



Technical Note

Large-Scale Controls on the Leaf Economic Spectrum of the Overstory Tree Species *Metrosideros polymorpha*

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Abstract: The role of intraspecific trait variation in functional ecology has gained traction in recent years as many papers have observed its importance in driving community diversity and ecology. Yet much of the work in this field relies on field-based trait surveys. Here, we used continuous canopy trait information derived from remote sensing data of a highly polymorphic tree species, *Metrosideros polymorpha*, to quantify environmental controls on intraspecific trait variation. *M. polymorpha*, an endemic, keystone tree species in Hawai'i, varies morphologically, chemically, and genetically across broad elevation and soil substrate age gradients, making it an ideal model organism to explore large-scale environmental drivers of intraspecific trait variation. *M. polymorpha* canopy reflectance (visible to shortwave infrared; 380–2510 nm) and light detection and ranging (LiDAR) data collected by the Global Airborne Observatory were modeled to canopy trait estimates of leaf mass per area, chlorophyll a and b, carotenoids, total carbon, nitrogen, phosphorus, phenols, cellulose, and top of canopy height using previously developed leaf chemometric equations. We explored how these derived traits varied across environmental gradients by extracting elevation, slope, aspect, precipitation, and soil substrate age data at canopy locations. We then obtained the feature importance values of the environmental factors in predicting each leaf trait by training random forest models to predict leaf traits individually. Of these environmental factors, elevation was the most important predictor for all canopy traits. Elevation not only affected canopy traits directly but also indirectly by influencing the relationships between soil substrate age and canopy traits as well as between nitrogen and other traits, as indicated by the change in slope between the variables at different elevation ranges. In conclusion, intraspecific variation in *M. polymorpha* traits derived from remote sensing adheres to known leaf economic spectrum (LES) patterns as well as interspecific LES traits previously mapped using imaging spectroscopy.

Keywords: imaging spectroscopy; leaf economic spectrum; intraspecific trait variation; *Metrosideros polymorpha*; Hawai'i



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1. Introduction

Community ecology and metrics for assessing functional diversity have traditionally focused on interspecific trait variation and species turnover along environmental gradients [1–3]. For example, the leaf economic spectrum (LES), which describes how plant traits covary, primarily describes interspecific trait variation [2]. Since the theory was developed, the role of intraspecific variation in the LES has been investigated with conflicting results [4–7]. For example, intraspecific variation patterns in montane boreal forests were contrary to community-level interspecific patterns that followed the LES [5]. In contrast, intraspecific variation in temperate rainforests did follow LES and contributed to overall trait variation within the community [4]. Moreover, quantifying the functional diversity of forest communities often ignores intraspecific variation by using species trait means

despite the importance of intraspecific trait variation in driving functional diversity—about 25% according to one meta-analysis [8]. Many studies agree that our understanding of functional diversity and community ecology could be enhanced by better incorporating intraspecific trait diversity [1,9–12].

Quantifying intraspecific trait variation on large geographic scales is possible with remote sensing, specifically imaging spectroscopy. Imaging spectroscopy is a remote sensing technique that captures a continuous portion of the electromagnetic spectrum from the visible (~380 nm) to the shortwave infrared (~2510 nm) at short (~5–10 nm) wavelength intervals. By sampling the spectra at high spectral resolution, these data capture surface chemistry [13,14], and when applied to vegetation, canopy traits (e.g., leaf mass per area, leaf nitrogen, lignin, etc.) can be estimated with demonstrable accuracy [15–17]. These data have been used to quantify functional diversity [18] and interspecific leaf trait patterns [19] at the landscape and regional levels.

Metrosideros polymorpha (‘ōhi‘a lehua) on Hawai‘i Island is an ideal model canopy tree species to study intraspecific trait variation. *M. polymorpha* spans the entirety of Hawai‘i Island across recent (<50 years) lava flows to older soils (~325,000 years old) and from sea level to the tree line (~9000 m). This species is highly polymorphic and has differentiated into four distinct genotypes that self-sort along elevation and soil substrate age gradients [20,21]. By quantifying canopy traits of *M. polymorpha* across Hawai‘i Island using imaging spectroscopy data, we can observe intraspecific trait variation of continuous canopies across broad environmental gradients on a large spatial scale (~10,000 km²). While prior studies have confirmed that interspecific and community-scale trait patterns follow LES across large spatial scales using imaging spectroscopy data [19], we investigated intraspecific variation with regard to the LES using the *M. polymorpha* model system across Hawai‘i Island.

2. Materials and Methods

2.1. Data Collection

M. polymorpha canopy spatial data were developed by Seeley et al. [22] using 2019 Arizona State University Global Airborne Observatory (GAO) data. The GAO houses a high-fidelity imaging spectrometer (380–2510 nm) and a boresight-aligned dual-laser light detection and ranging (LiDAR) scanner, which was used to develop island-wide visible to shortwave infrared (VSWIR) surface reflectance and top of canopy height (TCH) mosaics [23]. Between the summer of 2022 and winter of 2023, canopy location data of 5366 crowns were collected, and crowns were identified as either *M. polymorpha* or “other.” An island-wide support vector machine (SVM) model was trained using 70% of these crown data and a 96.0% accuracy was achieved when tested on the remaining 30%. The SVM was then used to classify all pixels with vegetation over one meter tall as either *M. polymorpha* or other vegetation. The model output was compared to a Bayesian Gaussian process classification (GPC) trained using the spatial information from the training crown data, and the results were spatially accurate according to the Bayesian GPC. Due to the large dataset size, ~152,000 pixels representing *M. polymorpha* canopies were selected from across Hawai‘i Island using systematic random sampling. To extract canopy height and trait data, we used GAO TCH from light detection and ranging (LiDAR) and canopy trait estimations were developed by applying universal chemometric algorithms to VSWIR reflectance data [15]. These algorithms have been used to quantify *M. polymorpha* canopy traits at six locations on Hawai‘i Island [24]. Note that the chemometric equations result in estimates of canopy trait information, so we focus on the relative values rather than the absolute values. The canopy traits estimated from VSWIR data included: leaf mass per area (LMA), total carbon (C), phenols, chlorophyll a and b (a+b), foliar nitrogen (N), cellulose, carotenoids, and phosphorus (P).

We next obtained environmental data on elevation, slope, aspect, precipitation, and soil substrate age (Figure S1). Spatial elevation data were collected from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) [25]. Slope and aspect spatial

data were derived from the SRTM DEM using the QGIS Terrain Analysis toolbox. Annual precipitation data (30-year normal from 1991 to 2020) were developed by the PRISM Climate Group [26], and soil substrate age datasets were produced by the U.S. Geological Survey [27]. To co-align the environmental conditions and *M. polymorpha* canopy trait data, we extracted environmental information from the center of each 2 m × 2 m *M. polymorpha* pixel in the Seeley et al. [22] *M. polymorpha* spatial distribution dataset.

2.2. Analysis

We first investigated the relative importance of environmental factors (elevation, slope, aspect, precipitation, and soil substrate age) in driving *M. polymorpha* canopy traits. The relative contribution of the environmental factors in driving canopy trait variation was assessed by training a random forest classifier for each canopy trait. Models were developed using the scikit learn Python package (version 1.1.3) [28] with standardized environmental data as the predictor variables and each canopy trait as the response variable. Predictor importance was calculated using the feature importance method built into the scikit-learn random forest model. The feature importance method calculates how often each predictor was used in the trees developed by the model.

Next, we compared the relationship between canopy traits and environmental factors. As prior studies have described elevation and soil substrate age as being primary drivers of genotypic variation in *M. polymorpha* [20,24,29–31], our analyses focused on these variables. Linear regression models were fit for each canopy trait–environmental factor (elevation, soil substrate age) pairing to understand their relationship. Additionally, linear regressions were fit and boxplots were developed to assess the relationship between canopy traits and soil substrate age at each elevation range. The slope and r^2 of each model were recorded. To visualize how canopy traits varied across elevation gradients, box plots of canopy traits grouped according to elevation alone and soil substrate age alone were developed. Boxplots were developed using the seaborn Python package (v. 0.11.2) [32]. For both the linear models and visualizations, elevation and soil substrate age were grouped into categories representing elevation (0–150, 150–300, 300–600, 600–900, 900–1200, 1200–1500, 1500–1800, 1800–2100, 2100–3000 m) and age ranges (0–500, 500–1000, 1000–5000, 5000–15,000, 15,000–50,000, 50,000–400,000 years). Elevation and soil substrate age were modeled using categories as a means of standardizing the data to better compare the trait–environment relationships between the environmental factors. For nonlinear canopy traits–environment relationships, as determined by checking residual normality and homoscedasticity, canopy traits were log-transformed. Dataset ranges were chosen to ensure a more even spread of canopy data within each range. To maintain a consistent group size, 57 pixels within each elevation–soil substrate age category were randomly selected.

To understand how environmental factors mediated trait relationships described by the LES, we developed paired plots between the foliar N and LMA, chlorophyll a+b, and P. Data were first grouped according to elevation and then soil substrate age range. Next, a regression line for paired traits within each elevation or soil substrate age range was calculated and plotted using the scikit learn Python package (version 1.1.3) [28].

3. Results

3.1. Canopy Trait Variation across Environmental Gradients

Intraspecific variation of canopy traits primarily followed elevation gradients. The random forest feature importance indicated that elevation is the primary driver of all *M. polymorpha* canopy traits. Precipitation was the second most important factor in predicting trait estimates. For chlorophyll a+b, carotenoids, total C, and nonstructural carbohydrates, soil substrate age was the third most important predictor, and for all other traits, soil substrate age was the least important predictor. Slope and aspect had similar levels of importance, with slope being the more informative variable in most cases (Figure 1).

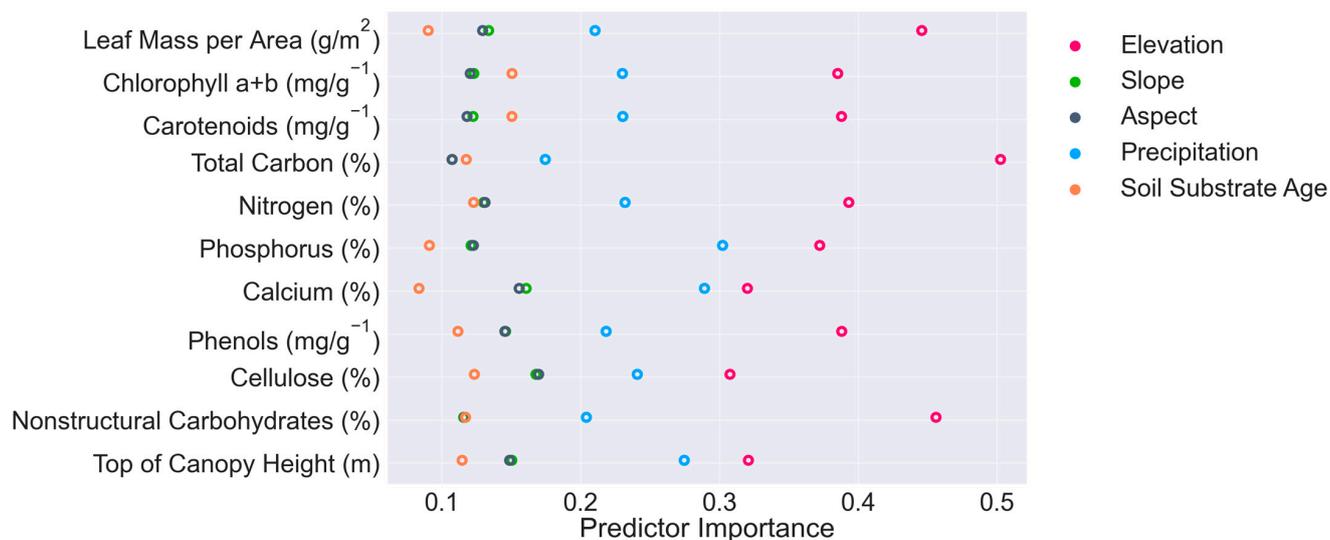


Figure 1. Random forest feature importance rankings of environmental factors in predicting canopy traits.

Except for TCH, elevation and soil substrate age had opposite relationships with *M. polymorpha* canopy traits. LMA was positively associated with elevation while all other traits were negatively associated with elevation. TCH was positively related to both elevation and soil substrate age. The relationship between elevation and all canopy traits, except phenols and TCH, was stronger than that of soil substrate age, as determined by the slope and r^2 . LMA had the strongest relationship with both environmental factors, followed by phenols and total C (Figure 2; Table 1). Across the elevation gradient, total C, phenols, cellulose, and TCH either peaked or had a minimum around 1200–1800 m. Chlorophyll a+b, carotenoids, and N variability decreased with increasing elevation, TCH variability peaked at middle elevations, and variability of cellulose increased positively with elevation (Figure 2). Canopy trait variability did not vary greatly with soil substrate age, and the relationship between traits and soil substrate age was primarily linear (Figure 2). When grouped according to elevation, the relationship between soil substrate age and canopy traits becomes more variable. While few consistent patterns emerged regarding the slope and r^2 , canopies at 150–300 m had larger slopes for many of the traits than those at other elevations (Table 1). Variability of the chlorophyll a+b, carotenoids, and N was higher on older soils (15,000–40,000 years) at low elevations (0–300 m). Visually, the relationship between soil substrate age and canopy traits appeared more parabolic in at some elevation ranges, while it remained more linear at others. For example, median N values peaked around 5000–50,000 years at most elevations, but the relationship remained linear at 1200–1500 m (Figure 3).

Table 1. Slope and r^2 of linear regression between *Metrosideros polymorpha* canopy traits and environmental factors. Rows below the elevation range title represent the relationship between soil substrate age and leaf traits within each elevation range. Elevation and soil substrate age were both treated as categorical rather than continuous variables. Elevation ranges were: 0–150, 150–300, 300–600, 600–900, 900–1200, 1200–1500, 1500–1800, 1800–2100, and 2100–3000 m. Age ranges were grouped as follows: 0–500, 500–1000, 1000–5000, 5000–15,000, 15,000–50,000, and 50,000–400,000 years.

		Leaf Mass per Area	Chlorophyll a+b	Carotenoids	Total Carbon	Nitrogen	Phosphorus	Phenols	Cellulose	Top of Canopy Height
Elevation	Slope	16.972	−0.118	−0.095	−2.256	−0.074	−0.037	−5.179	−0.500	0.121
	R^2	0.282	0.162	0.166	0.205	0.157	0.039	0.055	0.160	0.003
Soil Substrate Age	Slope	−6.908	0.098	0.083	1.702	0.073	0.027	6.934	0.443	0.437
	r^2	0.021	0.051	0.057	0.053	0.070	0.010	0.045	0.057	0.015

Table 1. Cont.

Elevation Ranges:		Leaf Mass per Area	Chlorophyll a+b	Carotenoids	Total Carbon	Nitrogen	Phosphorus	Phenols	Cellulose	Top of Canopy Height
0–150	Slope	−6.950	0.132	0.090	2.291	0.056	0.097	4.563	0.162	0.190
	r^2	0.032	0.086	0.061	0.131	0.042	0.108	0.028	0.014	0.003
150–300	Slope	−15.161	0.222	0.178	2.047	0.129	0.021	6.740	0.587	−0.110
	r^2	0.133	0.198	0.197	0.107	0.191	0.008	0.059	0.160	0.001
300–600	Slope	−8.200	0.141	0.116	1.254	0.097	0.000	4.973	0.449	0.576
	r^2	0.051	0.108	0.116	0.043	0.131	0.000	0.028	0.084	0.026
600–900	Slope	−7.346	0.095	0.082	2.063	0.069	0.033	9.178	0.552	0.397
	r^2	0.042	0.069	0.082	0.108	0.084	0.016	0.086	0.104	0.013
900–1200	Slope	−9.884	0.060	0.065	1.780	0.065	0.012	9.219	0.556	0.595
	r^2	0.074	0.034	0.058	0.097	0.076	0.002	0.099	0.119	0.024
1200–1500	Slope	−5.906	0.098	0.091	2.133	0.097	0.020	11.209	0.708	0.883
	r^2	0.028	0.091	0.123	0.137	0.176	0.008	0.151	0.196	0.068
1500–1800	Slope	−7.701	0.096	0.076	1.620	0.066	0.065	5.534	0.314	0.879
	r^2	0.047	0.091	0.092	0.074	0.098	0.066	0.034	0.041	0.067
1800–2100	Slope	−5.669	0.099	0.083	2.295	0.088	0.076	10.107	0.659	0.482
	r^2	0.013	0.060	0.068	0.118	0.113	0.068	0.085	0.117	0.020
2100–3000	Slope	−11.126	0.009	0.025	1.380	0.044	−0.062	3.900	0.357	0.186
	r^2	0.056	0.001	0.010	0.037	0.039	0.040	0.010	0.030	0.007

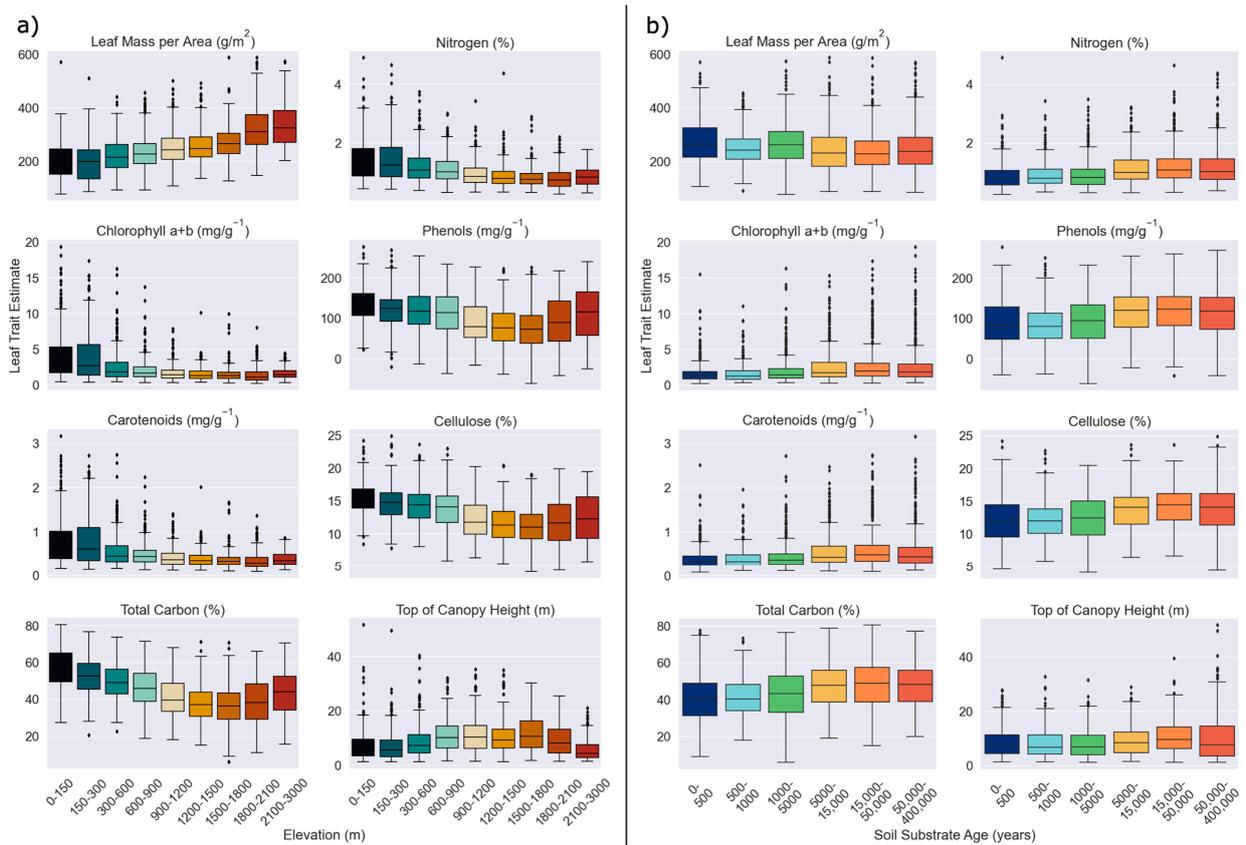


Figure 2. Boxplot of *Metrosideros polymorpha* canopy traits across its (a) elevation and (b) soil substrate age range on Hawai'i Island. Colors correspond to x axis values.

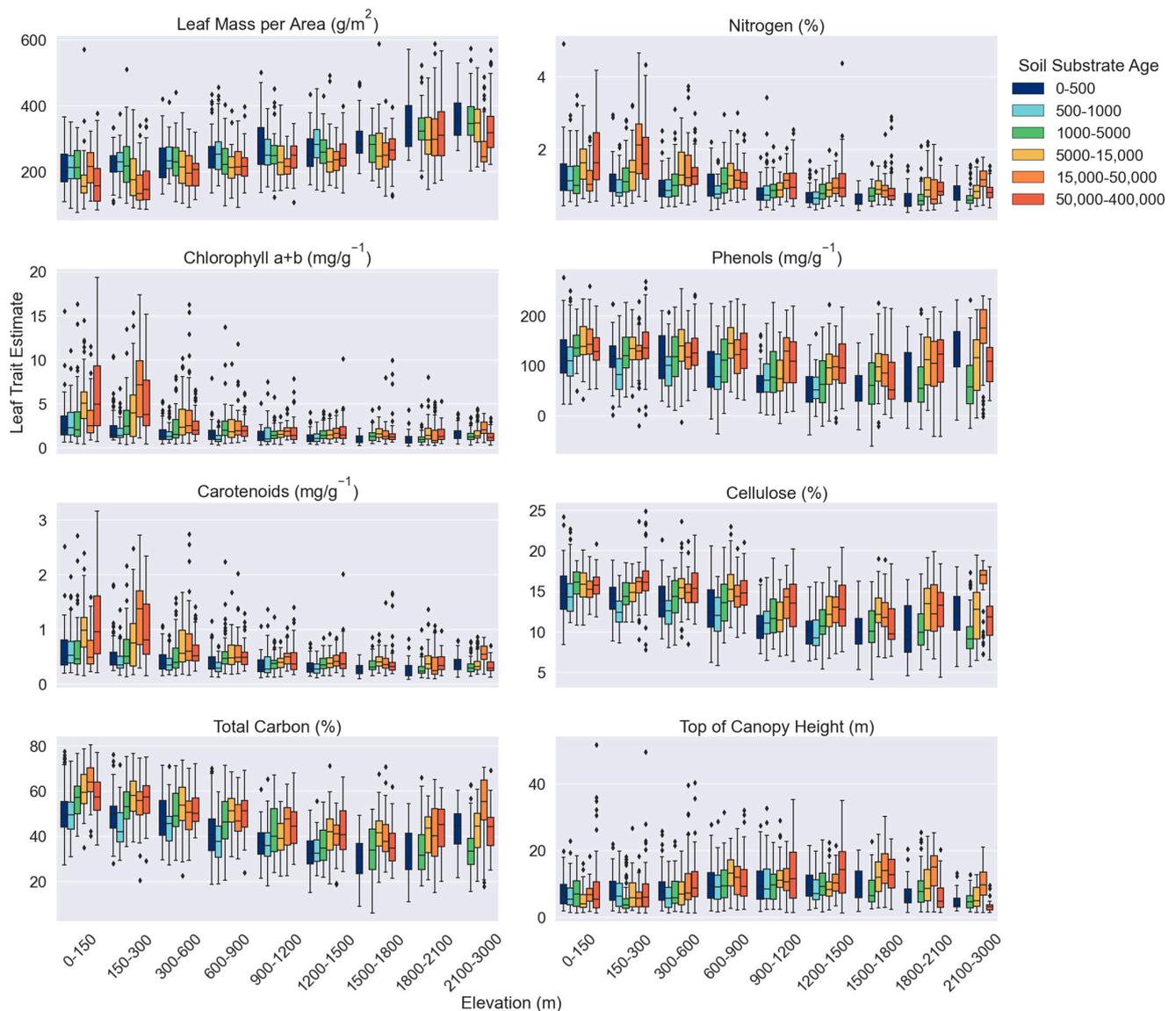


Figure 3. *Metrosideros polymorpha* canopy traits grouped according to elevation across a soil substrate age gradient.

3.2. Canopy Trait Relationships as Mediated by Environmental Factors

M. polymorpha canopy LMA and N were negatively correlated. High LMA and low N were most often observed at higher elevations while low LMA and high N were observed at low elevations. Further, there was a constriction of trait variability at higher elevations, as can be observed in coordinate space when LMA and N are plotted against each other (Figure 4). The slope of the relationship between LMA and N increased positively with elevation from -62.6 to -151.9 . Soil substrate age had a smaller effect on the relationship between these variables, though the slope decreased across soils of different geologic ages. *M. polymorpha* inhabiting soils aged 0–500 had a larger slope (-111.4) while *M. polymorpha* on older soil ages was the lowest (-86.6 ; Figure 5; Table S1).

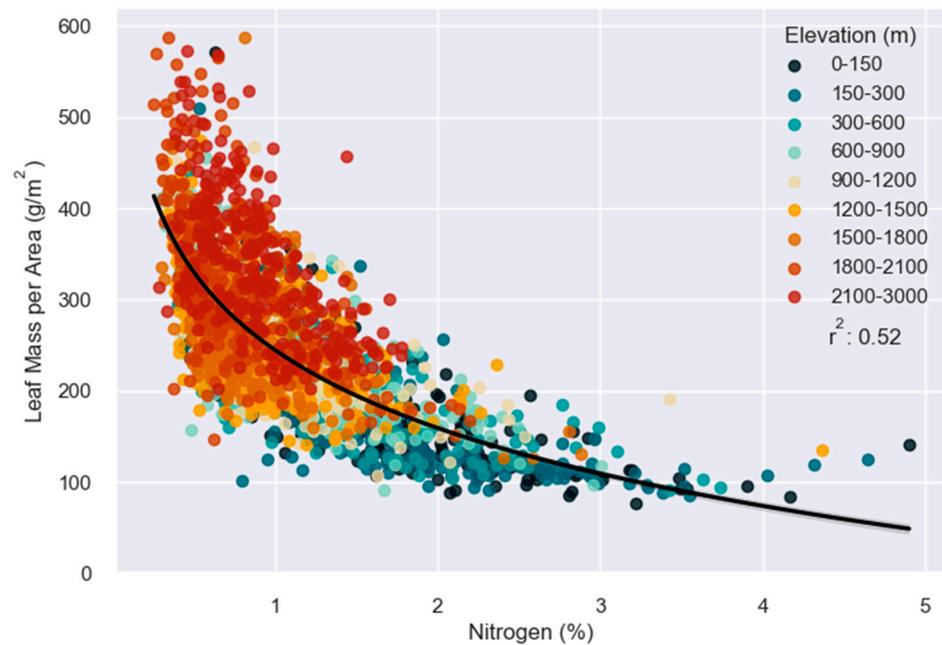


Figure 4. Leaf mass per area (LMA) plotted against canopy percent nitrogen (N). Colors represent elevation ranges. The black line represents the linear regression between $\log N$ and LMA.

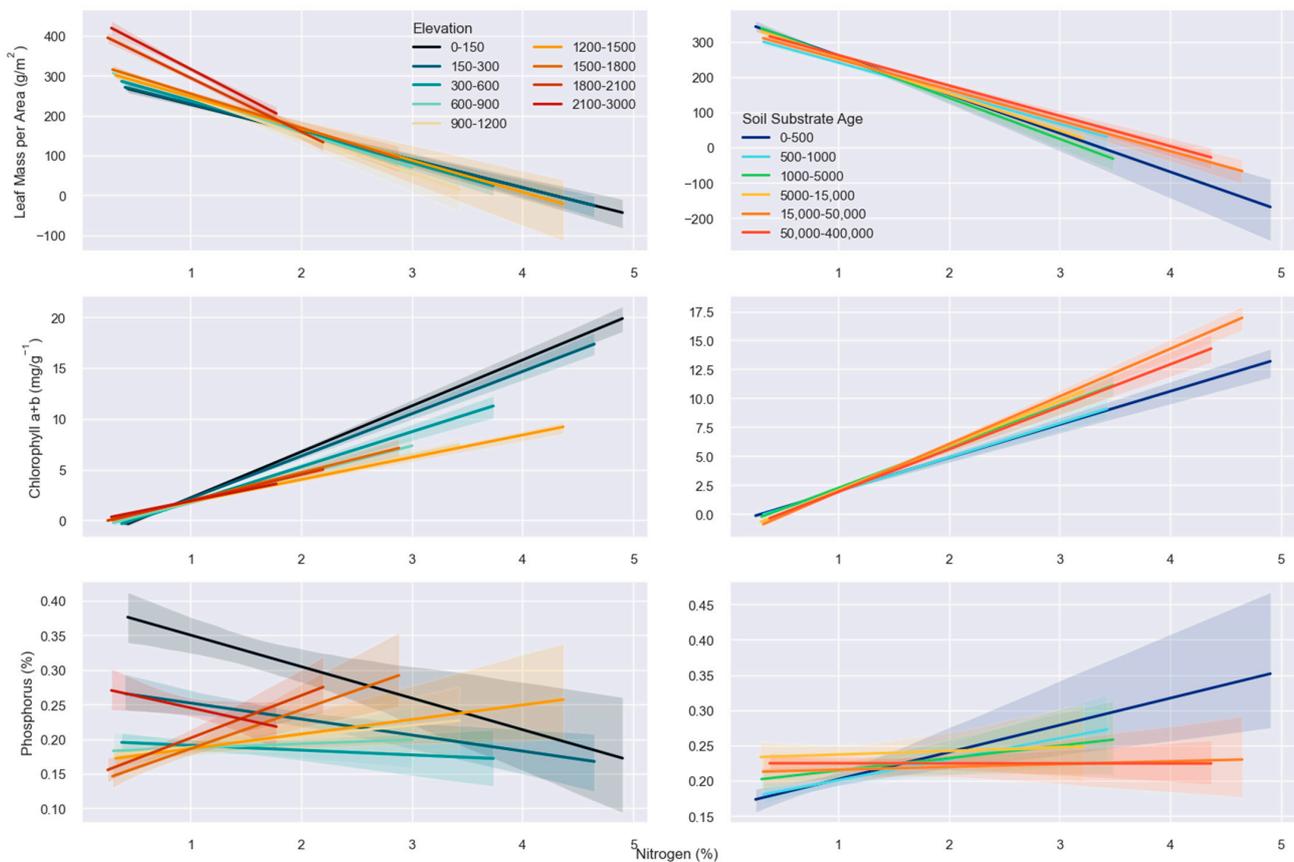


Figure 5. Linear regression plots where three canopy traits (leaf mass per area, chlorophyll a+b, and phosphorus) are plotted separately against canopy nitrogen. Colors in the left column represent elevation ranges while those in the right column represent soil substrate age ranges. See Table S1 for the slope and r^2 of each relationship.

The effect of elevation and soil substrate age on the relationship between chlorophyll a+b and N was like that of LMA and N. The slope between chlorophyll a+b and N decreased from 4.3 to 2.2 as elevation increased while that for soil substrate age peaked at 15,000–50,000 years old. The slope range was smaller for soil substrate age (2.8–4.0) than that for elevation. There were no consistent patterns between P and N for either elevation or soil substrate age. The slope for this relationship was near zero, and r^2 was consistently low (0.0001–0.102). Further, the relationship between P and N switched from negative to positive (Figure 5; Table S1).

4. Discussion

Intraspecific canopy traits of *M. polymorpha* across Hawai'i Island followed the global LES. Like the LMA-N relationship described by the LES [2], *M. polymorpha* exhibited a strong LMA-N relationship. Intraspecific variation is an important driver of community-level LMA-N relationship [4], and here we contribute to the body of literature describing intraspecific LMA-N relationships [4,33,34]. The *M. polymorpha* LMA-N relationship on Hawai'i Island was consistently negative, yet the slope decreased as elevation increased. Soil substrate age did not have a similar systematic effect on the LMA-N relationship. Further, the trait space occupied by *M. polymorpha* LMA-N variability constricted as elevation increased. This pattern of trait space constriction was observed using canopy traits estimated from imaging spectroscopy across elevation gradients in diverse Peruvian forests [19].

Intraspecific variation of *M. polymorpha* canopy traits was largely determined by elevation. Prior studies have observed strong morphological and physiological responses of *M. polymorpha* to elevation, describing differences in leaf size, shape, pubescence, stature, nitrogen use efficiency, and LMA, among others [29,35–41]. These traits have been shown to follow not only elevation but also soil substrate age gradients [37,38,42]. Further, *M. polymorpha* genotypes and their hybrids, many of which have unique chemical fingerprints [43] exist on specific elevation–soil substrate age combinations [20,21,44]. Prior studies focusing on *M. polymorpha* intraspecific variation used geographically separate sites or elevation gradients along a single slope [24,31]. Using data randomly sampled from across Hawai'i Island, we observed that elevation has the primary effect on *M. polymorpha* canopy traits, followed by precipitation. While soil substrate age was often the least important determinant of *M. polymorpha* canopy traits, the degree of leaf trait response to soil substrate age depended on elevation.

Elevation is a strong driver of plant traits globally and is thus a major component of the LES. Canopy traits such as LMA, specific leaf area, N, and $\delta^{13}\text{C}$ respond to elevation [2,19,45,46]. Canopy trait responses to elevational changes have been attributed to light availability, harsher environmental conditions at high elevations, growing season length, and temperature, among others [45,47,48]. Not only does elevation affect canopy traits directly, but it also mediates the effect of other environmental drivers. Here, we observed that the response of *M. polymorpha* canopy traits on soil substrate age differed based on elevation. Slope and aspect, which often mediates the effect of elevation on temperature and growing season length, had a lesser effect on canopy traits. Using six *M. polymorpha*-dominated sites on Hawai'i Island, Seeley et al. [24] reached the same conclusion as they determined that both canopy traits and VSWIR reflectance spectra were driven primarily by elevation, with soil substrate age being a secondary driver. While the occurrence of *M. polymorpha* across large environmental gradients allows for an investigation of intraspecific trait variation, this species has few analogs globally, and therefore, more work is needed to determine if the LES holds for intraspecific traits of other species.

5. Conclusions

Determining the drivers of intraspecific trait variation on large geographic scales allows us to better understand functional diversity, community ecology, and evolution, and manage for future climate scenarios [8–10,46,49–51]. As imaging spectroscopy coaligned

with LiDAR data [23] allows for accurate species classifications [52–58] and the estimation of canopy traits [15–17], it is a tool with which we can quantify intraspecific variation. Using imaging spectroscopy data from a model system, we demonstrated that intraspecific variation follows LES across broad environmental gradients. In the *M. polymorpha* model system, as with many systems, elevation was the primary driver of canopy trait variation. This work suggests that highly polymorphic species like *M. polymorpha* will adapt to environmental drivers like how trait selection and environmental filtering of diverse tree communities result in trait convergence based on site conditions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/rs15194707/s1>, Figure S1: Spatial data of the soil substrate age, annual precipitation, aspect, slope, elevation, and *Metrosideros polymorpha* presence for Hawai'i Island; Table S1: Slope and r^2 of the linear regression models between nitrogen and three canopy traits (leaf mass per area, chlorophyll a+b, and phosphorus) modeled separately for each trait.

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Data Availability Statement: *M. polymorpha* canopy trait data used in these analyses are openly available at Figshare: <https://doi.org/10.6084/m9.figshare.23605317.v1>, accessed on 12 September 2023.

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Conflicts of Interest: The authors declare no conflict of interest.

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