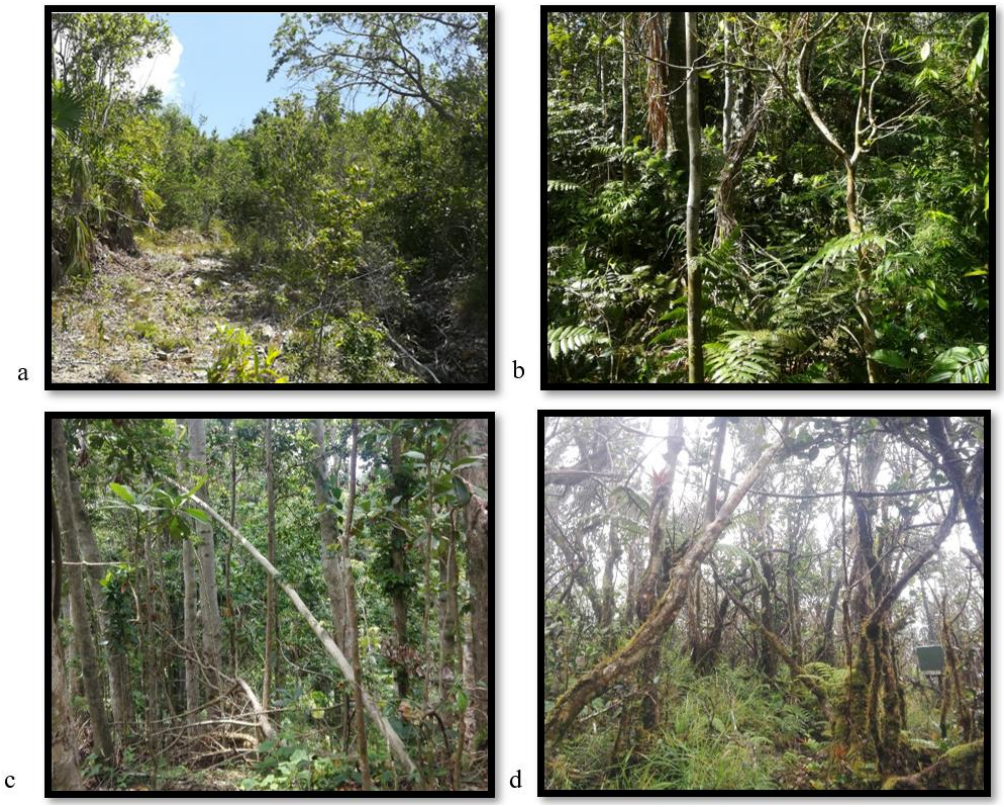

Figure 2. Sampling sites showing the range of conditions across gradients. On serpentine soils, (a) at 253 m.a.s.l. inside Susua State Forest, and (b) 875 m.a.s.l. inside Maricao State Forest. On volcanic soils, (c) the tabonuco forest at 380 m.a.s.l., and (d) the elfin woodland forest at 1010 m.a.s.l., both within El Yunque National Forest.

Species selection

This study focuses on woody species because they represent a major component of global carbon and climate dynamics, and their responses to ongoing and predicted climate change has major implications for both local and global scale processes (Dixon, et al., 1994). Using existing plot data, I measured traits on 3 - 5 individuals for species representing at least 80% of the total abundance of each plot (e.g., Garnier et al., 2004; Lavorel et al., 2008; Pakeman & Quested, 2007). Each species in each forest community was taken as an independent measure, even when the same species was distributed in different communities or gradients, in other words, trait measurements

were made for each species within each community and not extrapolated as is commonly done in other studies (e.g., Matteodo et al., 2013; Shen et al., 2019). A total of 10 species made up 80% of relative abundance in the volcanic gradient, resulting in 41 individuals sampled, whereas 59 species made up 80% of relative abundances on serpentine plots, resulting in 267 individuals sampled (Appendix 1). All samples in the serpentine gradient were collected between May 2018 and January 2019, and in the volcanic gradient during July 2018. Some samples for foliar nutrient content analysis were collected between January and February 2019 in both gradients.

Functional traits

A total of six functional traits were selected to represent resistance to drought, competitive capacity, hydraulic conductivity, and carbon storage (Appendix 2). Three of the selected traits are considered 'soft' traits and included: Specific Leaf Area (SLA, $cm^2.g^{-1}$), Leaf Dry Matter Content (LDMC - proportion), and Leaf thickness (LT - mm). The other three traits were considered 'hard' traits and includes: Basic Wood Density (Bwd – g.cm^3), Pore Density (PoreDens - # pores.mm^2), and Pore Diameter (PoreDiam - µm (Micra). Traits were measured following standardized protocols (Richter & Dallwitz, 2000; Garnier et al., 2001; Perez-Harguindeguy et al., 2013). Additionally, eleven foliar nutrient contents (Al, Ca, Fe, K, Mg, Mn, Na, P, and S) were quantified at the species level in each plot. These analyses were conducted at the Chemical Laboratory of the International Institute of Tropical Forestry (IITF, Río Piedras, Puerto Rico). All collected individuals of a species in each plot were combined, oven-dried at 65 ºC, and ground to pass through an 18 (1.00mm) mesh sieve (Molina, 2011). The total values of foliar nutrient content for Ca, K, P, Mg, Fe, Al, Mn, S, and Na were obtained using a Spectro SpectroBlue ICP Emission Spectrometer and reported as mg per g, after processing samples by wet oxidation using the Chao-Yong and Schulte (1985) method.

Climatic and edaphic data

Climatic data. Mean values of temperature (ºC) and precipitation (mm) for all plots (volcanic and serpentine) were downloaded from WorldClim (Fick & Hijmans, 2017). *Edaphic data.* For volcanic plots, soil data collected from 0-10 cm in the same sampling sites by Ping et al., (2013) were used. For serpentine soils, I randomly selected three coordinates within each forest

community for collecting soil samples using a basin with a core of 3 inches (7.62 cm) diameter by 6 inches (15.24 cm) depth. For soil pH, total soil carbon, and total soil nitrogen analyses, a cloth bag with a capacity of 1 kg was filled from three concentric cores and homogenized by mixing, then, and the remaining soil was discarded. Soil clods were broken by hand, and all samples were dried in a "solar dryer" (+/- 40ºC to avoid fungi growth). Soil samples were crushed using a Dynacrush Soil Crusher and passed through a 20 (0.85mm) mesh sieve. Samples were transported to the International Institute of Tropical Forestry (Río Piedras, Puerto Rico), where total carbon was measured as CO_2 by an infrared detector and total nitrogen was determined as N_2 by thermal conductivity cell and reported as percentages (%). For soil bulk density, a new core was sampled nearby (within 30 cm) and deposited in a different cloth bag. These samples were oven-dried at 105 ºC for 48 hours and weighed to a precision of 0.01 g at the end of the drying treatment. The specific volume of the core was calculated (694.99 cm^3) to estimate soil bulk density for each plot as the sample dry weight divided by the core volume.

Statistical analysis

All analyses were performed using the statistical programming language and software environment R (R Core Development Team 2018). First, to test the relevance of using elevation as a proxy of abiotic conditions, I compared Pearson correlation coefficients between elevation and other climatic (precipitation, temperature) and edaphic properties (total carbon, total nitrogen, pH, bulk density). Principle Component Analysis (PCA) was used to quantify the climatic and edaphic variables that differentiated volcanic and serpentine plant communities, to confirm initial observations that the two elevational gradients indeed differed in both climatic and soil properties.

To better understand generalities in trait-environment relationships, Pearson correlation coefficients were compared for all combinations of traits and abiotic variables. Next, to understand how the inclusion of trait types influences the interpretation of results, functional traits were divided into four categories reflecting "soft" and "hard" leaf and wood traits: 1) foliar 'soft' traits (SLA, LT, LDMC); 2) wood hydraulic traits ('hard' traits: Bwd, PoreDiam, PoreDens); 3) foliar nutrient content ('hard' traits: P, K, Mg, Ca, Fe, Al, Mn, Na, and S); and 4) all traits combined. For each trait, community weighted means were calculated using the *FD* package in R (Laliberte, Legendre, & Shipley, 2014), as the average of a species trait value within each site weighted by

its relative abundance within that site (Lavorel et al., 2008). Community weighted means are useful uni-dimensional trait indices used to assess community assembly as it relates to environmental conditions (Muscarella & Uriarte, 2016). To reduce the dimensionality of traits into two Principal Components, a PCA was used for each trait category (leaf, wood/hydraulic, nutrients) and the contribution of each trait to differentiation among study sites was quantified.

To test the major predictions of the stress gradient hypothesis of increased trait clustering with increasing environmental stress, trait variation was analyzed in multi-dimensional space. Functional Dispersion (FDis) was calculated, reflecting the average distance of individual species to the centroid of all species (weighted by species abundances) (Laliberte & Legendre, 2010). Functional dispersion describes the range of trait values in multivariate space, with large values indicating high dispersion of trait values among species within a community (and thus low similarity of trait values) and small values indicating clustering, or high similarity of traits within each community. Values of FDis were compared among trait categories and analysis of variance (ANOVA) was used to test for significant differences. This was also done to understand how the choice of traits measured influences the interpretation of functional dispersion. In the case of a significant ANOVA, LSD Fisher post-hoc analyses were used to distinguish trait categories. Finally, to further understand results predicted by the stress dominance hypothesis and test a major assumption of trait-based ecology, patterns of trait covariation were analyzed using Pearson correlation coefficients.

RESULTS

Relevance of using elevation as a proxy of abiotic conditions

Across serpentine plots, all climatic variables were significantly correlated. Elevation was positively correlated to precipitation ($r = .89$, $p < 0.05$) and negatively correlated to temperature (Appendix 3; $r = -.99$, $p < .001$). In comparison, edaphic variables were, in general uncorrelated except for total soil carbon, which was positively correlated to total soil nitrogen ($r = .92$, $p < 0.05$) and negatively correlated to soil bulk density ($r = -.88$, $p < 0.05$). Relationships between climatic and edaphic variables were not significant (Appendix 3; $p > 0.05$). Across volcanic plots, climatic variables were not significantly correlated to elevation. However, elevation was positively correlated to total soil nitrogen ($r = .99$, $p < 0.05$), and precipitation was positively correlated to soil bulk density ($r = .98$, $p < 0.05$) (Appendix 3). Elevation was similarly variable across both gradients, yet climatic variables (mean annual precipitation and mean temperature) were more variable across the serpentine gradient, while edaphic variables (total soil carbon and nitrogen (%), pH, and bulk density) were more variable across the volcanic gradient, with the exception of pH (Appendix 4).

The two PCA axes for abiotic conditions explained nearly 90% of the variation among all plots (Figure 3, Appendix 5). The first principal component (PC1) accounted for 73.2% with a high positive loading for total soil carbon (0.90) and a high negative loading for soil bulk density (-0.96). The second principal component (PC2) accounted for 16.5% with a high positive loading for elevation (0.58) and a high negative loading for temperature (-0.51). The serpentine plots were characterized by high values of soil pH, soil bulk density and temperature, whereas the volcanic plots were associated with high values of soil total carbon and total nitrogen. In general, the volcanic plots were more clustered in PCA space (representing lower environmental variability among plots) relative to serpentine plots.

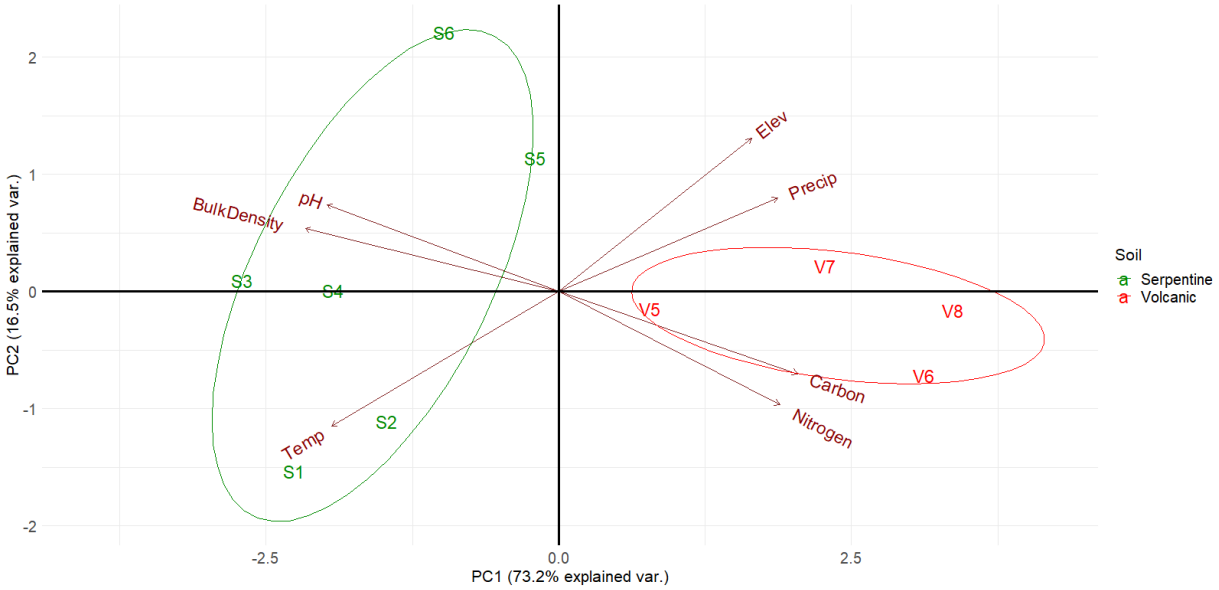

Figure 3: Principal component analysis of the first two axes (PC1 vs. PC2) for mean abiotic variables: Elevation (Elev, m); mean annual temperature (Temp, ºC); annual precipitation (Precip, mm); total soil carbon (Carbon, %); total soil nitrogen (Nitrogen, %); pH (1:1) H2O (pH); and Soil bulk density (BulkDensity, g·cm-3). Green datapoints depict serpentine sampling sites, red datapoints represent volcanic sampling sites. Ellipses indicate the conglomerate distribution of each elevational gradient.

A foundational assumption of trait-based ecology: Trait-environment relationships

Trait-environment relationships differed between gradients. In general, stronger relationships were found in plant communities on serpentine compared to volcanic soils (Table 1). For serpentine plots, correlations between environmental variables and all trait types (e.g. foliar 'soft' traits, wood hydraulic traits, and foliar nutrient traits) were found. Foliar traits were highly correlated with total soil nitrogen; wood traits were highly correlated with climatic variables; and foliar nutrient content traits were correlated with both soil and climatic variables. Across volcanic plots, only two significant correlations were found, both between foliar nutrient potassium content (K) and precipitation and bulk density. Significant trait-environment correlations were not shared between gradients.

Table 1. Pearson correlation coefficients for trait-environment relationships across study sites. All correlations between trait types were tested. If all correlations were included, the table would be quite large (15 traits x 6 abiotic factors) and difficult to read. Thus, for simplicity, only significant correlations are shown (p-value < 0.05). When a relationship was significant in one gradient, however, the relationship in the other gradient was also included in the table whether it was significant or not. In all cases, there were no significant relationships shared between the two gradients. The hyphen (-) indicates a non-significant relationship.

Serpentine			Volcanic		
Trait type	**Trait ~ Abiotic variable**	**Correlation coefficient**	**Trait type**	**Trait ~ Abiotic variable**	**Correlation coefficient**
Foliar	SLA ~ Nitrogen	-0.83	Foliar	SLA ~ Nitrogen	-
	LDMC ~ Nitrogen	0.84		LDMC ~ Nitrogen	-
Wood	Bwd ~ Precip	-0.84	Wood	Bwd ~ Precip	-
	PoreDens ~ Elev	-0.82		PoreDens ~ Elev	-
	PoreDens ~ Precip	-0.95		PoreDens ~ Precip	-
	PoreDens ~ Temp	0.82		PoreDens ~ Temp	-
	PoreDiam ~ Elev	0.85		PoreDiam ~ Elev	-
	PoreDiam ~ Precip	0.92		PoreDiam ~ Precip	-
	PoreDiam ~ Temp	-0.84		PoreDiam ~ Temp	-
Foliar nutrient content	Fe ~ Elev	0.84	Foliar nutrient content	Fe ~ Elev	-
	K ~ Precip	-		K ~ Precip	0.97
	K ~ BulkDensity	-		K ~ BulkDensity	1
	Mg ~ Precip	-0.83		Mg ~ Precip	-
	Mn ~ Elev	0.84		Mn ~ Elev	-
	Mn ~ Temp	-0.83		Mn ~ Temp	-

Functional variation in multiple dimensions and the stress dominance hypothesis

The two PCA axes of the foliar functional traits explained 85% of the variation among plots (Figure 4a, Appendix 5). The first principal component (PC1) accounted for 52.8% with a high positive loading for CWM LT (0.85) and a high negative loading for CWM LDMC (-0.88). The second principal component (PC2) accounted for 32.5% with a high negative loading for CWM SLA (-0.95). The two axes of the wood traits PCA explained 99% of the total variation among plots (Figure 4b, Appendix 5). The first principal component (PC1) accounted for 84.7% with a high positive loading for CWM PoreDens (0.94) and a high negative loading for CWM PoreDiam (-0.98). The second principal component (PC2) accounted for 14.6% with a high positive loading for CWM Bwd (0.55). Finally, the PCA axes for foliar nutrient traits explained 71% of the variance among plots (Figure 4c, Appendix 5). The first principal component (PC1) accounted for 42.2% with a high positive loading for CWM Na (0.9) and a high negative loading for CWM Mg (-0.67). The second principal component (PC2) accounted for 28.9% with a high positive loading for CWM Al (0.67) and a high negative loading for CWM S (-0.8). Serpentine plots were clustered in PCA

space for foliar 'soft' traits, wood hydraulic traits, and foliar nutrient traits. In contrast, volcanic plots were more dispersed in trait space, except for wood hydraulic traits (Figure 5).

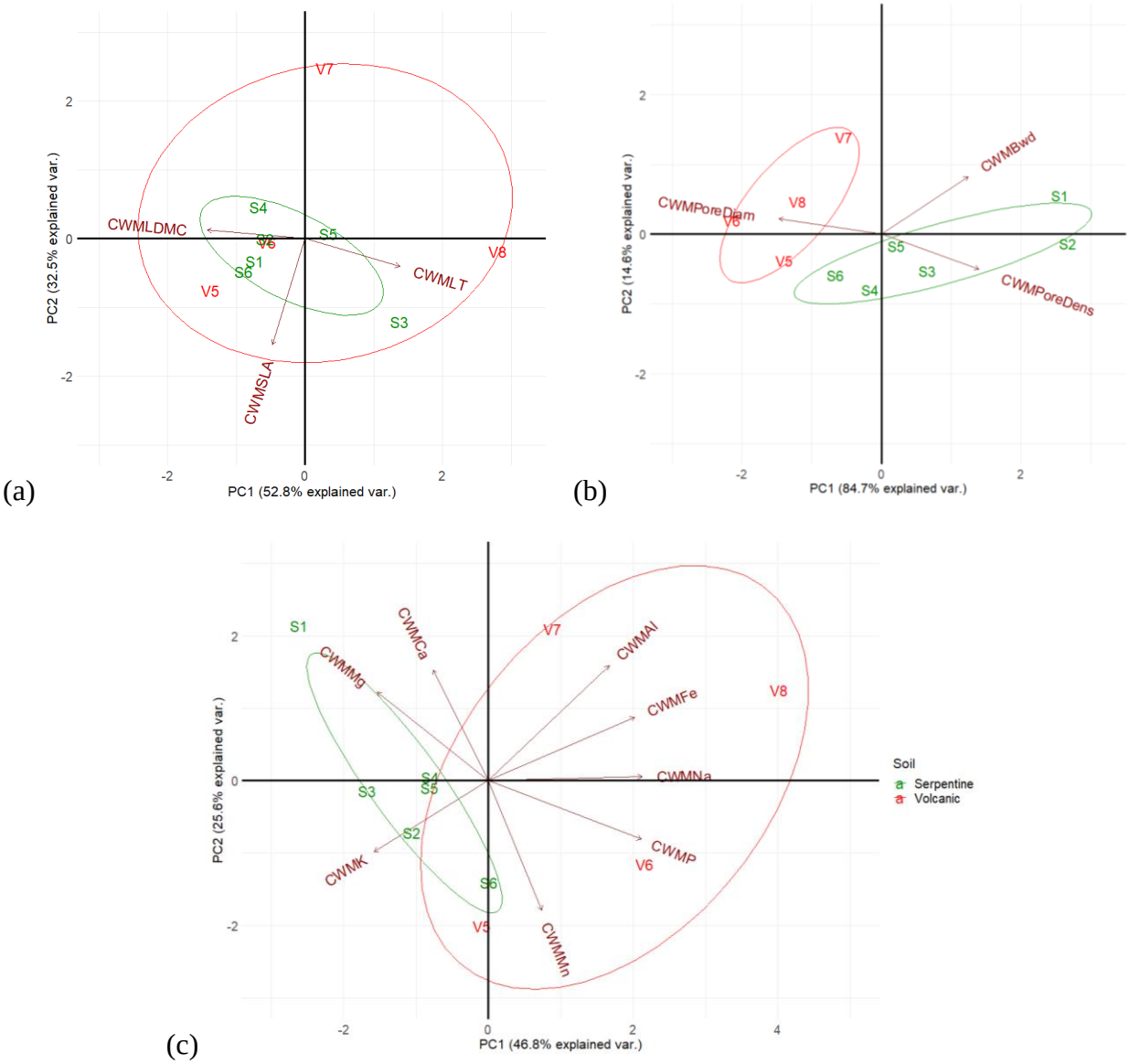

Figure 4: Principal component analysis (PC1 vs. PC2) of community weighted trait means. (a) Foliar traits: CWM LDMC (proportion), CWM SLA (cm2·g-1), and CWM LT (mm); (b) Wood traits: CWM PoreDiam (µm), CWM PoreDens (pores·mm-2), and CWM Bwd (g·cm3); (c) Foliar nutrient content (mg·g-1): CWM Ca, CWM Mg, CWM K, CWM Al, CWM Fe, CWM Na, CWM P, CWM Mn and CWM S. Green points represent serpentine sampling sites, red points represent volcanic sampling sites. Ellipses indicate the conglomerate distribution of each elevational gradient.

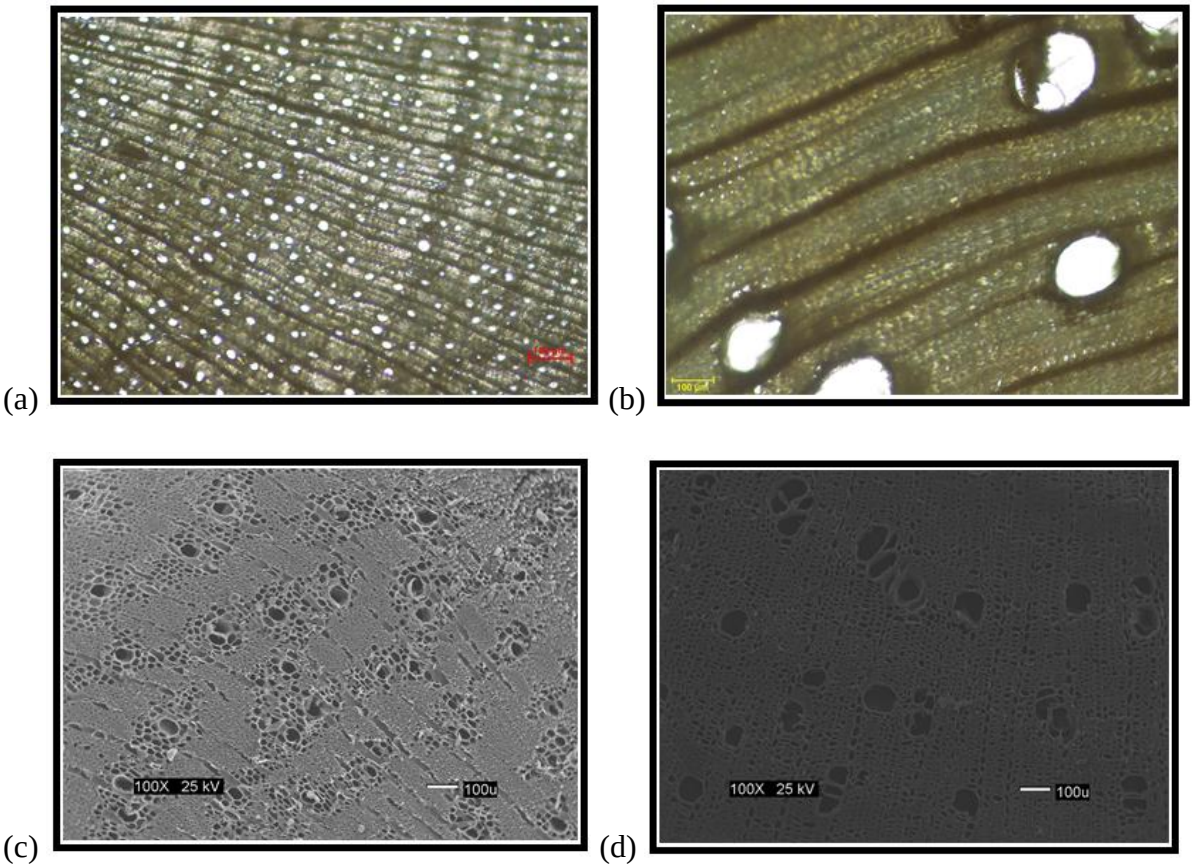

Figure 5. Photographs showing contrasting pore density and diameter across gradients. On serpentine soils, the lowest pore diameter value was represented by (a) *Gyminda latifolia* (S1), and the highest value was represented by (b) *Cecropia schreberiana* (S5). On volcanic soils, the lowest pore diameter value was represented by (c) *Tabebuia heterophylla* (V6), and the highest value was represented by (d) *Ixora ferrea* (V6). All photographs were taken at a magnification of 100X with either a light microscope (a, b) or a SEM microscope (c, d).

In multi-trait space, functional dispersion varied depending on the trait category used. For serpentine plots (Figure 6a, Appendix 6), functional dispersion (FD) for all traits significantly differed from FD calculated using all other trait categories ($p < 0.05$). Across both serpentine and volcanic sites, significant differences were found between FD calculated using foliar 'soft' traits and FD calculated using foliar nutrient traits ($p < 0.05$), and between wood hydraulic traits and foliar nutrient traits ($p < 0.01$). (Figure 6b, Appendix 6). In general, functional dispersion was higher for foliar nutrient traits than either foliar 'soft' traits (SLA, LDMC, LT) or wood hydraulic traits (Bwd, PoreDens, PoreDiam), which generally had comparable values of functional dispersion in either volcanic or serpentine gradients. Serpentine plots were more functionally dispersed for both foliar and wood traits ($p < 0.05$, see Appendix 7), in contrast to the PCA results and expectations based on the stress dominance hypothesis.

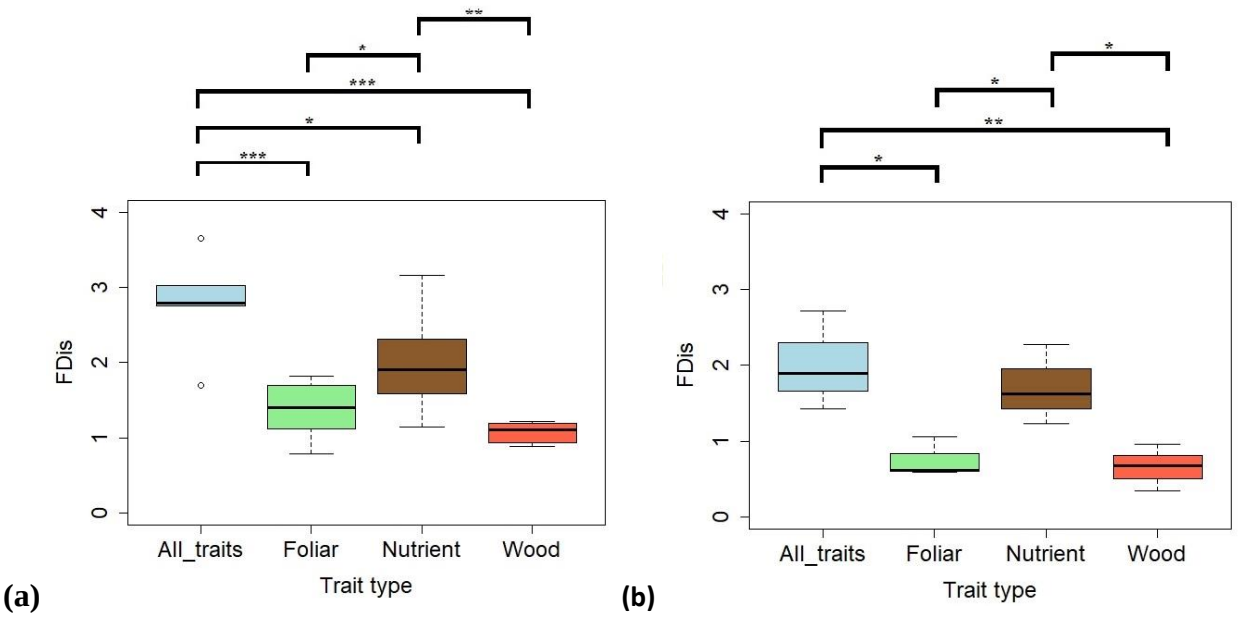

Figure 6: Functional diversity values for different trait categories: all traits (including foliar 'soft' traits, wood hydraulic traits, and foliar nutrient content), and each trait individually. Functional Dispersion (FDis) for (a) serpentine, and (b) volcanic plots. Asterisks represent significant differences between groups (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Trait covariation among trait types

In general, there were more trait-trait correlations on serpentine compared to volcanic soils for all trait types (Table 2). On serpentine soils, all trait type correlations were present. For example, foliar 'soft' traits were highly correlated with other foliar 'soft traits, wood hydraulic traits, and foliar nutrient content. Wood traits were strongly correlated to other wood traits and foliar nutrient content. Also, foliar nutrient traits were generally positively correlated to other foliar traits. Across volcanic soils, foliar and wood traits were uncorrelated. Foliar traits were strongly correlated with other foliar traits and foliar nutrient content. In comparison, wood traits were strongly correlated with foliar nutrient content, but not with other wood traits. Foliar nutrients were, in general, uncorrelated in volcanic plots.

Table 2. Pearson correlation coefficients for trait-trait covariation across study sites. All correlations between trait types were tested: foliar 'soft' traits (SLA, LDMC, LT), wood traits (Bwd, PoreDens, and PoreDiam), and foliar nutrient contents (Al, Ca, Mg, K, Fe, Na, P, Mn and S), for simplicity, only significant correlations are shown (p-value < 0.05). When a relationship was significant in one gradient, however, the relationship in the other gradient was also included in the table whether it was significant or not. Values in bold represent correlations shared between gradients. The hyphen (-) indicates a non-significant relationship.

Serpentine			Volcanic		
Trait type	**Trait - trait**	**Correlation coefficient**	**Trait type**	**Trait - trait**	**Correlation coefficient**
Foliar VS Foliar	SLA~ LT	-0.82	Foliar VS Foliar	SLA~ LT	-
	LDMC ~ LT	-		LDMC ~ LT	-0.63
Foliar VS Wood	LDMC ~ Bwd	0.66	Foliar VS Wood	LDMC ~ Bwd	-
Foliar VS Nut	SLA ~ Al	-	Foliar VS Nut	SLA ~ Al	-0.77
	SLA ~ Mn	0.30		SLA ~ Mn	-
	SLA ~ P	0.52		SLA ~ P	-
	LDMC ~ Na	-		LDMC ~ Na	-0.8
	LDMC ~ P	-0.37		LDMC ~ P	-
	LT ~ Al	-		LT ~ Al	0.79
	LT ~ Ca	0.30		LT ~ Ca	-
	LT ~ Fe	**-0.34**		**LT ~ Fe**	**0.98**
	LT ~ Mn	-0.29		LT ~ Mn	-
	LT ~ P	-0.31		LT ~ P	-
Wood VS Wood	Bwd ~ PoreDens	0.713	Wood VS Wood	Bwd ~ PoreDens	-
	Bwd ~ PoreDiam	-0.561		Bwd ~ PoreDiam	-
Wood VS Nut	Bwd ~ K	-0.38	Wood VS Nut	Bwd ~ K	-
	Bwd ~ Mn	**-0.28**		**Bwd ~ Mn**	**-0.66**
	Bwd ~ P	-0.77		Bwd ~ P	-
	PoreDens ~ Mg	0.34		PoreDens ~ Mg	-
	PoreDens ~ K	-		PoreDens ~ K	0.71
	PoreDens ~ P	**-0.53**		**PoreDens ~ P**	**-0.68**
	PoreDiam ~ K	0.36		PoreDiam ~ K	-
	PoreDiam ~ Mn	0.28		PoreDiam ~ Mn	-
	PoreDiam ~ P	**0.55**		**PoreDiam ~ P**	**0.69**
Nut VS Nut	Al ~ Ca	0.63	Nut VS Nut	Al ~ Ca	-
	Al ~ Fe	-		Al ~ Fe	0.85
	Al ~ Mg	0.41		Al ~ Mg	-
	Al ~ S	-		Al ~ S	-0.64
	Ca ~ Mg	0.55		Ca ~ Mg	-
	Fe ~ K	0.31		Fe ~ K	-
	K ~ Mn	0.35		K ~ Mn	-
	K ~ P	0.41		K ~ P	-
	Mn ~ P	0.35		Mn ~ P	-
	Na ~ S	0.45		Na ~ S	-

General results

In the volcanic gradient a total of 10 species made up 80% of relative abundance, resulting in 41 individuals sampled, whereas on serpentine plots a total of 59 species made up 80% of relative abundances, resulting in 267 individuals sampled (Appendix 1). The results were associated with two general factors: the environmental conditions, and the trait analysis (multiple dimensions,

multiple traits, and trait-trait correlations). First, based on abiotic conditions, the relevance of using elevation as a proxy of abiotic conditions was tested in both gradients. Whereas in serpentine plots all climatic variables were significantly correlated to each other, these correlations were not found across the volcanic gradient (Appendix 3). The PCA for abiotic conditions (Fig. 3, Appendix 5) explained 90% of the variation among plots. Both gradients were associated with high values of different abiotic conditions. Serpentine plots were associated with high values of soil pH, soil bulk density and temperature, whereas the volcanic plots were associated with high values of soil total carbon and total nitrogen. In addition, stronger trait-environment relationships were found in plant communities on serpentine compared to volcanic soils (Table 1).

Second, the trait analyses exhibited complementary results. The PCA results (Fig. 5), demonstrated that serpentine plots were clustered for foliar 'soft' traits, wood traits, and foliar nutrient content. In contrast, volcanic plots were more dispersed in trait space, except for wood hydraulic traits. In comparison, functional dispersion values were consistently higher for foliar nutrient traits than either foliar 'soft' traits or wood hydraulic traits in either gradient. Foliar 'soft' traits and wood hydraulic traits generally had comparable values of functional dispersion across volcanic or serpentine gradients (Fig. 6). However, serpentine plots were more functionally dispersed for both foliar and wood traits in contrast to PCA results and opposite to predictions from the stress dominance hypothesis. Finally, trait-trait covariation was higher on serpentine compared to volcanic soils for all trait types (Table 2).

DISCUSSION

Is elevation sufficient to capture abiotic variation across elevation?

The use of elevation as a proxy of abiotic conditions is not enough to generalize the variability of mountain environments. In the present study, elevation was only correlated to environmental factors in the serpentine gradient (Appendix 3, Figure 3) where precipitation increased and temperature decreased with increasing elevation. While temperature is known to vary predictably with elevation (decreasing an average of 0.68°C for each 100 m increase in elevation: Barry, 2008) the direction of change in precipitation with increasing elevation is much more variable (Anders & Nesbitt, 2015). Most studies report increasing precipitation with increasing elevation (Duckstein, Fogel, & Thames, 1973; Van Beusekom et al., 2015). However, some mountains show little variation in precipitation with elevation, while others show decreasing precipitation with increasing elevation (Pringle, Triska, & Browder, 1990; Barry, 2008). Other abiotic factors such as soil properties have a more complex relationship with elevation (e.g., Yüksek et al., 2013). Across serpentine plots, soil carbon and nitrogen tended to decrease with increasing elevation, contrary to other studies (Birk & Vitousek, 1986). The low values of soil carbon and nitrogen in serpentine soils found here are characteristic of the low nutrient availability of this soil type (Nicks & Chambers, 1995; Zhang et al., 2001; Kay et al., 2011). The increasing precipitation at higher elevations coupled with the high porosity and drainage of this soil type, likely lead to increased nutrient leaching (Cole, 1995), which may help to explain the lower soil nutrient content at higher elevations seen here. Yet, the tall, gallery forests that develop at high elevations on serpentine soils in this study, in comparison to other serpentine communities throughout the Caribbean (e.g., Ramírez & Castañeda, 2017) and around the world (e.g., Harrison et al., 2015), point to important interactions between climatic and edaphic properties, further emphasizing that other abiotic factors are important to consider in addition to elevation.

In contrast, total soil nitrogen and carbon tended to increase with increasing elevation on volcanic soils, as shown in other tropical volcanic mountains. Increased soil nutrient availability at higher elevations on volcanic soils is thought to be due to processes related to soil formation, with younger soil age occurring at higher elevations due to intermittent ash deposition (Pringle et al., 1990; Sparks, 2002; Cusack, 2013). Whereas soil at lower elevations result from the colluvial

deposition of volcanic rocks, and thus tend to be less nutrient rich. Soil nutrient availability is also likely influenced by land use history. Even though the Luquillo Mountains were proclaimed a reserve in 1876, agriculture, timber extraction, and charcoal production were allowed in some areas during 1912-1948 (Robinson, Bauer, & Lugo; 2014). It is thought that these activities primarily affected nutrient availability at middle and lower elevations (Weaver, 2012). Soil nutrient composition at higher elevations, at least in the volcanic gradient in this study, appears to be additionally influenced by the deposition of Saharan Dust (Ping et al., 2013), possibly due to the direct interception of trade winds at higher elevations. The contribution of Saharan Dust to soil inorganic inputs in Puerto Rico is still debated. However, Puerto Rico is located downwind of the largest airborne dust source originating in Africa, which generates a contribution of dry depositions between 53 and 73% (McClintock et al., 2019). Pett-Ridge et al. (2009) showed that Saharan dust contributes significantly to atmospheric inputs to soil in the Luquillo Mountains, also, Heartsill - Scalley et al. (2007) argue that its contribution, although detectable, may be minor. Interestingly, inputs of the inorganic ion K+ were extremely high in rainfall at mid-elevations in the Luquillo Experimental Forest, where the present study took place, which can only be attributed to non-marine inputs such as Saharan dust (Medina et al., 2013). This may help to explain variation in foliar K content which was positively related to precipitation and soil bulk density in the volcanic plots (discussed below).

In addition to variable environment-environment relationships, the abiotic environment itself dramatically differed between soil types (Figure 3). Serpentine forest communities were associated with higher values of soil pH, temperature and soil bulk density, and lower values of total soil carbon, soil nitrogen, and precipitation relative to volcanic forest communities. In comparison, volcanic plant communities were associated with high values of total soil nitrogen and carbon, and low soil bulk density reflecting increased soil water availability and increased accumulation of organic matter (Zhang et al., 2001; Dahlgren et al., 2004). Finally, there was higher environmental variability among serpentine plots compared to volcanic plots, which were environmentally less heterogenous, even though the elevational range between mountains was similar (serpentine: 253 - 875 m, volcanic: 380 - 1010 m). These results demonstrate the importance of including a broader assessment of abiotic conditions across elevation (Muenchow et al., 2013), and further discourages the use of elevation as a proxy for abiotic conditions.

Trait-environment relationships are variable

In serpentine soils, high values of bulk density and, presumably, lower water availability (Zhang et al., 2001) influence plant functional trait composition, as seen by higher wood density in lower elevation serpentine communities where conditions were warmer and drier (Figure 3). Higher wood density results in slower plant growth rate (Swenson & Enquist, 2007; Ordóñez et al., 2009), which is characteristic of other serpentine plant communities around the world (Harrison et al. 2015). Plants growing in water-limited systems are also known to develop hydraulic strategies that include greater pore density and smaller pore diameters (Figure 4b), favoring low water conduction and resistance to embolism (Olson et al., 2014), as evident in serpentine plant communities of this study. In comparison, the higher precipitation of volcanic sites can explain patterns of wood trait variation reported in this study. Functional traits in the volcanic gradient indicate weaker environmental selection. For example, low wood densiy values were found in all communities across the gradient. In the lower part of the mountain (tabonuco forest) low wood density values reflect higher growth rates in warmer conditions. In comparison, low values of wood density at the highest elevations (elfin woodland forest) suggests that, despite the increased water availability, the extreme conditions related to cloud immersion and wind, increases environmental stress (Howard, 1969; Gould et al., 2006). Indeed, SLA was higher in the lower elevation tabonuco and colorado forests compared to the higher elevation elfin woodland forests, which also had thicker leaves (Figure 4a). Despite the apparent stress at high elevations in volcanic soils, relative to serpentine plant communities, functional traits of volcanic communities indicate weaker environmental selection, in line with the stress dominance hypothesis.

The contrasting environmental conditions between volcanic and serpentine mountains appeared to influence the strength of the relationship between functional traits and the environment (Table 1), suggesting that the strength of selection for particular trait optima may be variable across environments and across traits (Butterfield & Callaway, 2013). If the strength of trait-environment relationships varies predictably across environmental gradients, this would help to explain why these relationships appear idiosyncratic when comparing different studies. For example, water was a major limiting factor underlying directional trends of foliar trait variation (Salazar, 2015), yet these results may be dependent on the scale and type of ecosystem studied (in the cited example, at a local scale in a tropical dry forest). Yet at global scales, soil fertility predominantly determines

foliar trait variation (Ordoñez et al., 2009). Thus, the slope of the relationship between SLA and the environment, for example, may be dependent on other external factors such as water availability (Reich et al., 1999; Wright et al., 2002, 2004). Determining predictable shifts in the relationship (i.e., the slope) between key plant traits and environmental variables are a necessary next step for reliably calibrating models designed to predict vegetation and productivity changes with global climate and land-use change (Wright et al. 2005).

In addition, the type of trait appeared to affect the strength of the trait-environment relationship. In serpentine plant communities, there was a high number of significant relationships between traits and environmental factors. Foliar traits (SLA, LDMC) were highly correlated to total soil nitrogen. The low availability of soil nutrients in serpentine soils may severely limit plant development and survival (Epstein & Bloom, 2005), thus influencing plant functional traits more strongly (Grossman & Takahashi, 2001) compared to volcanic soils. In general, foliar nutrient traits were not correlated to climatic variables. Thus, 'soft' traits appeared more labile across environmental conditions, reflecting their cheaper construction costs and higher plasticity (Wright et al., 2004). Like other studies, foliar nutrient content was correlated with climatic variables (elevation, precipitation, temperature) likely due to interactions between climate and soil characteristics (Ordoñez et al., 2009). In addition, wood traits (Bwd, PoreDens, PoreDiam) were primarily correlated to climatic variables, with more conservative hydraulic strategies (higher PoreDens and lower PoreDiam) and thus increased resistance to cavitation and embolism (Rosas, 2019) in areas of lower water availability and higher soil density.

In contrast, among all traits measured in volcanic plots, only foliar K (potassium) was positively associated with precipitation and soil bulk density, as reported in Brockley (1976). High levels of K+ in rainfall are thought to be primarily due to non-marine inputs, such as an influx of Saharan dust (Medina et al. 2013). However, higher ion concentrations were reported below cloud line, because cloud formation doesn't typically allow dry deposition of airborne particles (Medina et al. 2013). Our results confirm this pattern, with higher values of foliar K in low-lying tabonuco forests and lower values of foliar K in high elevation elfin forests. Foliar K is involved with stomatal conductance and is thought to predict a plants' response to drought conditions (Wang et al., 2013). Thus, increased drought intensity and frequency (Jennings et al., 2014), may be offset by physiological responses of plants in these communities. High differences in the quantity of

correlations between both gradients suggests that relationships between trait and abiotic factors are variable across different environments (Butterfield & Callaway, 2013). In general, serpentine communities had greater environmental pressure, as evidenced by more conservative hydraulic strategies (larger PoreDens and smaller PoreDiam) (Rosas, 2019) and stronger trait-environment relationships. Because climate change scenarios predict increased drought in this area (Angeles et al., 2007; Jennings et al., 2014; Van Beusekom et al., 2015), conservative hydraulic strategies may result in less sensitivity to climate change. Less variation of 'soft' traits across elevation lends further support to the idea that serpentine plant communities are less sensitive to climate change (Harrison et al., 2015).

Functional variation in multiple dimensions and the stress dominance hypothesis

The magnitude of trait variation may also depend on the type and number of trait axes included. In two dimensions (PCA analyses using CWM values), the magnitude of trait variation in different environments was highly dependent on the trait type used. Serpentine plant communities appeared clustered in PCA space regardless of the trait type used (foliar 'soft' traits, wood traits, or foliar nutrient traits). In contrast, volcanic plant communities appeared clustered only when using wood traits. Wood traits have been shown to be less labile compared to leaf traits, due to the higher energetic costs associated with wood construction. As a result, wood trait variation is, generally, smaller than leaf trait variation (Wright et al., 2004; Chave et al., 2009) which tends to be more variable across environmental gradients. In other words, when using two trait axes, volcanic communities appeared more dispersed while serpentine communities appeared more clustered, in line with expectations from the stress dominance hypothesis of increased clustering with increased stress.

Arguably, a multi-dimensional approach provides a better characterization of ecological strategies across plant communities (e.g., Petchey, Hector, & Gaston, 2004; Mason et al., 2005; Schleuter et al., 2010). Metrics of functional dispersion were developed to explain the similarity of species in n-dimensional trait space (Laliberte & Legendre, 2010). When all trait types were included, values of functional dispersion were higher regardless of soil type. In general, functional dispersion was higher on serpentine soils, contrary to results shown in two dimensions and contrary to predictions based on the stress dominance hypothesis (SDH). This result can be understood

considering environmental variation between sites. The SDH proposes the coexistence of species with similar trait values and thus less niche differentiation in stressful or harsh environments (Grime, 1977; Adler et al., 2013). In environments with persistent limiting factors (such as low soil fertility), the adaptation of different strategies in response to the same stress variable can result in high niche differentiation (Butterfield & Callaway, 2013), resulting in the coexistence of functionally distinct species due to environmental stress rather than from competition or limiting similarity among species (Funk et al., 2016). In this case, high niche differentiation in response to stress may reflect a diversity of ecological strategies for stress avoidance or stress tolerance (Ludlow, 1989). In serpentine plant communities, soil characteristics appear to be a more limiting factor for plant development in comparison with climatic factors, as shown in other studies comparing plant communities on serpentine and non-serpentine soils (Fernandez-Going et al., 2013; Harrison et al., 2015).

Trait covariance depends on specific site conditions

Multiple studies suggest that including different trait types may better reflect the multi-dimensional functionality of plant responses to elevation (Kraft, Godoy, & Levine, 2015; Umaña & Swenson, 2019b). Trait covariation supports the idea that functional traits do not vary independently, where a high correlation between traits may indicate that the traits share similar roles in community assembly, respond similarly to environmental conditions, or share a common genetic control (Wright et al., 2007). In this study, trait covariation was generally stronger in serpentine plots relative to volcanic plots (Table 2). This result suggests that environmental filtering and environmental conditions may help to explain differences in the strength and direction of trait-trait correlations across studies, possibly explaining why these relationships appear idiosyncratic across systems and species (e.g., Westoby & Wright, 2006; Ishida et al., 2008; Fajardo & Piper, 2011). Thus, trait covariation may depend on the abiotic conditions in a specific location. It is possible that the harsh environmental conditions typical of serpentine soils are a stronger environmental filter (relative to volcanic soils) and thus more strongly restrict trait values, resulting in tighter correlations between traits and less trait variation around the optimal value (less scatter). This finding loosely supports the stress dominance hypothesis. In general, patterns of trait covariation across serpentine and volcanic sites reflect important tradeoffs in plant function. For

example, wood-wood correlations (present only in serpentine plots) reflect higher hydraulic pressure due to lower precipitation and higher soil bulk density in serpentine soils (Figure 3).

Across both gradients, correlations between wood and foliar nutrient traits imply linkages between plant water and nutrient status. For example, low values of leaf P may reduce vessel pore diameter (e.g., Cai et al., 2017) and increase vessel pore density (e.g., Lovelock et al., 2006), because P defficiency is correlated with hydraulic limitations. Thus lower leaf P availability will decrease hydraulic conductivity (Lovelock et al., 2006). In the present study, leaf P was negatively correlated with pore density (serpentine: -0.53, volcanic: -0.68) and positively correlated to pore diameter (serpentine: 0.55, volcanic: 0.69), suggesting that low P availability may cause strong environmental filtering (Van der Sande et al., 2015), selecting for more conservative wood strategies (Rosas, 2019). Aditionally, across both gradients, foliar nutrients were highly correlated suggesting that analyzing a subset may be sufficient when funding is limited. Foliar nutrients were also generally correlated with wood traits, suggesting that leaf nutrients may possibly be eliminated in large trait campaigns, if funding is a major constraint and other 'hard' traits are measured.

Even though a growing number of studies quantify trait variation, these studies emphasize what are known as ‘soft’ traits (e.g., Reich, Ellsworth & Walters, 1998; Tardieu, Granier & Muller, 1999; Wilson, Thompson & Hodgson, 1999; Evans & Poorter, 2001; Ackerly et al., 2002; Hodgson et al., 2011). The present study provides justification for the need to include ‘hard’ traits (especially those related to hydraulic function) to understand how the environment shapes plant communities across elevation. Few correlations were found between foliar and wood traits, questioning the generality of the leaf economic spectrum which assumes that traits like specific leaf area reflect a tradeoff in plant growth strategies. Specific leaf area is likely one of the most widely measured functional traits at global scales due to its ease of measurement. However, the results shown here defy the high deduction power that many studies have assigned to SLA, exhibiting a growing disconnect between ‘soft’ traits that are only loosely correlated to physiological or demographic processes (Belluau & Shipley, 2018), and patterns of community assembly.

CONCLUSION

1. The use of elevation as a proxy of abiotic conditions is not enough to generalize the variability of species richness or trait patterns across mountains. This conclusion appears obvious but is not well integrated into trait-based ecology. The results shown here demonstrate the need to include additional abiotic factors (in addition to elevation) to explain patterns of functional trait diversity.
2. The need to measure abiotic factors across environmental gradients is further seen in the variable relationships between traits and climatic and edaphic properties. It is highly likely that the slope of the relationship between functional traits and environmental variables is dependent on, and thus predicted by, environmental conditions with tighter trait-environment relationships in areas where the strength of selection is stronger, such as in climatically or edaphically harsh environments. Similarly, trait-trait covariation may be dependent on environmental variation. As a result, more work should focus on synthesizing the slope of trait-environment and trait-trait relationships.
3. The ability to distinguish trait variation in different environments depends on the trait type, likely a result of variable trait-environment relationships. Trait-based studies will need to evaluate the costs and benefits of including both 'soft' and 'hard' traits, particularly if growing evidence demonstrates that 'soft' traits are not correlated to 'hard' traits, as pervasively as currently believed.
4. This study provides multiple lines of evidence in support of the stress dominance hypothesis yet highlights an important and often overlooked subtlety. The direction of stress across elevation is highly variable across mountains, further emphasizing that elevation alone should not be used to synthesize patterns of species or trait diversity.
5. Finally, this project represents the first synthesis of forest inventory data for serpentine woody plant communities. It is among the few studies detailing functional diversity gradients in Puerto Rico and the Caribbean (Muscarella et al., 2015; Swenson et al., 2011b), and the only study detailing functional diversity of tropical serpentine plant communities. The application of trait-based approaches is particularly relevant in Puerto Rico and the Caribbean where high environmental heterogeneity across small spatial scales produces one of the world's richest biodiversity hotspots.

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APPENDIX

Appendix 1: Plots selected for this study. Serpentine sites are indicated by the letter "S" and volcanic sites are indicated by the letter "V". Asterisks indicate the number of species that represent 80% of the total abundance of each plot.

Cod	Station	Altitude (m)	Municipio	Total number of species	Number of species (80% ab) *	Number of families (80% ab) *
S1	Susua	253	Yauco	19	12	8
S2	Susua	296	Yauco	9	4	3
S3	Susua	347	San German	17	6	6
S4	Maricao	421	San German	11	6	5
S5	Maricao	786	Maricao	22	17	14
S6	Maricao	875	Maricao	21	14	14
V5	Tabonuco forest	380	Río Grande (El Verde)	7	3	2
V6	Palo colorado forest	751	Río Grande (Toro Trail II)	6	3	3
V7	Sierra palm forest	835	Río Grande (Mt. Britton)	1	1	1
V8	Elfin Woodland vegetation	1010	Río Grande (Yunque Peak)	4	3	3

Appendix 2: Description of the functional traits measured and their relevance to plant function.

Trait	Unit	Class	Interpretation	# of measurements per individual
Specific Leaf Area (SLA)	cm2/g	Carbon fixation and drought evasion	Related to photosynthetic and growth rate. Large SLA indicates greater hydraulic availability.	5
Leaf Dry Matter Content (LDMC)	Prop. *		Related to the leaf's capacity of defense, longevity, and carbon fixation.	5
Leaf Thickness (LT)	mm	Resistance to drought and temperature variation	Related to the capacity to avoid drought and physical defense, large values represent a high cost of construction.	5
Basic Wood Density (Bwd)	g/cm3	Competitive capacity and resistance to drought	Related to growth and hydraulic capacity, a large Bwd indicates slow growth and low hydraulic capacity.	1
Pore Diameter (PoreDiam)	µm	Hydraulic security in drought conditions	Related to longitudinal hydraulic conductivity and overcoming embolism. In soils with low-water availability, species will have small diameters (hydraulic security); in contrast, a high-water availability will generate bigger diameters (hydraulic efficiency).	30
Pore Density (PoreDens)	# Pores/ mm2		Related to the hydraulic conductivity, here, a large pore density indicates a low probability of embolism, greater resistance to drought, and better hydraulic security for small pore size.	10

* Means proportion.

Appendix 3. Pearson correlation coefficients of abiotic variables across study sites: Elevation (Elev, m); mean annual temperature (Temp, ºC); annual precipitation (Precip, mm); total soil carbon (Carbon, %); total soil nitrogen (Nitrogen, %); pH (1:1) H2O (pH); and bulk density (BulkDensity, g·cm-3).. The values above the diagonal represents the p-value, and the values below the diagonal represent the correlation coefficient. Values in bold represent a significant p-value (< 0.05).

Serpentine	**Elev**	**Precip**	**Temp**	**Carbon**	**Nitrogen**	**pH**	**Bulk Density**
Elevation		**0.02**	**0.00**	0.69	0.44	0.37	0.85
Precipitation	0.89		**0.01**	0.63	0.36	0.35	0.94
Temperature	-0.99	-0.92		0.74	0.45	0.44	0.79
Carbon	-0.21	-0.25	0.18		**0.01**	0.52	**0.02**
Nitrogen	-0.39	-0.46	0.39	0.92		0.79	0.15
pH	0.45	0.47	-0.4	-0.33	-0.14		0.41
Bulk density	-0.1	-0.04	0.14	-0.88	-0.66	0.42	

Volcanic	**Elev**	**Precip**	**Temp**	**Carbon**	**Nitrogen**	**pH**	**Bulk Density**
Elevation		0.16	0.05	0.41	**0.01**	0.80	0.16
Precipitation	-0.84		0.05	0.19	0.21	0.75	**0.02**
Temperature	-0.95	0.95		0.37	0.09	0.92	0.10
Carbon	0.60	-0.81	-0.63		0.39	0.25	0.10
Nitrogen	0.99	-0.79	-0.91	0.61		0.71	0.19
pH	-0.20	0.25	0.08	-0.75	-0.29		0.57
Bulk density	-0.84	0.98	0.90	-0.90	-0.81	0.43	

Appendix 4: Mean and Standard deviation of abiotic conditions measured in each gradient

Abiotic variable	SERPENTINE		VOLCANIC	
	Mean	**SD**	**Mean**	**SD**
Elevation (m)	496	266	744	266
Precipitation (mm)	2208	324	2922	115
Temperature (°C)	23	2	20	1
Total soil Carbon (%)	6.5	1.5	15.9	5.9
Total soil Nitrogen (%)	0.4	0.1	0.7	0.1
pH (1:1) H_2O	6.8	0.5	4.4	0.3
Soil Bulk Density (g.cm3)	0.9	0.1	0.5	0.2

Appendix 5: Loading of the first three Principal Components (Dim) in the principal component analysis (PC1 vs. PC2) of the evaluated variables: mean abiotic values (Figure 3), CWM foliar functional traits (Figure 4a), CWM wood functional traits (Figure 4b), and CWM foliar nutrient contents (Figure 4c). The eigenvalues for each axis and cumulative variance explained, is also included.

Evaluated variables group	Variable	PC1	PC2	PC3
Abiotic conditions mean value (Figure 3)	Elev	0.73	0.58	0.36
	Precip	0.83	0.35	-0.41
	Temp	-0.86	-0.51	0.02
	Total Carbon	0.90	-0.31	0.13
	Total Nitrogen	0.83	-0.43	0.21
	pH	-0.87	0.33	0.30
	Bulk density	-0.96	0.24	-0.08
	Eigenvalue	5.12	1.15	0.46
	Proportion of variance explained	73.21	16.49	6.52
	Cumulative variance explained	73.21	89.71	96.23
Foliar functional traits community weighted means (Figure 4a)	CWMLeaftickness	0.85	-0.25	-0.46
	CWMSLA	-0.29	-0.95	0.08
	CWMLDMC	-0.88	0.07	-0.47
	Eigenvalue	1.58	52.85	52.85
	Proportion of variance explained	0.97	32.51	85.36
	Cumulative variance explained	0.44	14.64	100.00
Wood functional traits community weighted means (Figure 4b)	CWM.Bwd	0.84	0.55	-0.03
	CWM.PoreDens	0.94	-0.34	-0.09
	CWM.PoreDiam	-0.98	0.15	-0.11
	Eigenvalue	2.54	0.44	0.02
	Proportion of variance explained	84.68	14.63	0.69
	Cumulative variance explained	84.68	99.31	100.00
Foliar nutrient contents community weighted means (Figure 4c)	CWM.Al	0.62	0.67	-0.30
	CWM.Ca	-0.38	0.53	-0.66
	CWM.Fe	0.79	0.43	0.07

	CWM.K	-0.58	-0.57	-0.16
	CWM.Mg	-0.67	0.35	-0.15
	CWM.Mn	0.40	-0.75	-0.33
	CWM.Na	0.90	0.01	-0.39
	CWM.P	0.89	-0.14	0.30
	CWM.S	0.29	-0.80	-0.35
	Eigenvalue	3.79	2.60	1.06
	Proportion of variance explained	4.22	2.89	1.18
	Cumulative variance explained	42.16	71.02	82.80

Appendix 6: Post-hoc LSD Fisher test results for: Functional Dispersion (FDis) in (a) serpentine and (b) volcanic (b) sites. Indices evaluated between trait types: all traits (foliar, wood, and foliar nutrient content), and each trait type individually (foliar 'soft', wood hydraulic, or foliar nutrient traits). Asterisks represent significant differences between groups (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Functional diversity indices and evaluated gradient	**Trait type comparison**	**diff**	**Lwr.ci**	**Upr.ci**	**p-value**	**Significance**
FDis – Serpentine gradient (Figure 6a)	Foliar – All traits	-1.42	-2.04	-0.80	0.0001	***
	Nutrient – All traits	-0.79	-1.41	-0.17	0.02	*
	Wood – All traits	-1.71	-2.33	-1.09	0.00001	***
	Nutrient – Foliar	0.63	0.01	1.25	0.05	*
	Wood – Foliar	-0.29	-0.91	0.33	0.33	
	Wood - Nutrient	-0.93	-1.55	-0.31	0.01	**
FDis – Volcanic gradient (Figure 6b)	Foliar – All traits	-1.26	-2.13	-0.38	0.01	*
	Nutrient – All traits	-0.30	-1.18	0.58	0.45	
	Wood – All traits	-1.36	-2.23	-0.48	0.01	**
	Nutrient – Foliar	0.96	0.08	1.84	0.04	*
	Wood – Foliar	-0.10	-0.98	0.78	0.80	
	Wood - Nutrient	-1.06	-1.94	-0.18	0.02	*

Appendix 7. Type I ANOVA test results for Functional Dispersion (FDis) between trait types: all traits (foliar, wood, and foliar nutrient content), and each trait type individually (foliar 'soft', wood hydraulic, or foliar nutrient traits). Indices evaluated in (a) serpentine and (b) volcanic sites. Asterisks represent significant differences between the groups ($p < 0.05$).

Functional diversity indices and evaluated gradient	**Factor**	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**p-value**	**Significance**
FDis – All traits	Soil	1	1.20	1.20	2.95	0.13	
	Residuals	7	2.84	0.41			
FDis – Foliar	Soil	1	0.75	0.75	5.65	0.05	*
	Residuals	7	0.93	0.13			
FDis – Foliar nutrient content	Soil	1	0.17	0.17	0.39	0.55	
	Residuals	7	2.99	0.43			
FDis – Wood	Soil	1	0.35	0.35	8.67	0.02	*
	Residuals	7	0.28	0.04			