

*Full Length Research Article***Leaf Traits of *Parashorea malaanonan* Along Elevational Gradient in Mount Makiling Forest Reserve, Philippines**Marsh Reginald Bico Ebale<sup>1</sup>, Jonathan Ogayon Hernandez<sup>2</sup>, Crusty Estoque Tinio<sup>2,\*</sup><sup>1</sup> Forestry Development Center, College of Forestry and Natural Resources, University of the Philippines Los Baños, Los Baños, Philippines<sup>2</sup> Department of Forest Biological Sciences, College of Forestry and Natural Resources, University of the Philippines Los Baños, Los Baños, Philippines\* Corresponding Author. E-mail address: [cetinio@up.edu.ph](mailto:cetinio@up.edu.ph)

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## ABSTRACT

Studying leaf trait variation and relationships along elevational gradients will enhance our understanding of how plants respond to changing environmental conditions. Thus, we analyzed the leaf traits variation in ecologically and economically important *Parashorea malaanonan* and the potential influence of environmental covariables (rainfall, relative humidity, and air temperature) on leaf traits along an elevational gradient in Mount Makiling Forest Reserve (MMFR). Three sampling sites were selected based on elevation, i.e., low (400–500 masl), mid (500–600 masl), and high (> 600 masl). The leaf samples were collected from seedlings, saplings, and adult trees of *P. malaanonan*. There was no significant variation in most of the measured leaf traits, leaf area (LA), specific leaf area (SLA), leaf thickness (LT), leaf length-to-width ratio (L:W) across sampling sites, except vein density (VD). The SLA and LT at high elevations are significantly and negatively correlated ( $r^2 = 0.7396$ ). The environmental covariables had a significant ( $p < 0.05$ ) impact on the leaf traits of *P. malaanonan*. The observed variation in some leaf traits may have been influenced by the elevation gradient and its associated environmental conditions. Thus, *P. malaanonan* may have developed adaptive mechanisms to cope with the changing environment.

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**1. Introduction**

Leaf functional traits are good indicators of plant resource use and resource-acquisitive strategies. These strategies were identified based on the environmental gradient of available resources and increasing elevation (Ding et al. 2019). The resource-conservative strategy is the mechanisms of species in high elevation due to limited resources available to them. This strategy is evident in attributes such as reduced leaf size, lower specific leaf area, thicker leaf, higher leaf length-to-width ratio, and lower vein density. Contrarily, the abundance of resources at lower elevations can result in a resource-acquisitive strategy, leading to larger leaf size, higher specific leaf area, thicker leaf, and lower vein density (Marod et al. 2018; Midolo et al. 2019; Ochoa-beltrán et al. 2021; Yang et al. 2021). Some of the important leaf traits indicative of either resource-use or resource-acquisitive strategy include leaf area, specific leaf area, leaf thickness, leaf toughness, vein density, leaf mass to area ratio (LMA), leaf length to width ratio, leaf nitrogen mass ( $N_{\text{mass}}$ ),

leaf nitrogen area ( $N_{\text{area}}$ ), and among others (Cruz-Maldonado et al. 2021; Midolo et al. 2019; Sack and Scoffoni 2013; Shi et al. 2018; Yang et al. 2021). The specific leaf area, leaf life span, mass-based nitrogen, and mass-based assimilation are some traits associated with the plant's growth, survival, and light requirement (Poorter and Bongers 2006). However, the extent of the association may vary depending on site characteristics (e.g., elevation and environmental conditions). There are existing patterns in the relationship of elevation to leaf traits, such that as the elevation increases, the leaf area decreases (Liu et al. 2020; Marod et al. 2018), specific leaf area increases (Marod et al. 2018), leaf thickness increases (Marod et al. 2018) leaf length-to-width ratio increases (Guo et al. 2018), and vein density decreases (Blonder and Enquist 2014). The mean annual temperature and leaf mass: area ratio was also significantly correlated with  $N_{\text{mass}}$  and  $N_{\text{area}}$  at high elevation (Read et al. 2014). Although the leaf trait-elevation relationship is well documented in the literature, the patterns in a relationship may vary depending on the prevailing environment and species under investigation amid a changing climate. This highlights the need to study species-specific variation to elucidate contrasting patterns relative to their respective environments.

Species-specific trait variations along elevational gradients induced by diverse environmental conditions have long been studied but predominantly in temperate regions (Yang et al. 2021). Sales-Come and Hölscher (2010) conducted one of the few studies in tropical forests, focusing on specific leaf area, stomatal conductance, leaf size, and other tree variables. They found a significant correlation between the traits of Dipterocarpaceae species, revealing that as elevation increases, species display highly specialized leaf characteristics. Due to the diverse species composition, complex ecological processes, varying climatic influences, and other biotic factors in tropical ecosystems, leaf functional traits have received limited research attention, especially in high mountain areas (Udayakumar and Sekar 2021). Hence, additional studies on leaf trait variation along elevational gradients in tropical forest ecosystems can provide insights into how ecologically and economically important tree species develop adaptation strategies and resource acquisition patterns among species in complex ecosystems.

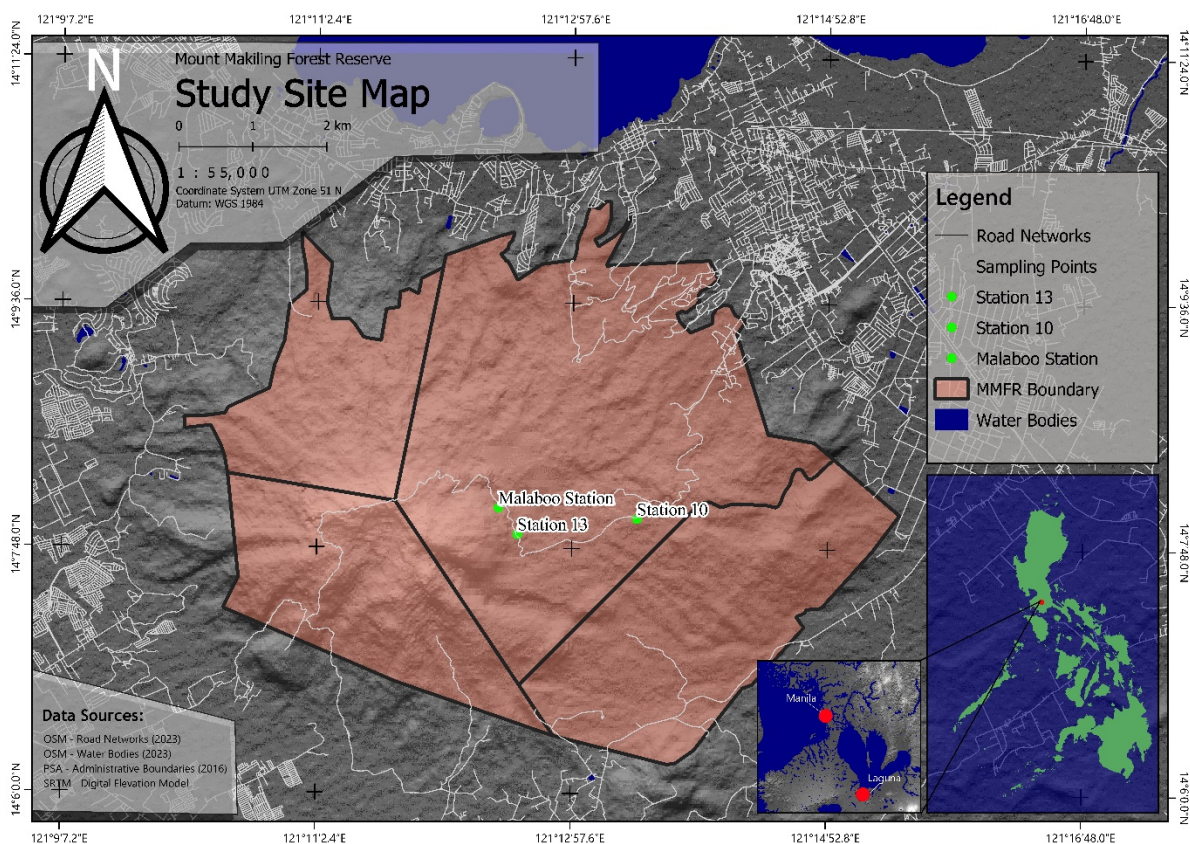
An ecologically and economically important tree species worthy of a study on leaf trait variation along elevation gradients is *Parashorea malaanonan*, a member species of the timber family Dipterocarpaceae. While threats to the species have been controlled hence, classified as least concern (Randi et al. 2019), however, it is projected to face a decline in its suitable habitat due to the impacts of climate change on tree species in the tropics (Tumaneng et al. 2019). *P. malaanonan* traits vary along the elevational gradient based on the growth-limitation hypothesis and plant economics spectrum (Reich 2014). Although *P. malaanonan* is widely distributed in the Philippines, research on the variation of leaf traits in response to environmental factors such as temperature, relative humidity, and rainfall is also limited. Consequently, the present study analyzed the variations and correlations of leaf traits in *P. malaanonan* along an elevational gradient in Mount Makiling Forest Reserve (MMFR). We also determined the potential influence of the environmental covariables (rainfall, relative humidity, and air temperature) on leaf traits. Our study will enhance the important knowledge of leaf traits on tree species in tropical forest ecosystems and inform future conservation efforts by revealing species leaf adaptive strategies in response to changing environmental conditions.

## 2. Materials and Methods

### 2.1. Study Site Description and Selection

The study was carried out at the MMFR, an ASEAN Heritage Park located  $14^{\circ} 8' N$  and  $121^{\circ} 12' E$  and lies within 65 km of Metro Manila, Philippines (Fig. 1). Specifically, sampling sites were located in the Molawin-Dampalit Subwatershed, which spans an elevational range of 20 to 1,143 meters above sea level (masl). It is the largest watershed zone among the subwatersheds in MMFR. The site comprises tropical lowland rainforest and lower montane forest formations (Pampolina et al. 2023). Regarding species composition, the most dominant species in the said watershed is *Diplodiscus paniculatus*, followed by *Celtis luzonica* and *Pinanga insignis*. Further, it is notable that critically endangered species such as *P. malaanonan* and *Diospyros blancoi* were also present at the site (Castillo et al. 2018).

Three sampling sites were selected based on elevation, representing low, mid, and high elevations (Fig. 1). The elevation difference was identified based on its area and the presence of *P. malaanonan*. The low elevation is located at Station 10 ( $140^{\circ} 08' 5.7'' N$ ,  $121^{\circ} 12' 24.4'' E$ ) with an elevation of 400–500 masl and covers 716.29 ha. It has an average light intensity of 982 lux. The mid-elevation was at station 13 ( $140^{\circ} 07' 54.1'' N$ ,  $121^{\circ} 12' 33'' E$ ) with an elevation of 501–600 masl covering 455.28 ha and an average light intensity of 1,318 lux. Lastly, the highest elevation was located at Malaboo station ( $140^{\circ} 07' 54.4'' N$ ,  $121^{\circ} 13' 10.1'' E$ ), which had an elevation of greater than 600 masl, covering 341.88 ha and had an average light intensity of 1,283 lux.



**Fig. 1.** Location map of the study sites in Molawin-Dampalit Subwatershed, MMFR, Philippines (Notes: Low elevation (Station 10), Mid-elevation (Station 13), High elevation (Malaboo Station)).



## 2.2. Tree Species Description

*P. malaanonan* is indigenous to Brunei, Kalimantan, Sabah, and the Philippines. Its population is declining due to massive land conversion and agricultural practices. The IUCN Red List of Threatened Species classifies it as “Least Concern” (Randi et al. 2019), while the DAO Red List of Threatened Philippine plants and their category classify it as “Non-threatened under the category of Other Wildlife Species”. Furthermore, the species can be found in lowland Dipterocarp forests up to 1,000 masl (Randi et al. 2019) and in lowland tropical rainforests at altitudes up to 1,300 masl in the Philippines (Abasolo et al. 2009). The species has been identified as one of the dominant dipterocarp tree species, with an importance value of 8.878, in the Molawin-Dampalit Subwatershed of the MMFR (Castillo et al. 2018; Tumaneng et al. 2019). Moreover, a high species diversity index (3.52) in the Molawin-Dampalit Subwatershed was also reported, indicating that despite the presence of many plant competitors, *P. malaanonan* was able to dominate the area and adapt to the environment (Castillo et al. 2018).

*P. malaanonan* can reach a height of 35 to 60 meters and a diameter at breast height of 200 centimeters, with a flat and spreading crown (Abasolo et al. 2009). The leaves are complete, alternate, and scattered, with a prominent midrib and five to eight pairs of equally pinnate nerves (Fig. 2). Its flowers display a yellow hue with a pink tinge, while its fruits have five elongated wings that mature in three to four months, depending on the climate. Lastly, the bark has broken ridges of 3.8 to 4.3 cm thick.



**Fig. 2.** The study species *P. malaanonan* shows (a) seedlings and (b) adult trees growing in Molawin-Dampalit Subwatershed, MMFR.

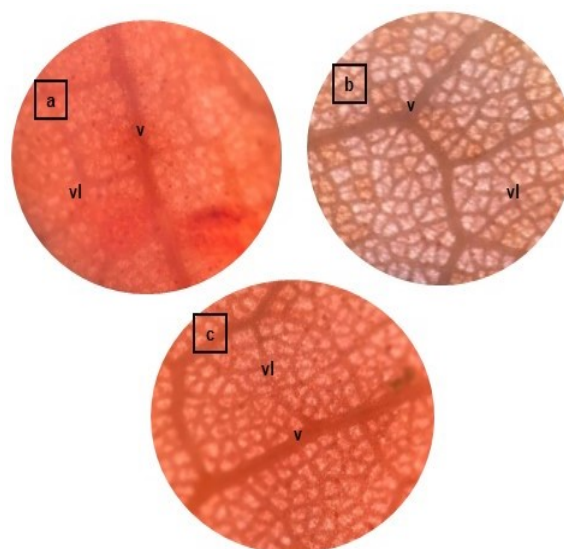
## 2.3. Field Sampling

Three sampling sites (Station 10, Station 13, and Malaboo Station) along the elevational gradient were identified. At each identified sampling site, a purposive sampling plot with an adult tree with a reproductively mature diameter at breast height (DBH) of at least 30 cm was established. Saplings and seedlings were purposively selected based on their availability under the forest canopy of the selected adult trees. Individuals with 5–10 cm DBH were categorized as saplings, while those with a root collar diameter (RCD) of less than 5 cm were categorized as seedlings (Sangeeta 2015).

From each site, fully expanded and healthy leaf samples ( $N = 2-6$ ) were collected for the measurement of leaf traits, such as leaf area (LA), specific leaf area (SLA), leaf thickness (LT), vein density (VD), and the ratio of leaf length to width (L:W) across the three life-history stages (seedlings, saplings, and adult trees). The samples were kept in a sealed plastic bag until further analysis in the laboratory. Only the adult tree leaf samples were collected at the high and low elevations, while only leaves from seedlings and saplings were collected at the mid-elevation due to sample availability and height of the mother tree. There were six individual seedlings in each sampling site. Also, six individuals of saplings were collected at the high and mid-elevations, but only five samples were collected at the low elevation. The total number of individuals collected for low, mid, and high elevations was 14, 12, and 15, respectively.

#### 2.4. Leaf Traits Measurements

Leaf traits were measured by collecting and measuring leaf traits (Pérez-Harguindeguy et al. 2013). The LA ( $N = 2-6$ ) was measured using the grid method by multiplying the total number of squares per replicate by  $0.25 \text{ cm}^2$ . The SLA ( $N = 2-6$ ) was computed by dividing the LA by the oven-dry mass of the leaves (dried at  $60^\circ\text{C}$  for 48 h), including the petiole. The leaf thickness (LT, in cm) was determined using a high-resolution digital caliper ( $0.01 \text{ mm}$ , accuracy:  $\pm 0.02$ ) at oven-dry weight conditions. The measurement of LT ( $N = 2-6$ ) was consistently done in only one section (i.e., middle) of the leaves. Furthermore, the length-to-width ( $N = 2-6$ ) ratio of the leaves was measured using a ruler. The length was measured from the base to the apex of the leaf, while the width was measured at the middle portion of the leaf (in cm). Lastly, leaf samples were cleaned with distilled water, and a middle portion of each leaf sample was cut into a square. The cut pieces of leaves were placed in tubes with a series of ethyl alcohol solutions (95%, 80%, 70%) applied weekly. When the veins were visible, the vein length was measured using a compound light microscope (Olympus, MicroBlue) at  $10\times/0.25$  magnification. The area of the field of view (FOV) and total vein length were then measured using Image Processing and Analysis software (ImageJ). Finally, the vein density in  $\text{cm}^{-1}$  was calculated using the formula: area of the FOV divided by the total vein length (Fig. 3).



**Fig. 3.** Leaf veins of *P. malaanonan* at  $10\times$  magnification showing (a) veins of an adult tree at high elevation, (b) veins of a sapling at mid-elevation, and (c) veins of a seedling at low elevation (Notes: v: veins, vl: veinlets).

## 2.5. Data Collection and Analysis of Environmental Covariables

A 5-year (2017–2021) secondary data on mean annual precipitation, mean annual relative humidity, and mean annual temperature of the study site was provided by the National Agromet Station in the University of the Philippines-Los Baños (NAS-UPLB). Primary data on light intensity and canopy closure was also collected from the study sites. The light intensity (lux) was measured using the light meter (Data logging, Digital Light Meter). Five light intensity readings were taken at each site within a day of data gathering; then, the averages were computed. The canopy closure (in % taken from four cardinal directions) at each site was also measured using a spherical densiometer (Forest densiometers, MODEL-C). Canopy closure is computed by multiplying the number of square counts covered by the crown by 1.04. Then, the difference between 100 and that product is the canopy closure. Regarding the analysis of environmental covariables, in the first dataset, the primary data of canopy closure and secondary data of rainfall, relative humidity, and temperature in MMFR were then pooled and analyzed using the multivariate analysis of variance (MANOVA) in R. In the second dataset, the value of canopy closure was removed; thus, only the secondary data (rainfall, air humidity, and temperature) were pooled and analyzed for their effects on the leaf trait variation.

## 2.6. Data Analysis

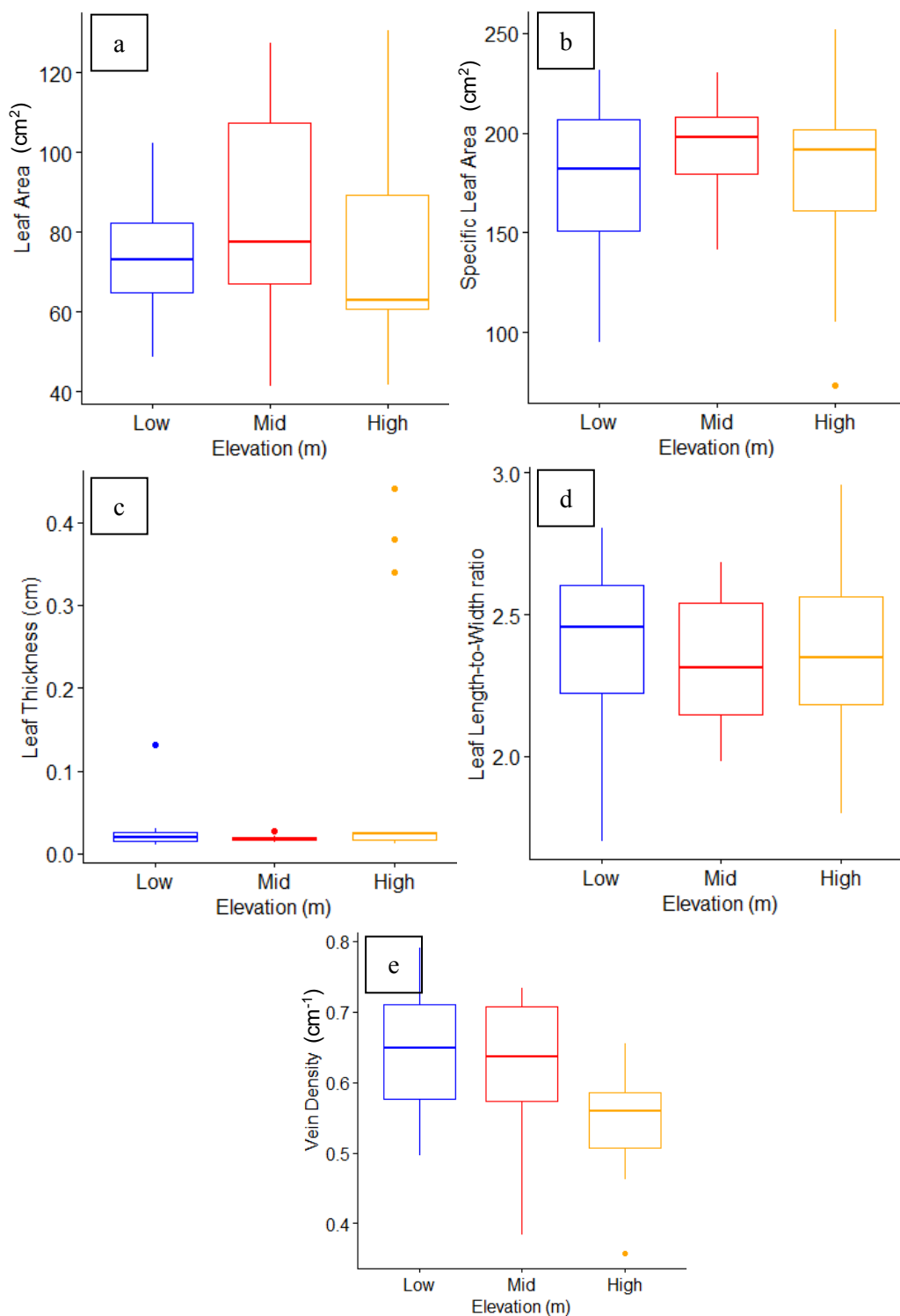
All the statistical analyses were performed in R statistical software (version R-5.12.8) at a significance level of  $\alpha = 0.05$ . The normality distribution of the collected data was determined using the “Shapiro.test” package. In analyzing the relationship of *P. malaanonan* leaf traits along an elevational gradient, the “dplyr” package was used to generate the mean values of leaf traits in each elevation, and an “aov” package was used to determine the significance of the variation of leaf traits. The “multcomp” package was used to determine the multiple comparisons among elevation that uses post-hoc Tukey’s Honest Significant Difference (HSD). The “cor.test” package was also used to assess the significance of the relationship between leaf traits in each sampling site. Finally, MANOVA was used to examine the pooled response of leaf traits to environmental covariables.

## 3. Results and Discussion

### 3.1. Results

#### 3.1.1. Leaf trait variation along elevational gradients

This study recorded the highest mean LA (84.0 cm<sup>2</sup>) and SLA (193 cm<sup>2</sup>) at the mid-elevation. In comparison, the lowest LA (73.4 cm<sup>2</sup>) and SLA (174 cm<sup>2</sup>) were recorded at the low elevation (**Fig. 4a** and **Fig. 4b**). In LT, the highest is 0.0932 cm (**Fig. 4c**) was found at high elevation while the lowest is at mid-elevation is 0.0189 cm (**Fig. 4c**). Both the low and high elevations exhibited the same L:W (i.e., 2.38), whereas the mid-elevation had L:W of 2.33 (**Fig. 4d**). The mean VD was observed to be higher at low elevation (0.643 cm<sup>-1</sup>), with the lowest value occurring at high elevation is 0.544 cm<sup>-1</sup> (**Fig. 4e**). Statistically, however, we found no significant differences in the LA, SLA, LT, and L:W of *P. malaanonan* across elevational gradients, except in VD ( $p = 0.0125$ ).

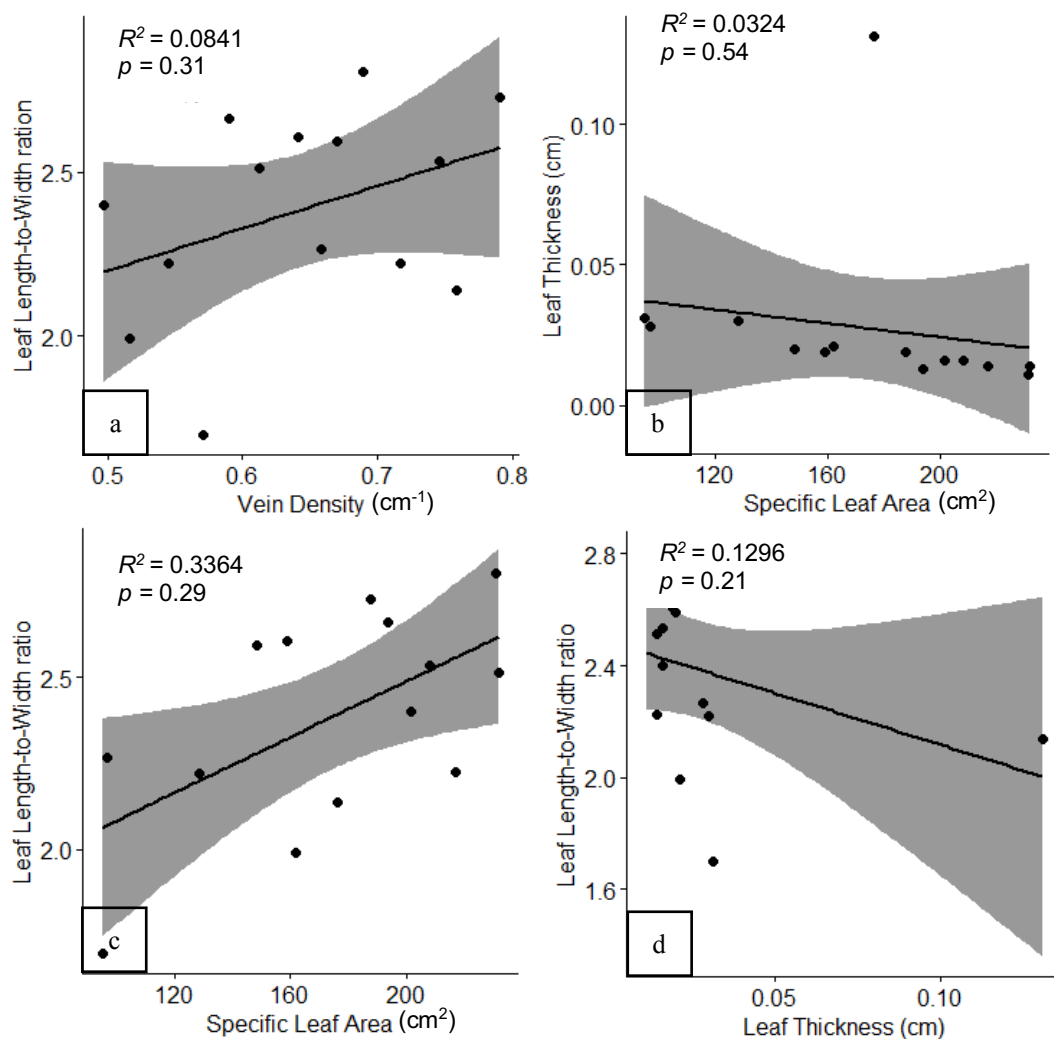


**Fig. 4.** Mean (a) LA, (b) SLA, (c) LT, (d) L:W, and (e) VD of *P. malaanonan* at different elevations in MMFR.

### 3.1.2. Leaf traits-elevation relationship

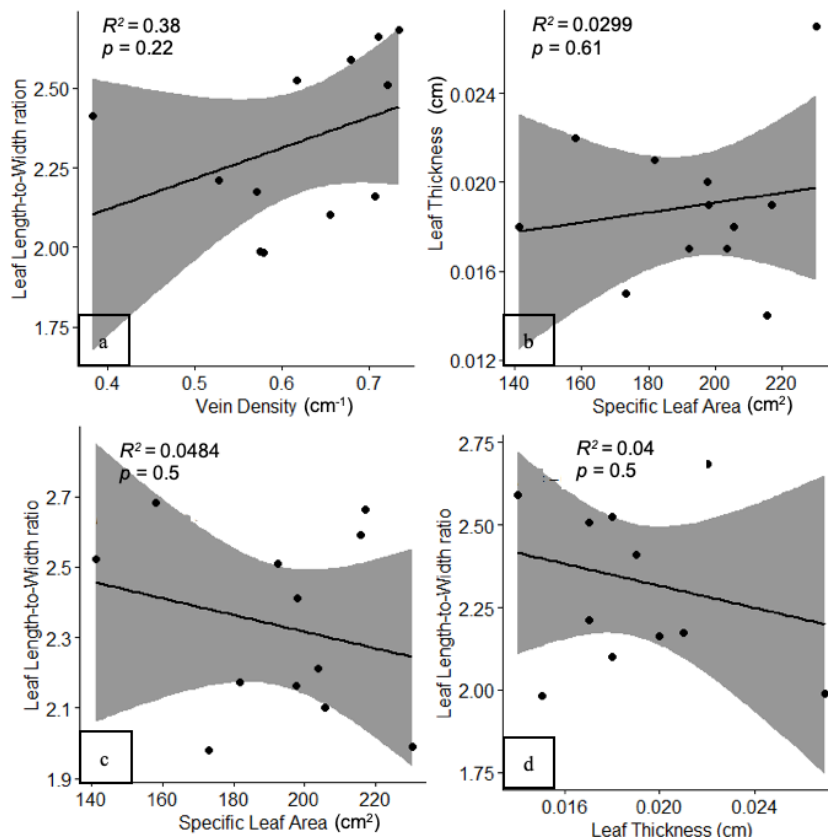
There was no significant relationship between VD and L:W (**Fig. 5a**) and SLA and LT (**Fig. 5b**). Contrarily, SLA and L:W had a significant ( $p = 0.029$ ) relationship observed at the low elevation (**Fig. 5c**). There was also no significant relationship between LT and L:W (**Fig. 5d**). The correlation between SLA and L:W showed a small linear correlation ( $r^2 = 0.3364$ ), indicating that

33.64% of the variation of SLA can be explained by the variation found in the L:W. At mid-elevation, no significant relationship existed in any of the traits measured (**Fig. 6a** to **Fig. 6d**). At high elevations, the relationship between VD and LW (**Fig. 7a**) was not significant. However, the relationships between SLA and LT (**Fig. 7b**), SLA and LW (**Fig. 7c**), and LT and LW (**Fig. 7d**) were found to be significant (p-values of 0.00003, 0.038, and 0.019, respectively). The SLA and LT had a strong linear correlation ( $r^2 = 0.7396$ ), while the LT and LW had a small linear correlation ( $r^2 = 0.3481$ ). The analysis of the relationship between traits along elevation revealed no significant relationship between VD and L:W (**Fig. 8a**), while there is a significant relationship between SLA and LT (**Fig. 8b**), SLA and LW (**Fig. 8c**), and LT and LW (**Fig. 8d**), with p-values of 0.00003, 0.038, and 0.019, respectively. A small linear correlation between SLA and LT ( $r^2 = 0.3481$ ) indicates that higher LT results in lower SLA.

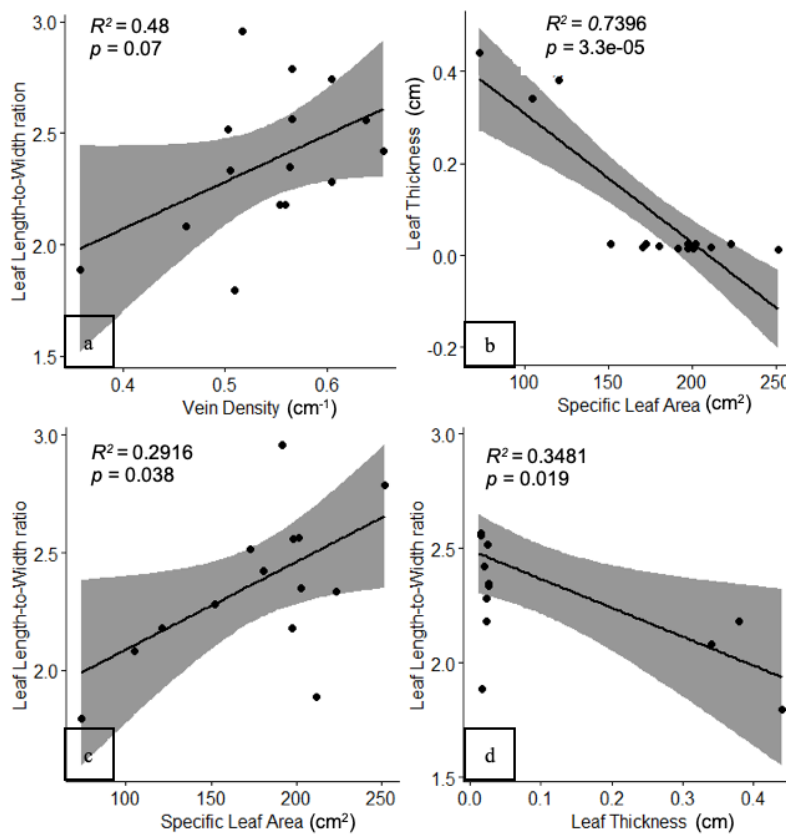


**Fig. 5.** Relationship between leaf traits of *P. malaanonan* at low elevation showing (a) VD to L:W, (b) SLA to LT, (c) SLA to L:W, and (d) LT to L:W.

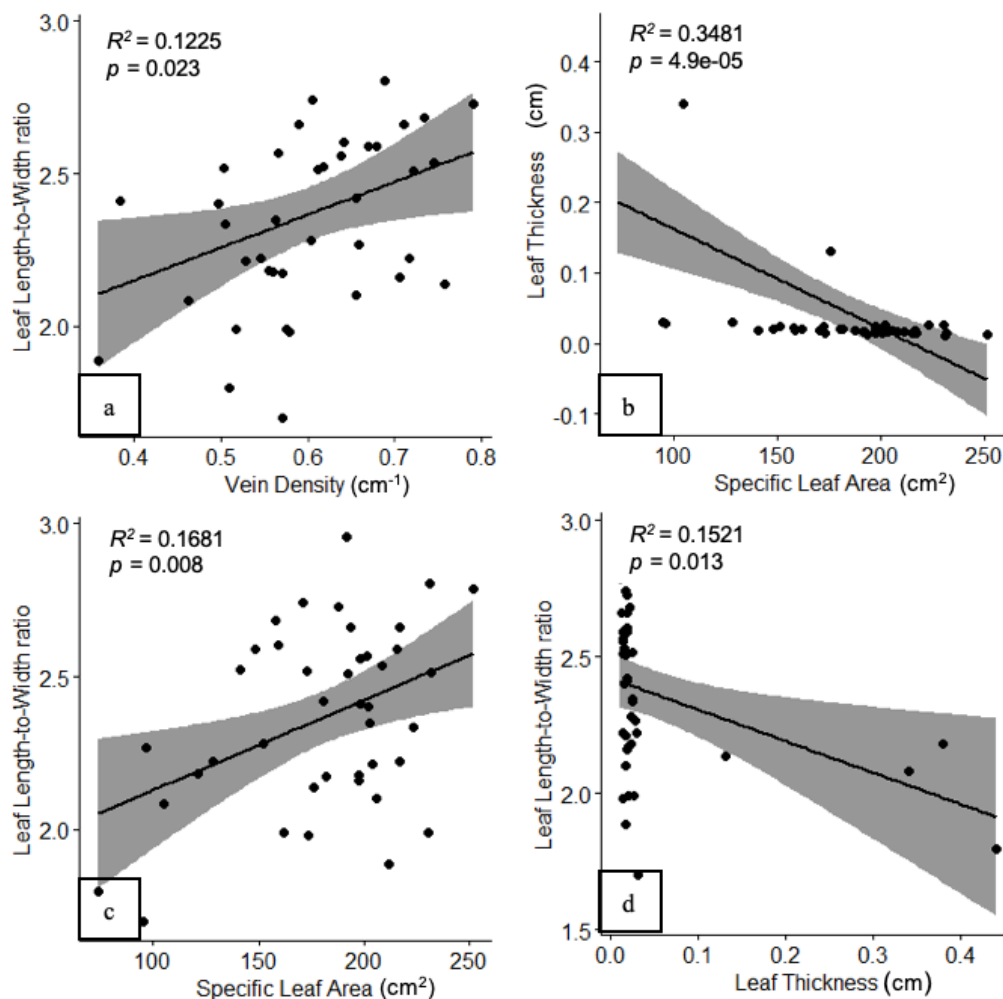




**Fig. 6.** Relationship between leaf traits of *P. malaanonan* at mid-elevation showing (a) VD to L:W, (b) SLA to LT, (c) SLA to L:W, and (d) LT to L:W.



**Fig. 7.** Relationship between leaf traits of *P. malaanonan* at high elevation showing (a) VD to L:W, (b) SLA to LT, (c) SLA to L:W, and (d) LT to L:W.



**Fig. 8.** Relationship between leaf traits of *P. malaanonan* along elevation showing (a) VD to L:W, (b) SLA to LT, (c) SLA to LW, and (d) LT to L:W.

3.1.3. Potential influence of environmental covariables on leaf traits of *P. malaanonan*

This study determined the effect of the explanatory variable (canopy closure, relative humidity, and temperature) on the response variable (LA, SLA, LT, L:W, and VD). Based on Dataset\_1, this study found that all the explanatory variables, such as canopy closure, rainfall, relative humidity, and temperature, significantly affected the LA, SLA, LT, L:W, and VD response at a population level (Table 1). It suggests that the leaf of *P. malaanonan* has an adapting mechanism in response to changing environmental conditions. Furthermore, Dataset\_2 discovered no significant effect on the response variables based on the three secondary data collected from NAS-UPLB (Table 1).

**Table 1.** Summary of the Type II MANOVA: Pillai test statistic

Covariable	Dataset_1 (p < 0.05)	Dataset_2 (p < 0.05)
Canopy (%)	S	-
Rainfall (mm)	S	NS
Relative Humidity (%)	S	NS
Temperature (°C)	S	NS

Notes: S = significant, NS = not significant. In Dataset\_1, the model used was the pooled data of four covariables identified (canopy density, rainfall, relative humidity, and temperature). In Dataset\_2, the model used was the pooled data of three covariables identified (rainfall, relative humidity, and temperature).

### 3.2. Discussion

#### 3.2.1. Leaf traits of *P. malaanonan* along elevational gradients

Our findings were consistent with that of [Blonder and Enquist \(2014\)](#), who discovered that VD was negatively correlated with elevational gradient. In contrast, [Rodríguez-Ramírez et al. \(2021\)](#) discovered a positive relationship between vein density and elevation of *Magnolia* spp. Previous results were attributed to different functional groups of plants based on their growth and/or survival strategy ([Albert et al. 2010](#)). They discovered that the relationship was affected by both the gradient portion and the environmental requirement. Also, the presence of resources in the sites may be a factor that contributed to this variation ([Reich 2014](#)) based on the leaf economic spectrum theory ([Westerband et al. 2021](#)). In the case of *P. malaanonan*, because it is a slow-growing species, it prefers a resource-conservative strategy in a resource-limited environment ([Newberry et al. 2011](#); [Ouédraogo et al. 2013](#)). *P. malaanonan* is classified as a species belonging to the family of slow traits ([Tumaneng et al. 2019](#)), which could influence its behavior in a different environment. It is partly related to the species' resource-conservative strategy, in which, due to the limited resources available at higher elevations, they require specialized traits that can conserve resources (e.g., water and nutrients) for their growth and survival, as opposed to low elevation, which is more resource-rich in comparison to high elevation ([Bai et al. 2015](#); [Reich 2014](#); [Umaña and Swenson 2019](#)). These findings support the results of [Rodríguez-Ramírez et al. \(2021\)](#), who claimed that leaf vein morphology varied within species as elevation increased. Furthermore, functional traits may withstand progressive environmental changes, but some may change subtly, as observed in the other leaf traits (LA, LT, and L:W) used in the present study ([Marod et al. 2018](#)). The findings also support [Gorné et al. \(2020\)](#) reports that evergreen species can be found in a resource-conservative strategy of the plant economic spectrum.

Similar to our findings, [Hernandez-Calderon et al. \(2014\)](#) discovered no significant relationship between LA and elevational gradient as individuals may require a large leaf area to capture light while also having lower photosynthetic efficiency driven by increased leaf tissue density, suggesting that although leaf area is higher at mid-elevation, their relative change to increasing elevation is expected to vary because elevation alone does not significantly impact plant growth rather due to environmental conditions ([Midolo et al. 2019](#)). Further, this is largely attributed to the predominantly understory location of the collected leaf sample, which resulted in no significant relationship between LA and elevational gradient ([Liu et al. 2020](#)). Moreover, our results indicated that the variation was primarily due to the relationship between high and low elevations ( $p = 0.0134$ ). According to [Sack and Scoffoni \(2013\)](#), high vein density provides advantages against insect herbivory, whereas low elevation is more prone to insect herbivory than high elevation. As a result, the mean VD was significantly higher at low elevation than at high elevation in the present study.

#### 3.2.2. Relationship between leaf traits along an elevational gradient

Results indicated a marginal relationship between leaf traits, possibly due to the abundant resources at the mid-elevation site. Based on our observation during fieldwork, many seedling individuals of *P. malaanonan* are present at the mid-elevation site, indicating the availability of resource-rich areas where these seedlings can thrive without the need for specialized traits to survive ([Wilson et al. 1999](#); [Wright et al. 2004](#)). Here, the observed significant relationship

between SLA and LT of *P. malaanonan* at high-elevation sites can be attributed to the plant's adaptive strategies related to temperature, UV radiation, light intensity regulation, water conservation, and herbivore defense. Plants generally develop a protective mechanism (increasing LT) from physical hazards due to lower temperature (Midolo et al. 2019) at higher elevations while simultaneously decreasing SLA due to sunlight exposure (Midolo et al. 2019; Ochoa-Beltrán et al. 2021). Results support Shen et al. (2019) findings that with increasing elevation, changes in resource-acquisitive (SLA) and resource-conservative (LT) behavior can be observed. SLA is found to be higher in resource-rich areas to capture more light for photosynthesis, and at high elevations, it tends to decrease due to exposure to sunlight. It can result in an increase in LT as the species-protective mechanism (Marod et al. 2018). This tendency partly confirms that the leaf economic spectrum works at high elevations, exemplified by the resource-conserving strategy evident in *P. malaanonan*.

Leaf traits differ depending on the available resources and the prevailing environmental conditions. This problem is explained by the correlation of determination. The percentage that each functional trait can explain the values of the others ranges only from 12.25% to 34.81%. It means that in terms of predicting the values of functional traits, the leaf traits of *P. malaanonan* in MMFR have a lower correlation with each other. The significant relationship between these functional traits indicates a common cross-species pattern of intraspecific leaf trait variation along the elevational gradient in *P. malaanonan* within MMFR (Midolo et al. 2019). Furthermore, because the leaf vein length per leaf area (VD) and specific leaf area are thought to be analogous (Sack and Scoffoni 2013), the same significant small relationship between SLA and VD to the L:W was observed in this study.

### 3.2.3. Potential influence of environmental covariables on leaf traits of *P. malaanonan*

The observed variation in leaf traits of *P. Malaanonan* cannot be attributed exclusively to elevational gradient as the environmental conditions unique in each site may have also played a role in influencing this variability (Pratama et al. 2023; Stiegel and Mantilla-Contreras 2018). Here, we found that the main or combined effects of canopy closure, temperature, relative humidity, and rainfall (Dataset\_1) significantly affected the leaf traits variation in *P. malaanonan*. In Dataset\_2, the result shows that when the canopy closure was removed in the combined environmental variables, either variable (e.g., rainfall, relative humidity, air temperature) had no significant effect on the population level. Hence, canopy closure could influence how other variables affect the leaf traits. For instance, according to Flerchinger et al. (2015), air temperature differs between the above and lower canopy, affecting the environmental conditions of species in different forest layers. Further, VD correlated with elevation and mean annual temperature and precipitation (Zhang et al. 2018). Similarly, Shi et al. (2018) observed comparable findings where mean annual rainfall negatively impacted LT and positively influenced SLA. This leaf trait responses may have been due to the tradeoff in which LT increases as a defense mechanism against harsher environmental conditions while also increasing SLA in lower elevations as an adaptation to increase photosynthetic efficiency (Ochoa-Beltrán et al. 2021). This tendency underscores the importance of climate patterns in understanding leaf trait responses in a changing environment. Environmental factors, specifically light and climatic conditions, significantly impacted functional leaf traits (Stiegel and Mantilla-Contreras 2018). The result shows that in conservation strategies for *P. malaanonan*, canopy density is also vital due to its effect on other environmental factors.

#### 4. Conclusions

This study investigated for the first time the variations in leaf traits of *Parashorea malaanonan* along an elevational gradient in the Mount Makiling Forest Reserve. Here, vein density showed significant elevation-related changes, while leaf area, specific leaf area, leaf thickness, and leaf length-to-width ratio showed no such pattern. A strong correlation ( $r^2 = 0.7396$ ) between SLA and LT was also observed at high-elevation sites. Moreover, environmental covariables (canopy closure, rainfall, relative humidity, and temperature) may have also played a role in influencing the observed variation in some of the leaf traits measured, highlighting their impact on *P. malaanonan*'s development of adaptive strategies. Overall, the elevation gradient influenced the significant variations ( $p = 0.0125$ ) observed in certain leaf traits, encompassing varying environmental conditions that potentially contribute to the elevation-driven variability. The present study's findings can provide insights into how ecologically and economically important tree species develop adaptation strategies and resource acquisition patterns among species in complex forest ecosystems.

#### Acknowledgments

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