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# Soil nutrients determine leaf traits and above-ground biomass in the tropical cloud forest of Hainan Island

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Identifying soil characteristics associated with the plant's resource use and acquisition strategy at different scales could be a crucial step to understanding community assembly and plant strategy. There is an increasing trend that plant functional properties can be an important driver of ecosystem functioning. However, major knowledge gaps exist about how soil abiotic properties, shape species diversity, above-ground biomass (AGB) and plant functional diversity in the Bawangling tropical forest (TCF) of Hainan island. Hence we hypothesized that plant functional traits and above-ground biomass would be strongly associated with soil abiotic factors given their direct relationship to soil resource acquisition and use. Here, we used 12 plant functional traits (FTs), above-ground biomass (AGB), and five soil nutrients in the Bawangling tropical cloud forest of Hainan Island by using a polynomial regression model and multivariate correlations to show relationship and identify how plants allocate their limited resources to adapt to their surroundings. Various phytosociological attributes were assessed and an Importance Value Index (IVI) value was calculated for each species to determine the dominant species. More than half of the total variations could be attributed to interspecific variations in H, DBH, LA, LMA, and LDW. From a taxonomic perspective; we found that species-level variance was more significant for plant functional traits and soil nutrients like TN, AP, TP, and OM. On the other hand, variation in specific stem density (SSD), leaf thickness (LT), leaf phosphorus (LP) and leaf soluble sugar (LS) was an exception for these tendencies. Among soil nutrients, soil nitrogen and phosphorus significantly impact the species and functional traits. Furthermore, the soil AN and TP we also found to have a comparatively strong positive relationship with above-ground biomass (AGB) as compared with other soil nutrients. The morpho-physiological functional traits showed a trade-off between conservative and acquisitive resource usage. These variations suggested that the relationships of functional traits, AGB, and species with soil nutrients mainly AN and TP in tropical cloud forests can directly affect the growth, reproduction, and survival of the species and are beneficial for the species co-existence and maintenance of biodiversity.

## KEYWORDS

Bawangling, functional diversity, soil nutrients, above-ground biomass, principal component analysis

## Introduction

Forests are the primary component of terrestrial ecosystems, offering diverse ecological services and ensuring people's safety (Borma et al., 2022). There is a high level of biodiversity in the tropical forests, and strongly weathered soil is needed for the growth of these forests. There is a high diversity in the distribution of plant species and soils within a tropical region (Fujii et al., 2018). The tropical cloud forest has a distinct community structure, remarkable species, and distinctive habitats. Functional traits and phylogeny have been studied by several researchers (Luna-Vega and Magallón, 2010; Long et al., 2011, 2015a; Kang et al., 2017). In the humid tropics of Africa, America, and Asia, all the higher-elevation forests are covered mainly by mist or clouds (Bubb et al., 2004). Tropical cloud forests have more deformed trees covered by epiphytes than low-altitudinal tropical forests. When forests are compared at lower altitudes, their stand environment is defined by stronger winds, higher amounts of UV radiation, more frequent fogs and lower air temperatures. The preservation and stability of species variety in the community is the foundation of forest ecosystems' stability and versatility of line of sight (Maestre et al., 2012). The species preservation strategy from a geographical pattern, functional features, and pedigree structure is revealed at equal angles (Kraft et al., 2008; Paine et al., 2011; Pearse et al., 2013). In Chinese vegetation, secondary forests are mostly found in Yunnan and Hainan Island (Bubb et al., 2004). In the previous findings, species richness and composition of the TCF were recognized in Yunnan (Shi and Zhu, 2009). Hainan Island's tropical cloud forest community structure was also studied in the past on TCF's community structure and species richness. Still, there was no comprehensive research on the Association and ordination between soil nutrients and functional diversity in a tropical cloud forest of Hainan Island. Hence, further research is needed to fill this gap.

Ecologists have studied the community-building mechanism using functional and phylogenetic diversity over the last ten years (Webb et al., 2002; Swenson et al., 2012; Swenson, 2013). The functional diversity of plants is known by their response under environmental stress, renewal reproduction, and resource acquisition stratifies. Plant functional characteristics (PFT) also indicate a plant's evolutionary response to climate, competition, carbon gain, defense, life cycle and water relations (Wright et al., 2004). Ecologists increasingly recognize variation in PFT as a factor in community formation (Weiher and Keddy, 1999; McGill et al., 2006). PFTs significantly influence ecosystem processes, can anticipate ecosystem responses to environmental shifts and are crucial in defining how plant species interact with their surroundings (Cornelissen et al., 2003). The prevalent trait variations origin can be understood using strategies focusing on the significance of functional variations between species (Weiher and Keddy, 1998) and individuals (Paine et al., 2011). Systematic collection of characteristic features to determine the usefulness of certain traits in co-existing species can be assessed using different typical techniques such as field data and null models (Weiher et al., 1998; Kraft et al., 2008).

The functional traits are divided into different categories within individual plant organs, i.e., leaves (Wright et al., 2004; Li et al., 2015) and stem (Chave et al., 2009; Zanne et al., 2010) for supporting a limited set of possible trait combination; we have collected empirical evidence. According to the other studies, the plant organs are mostly

inconsistent and are geographically or taxonomically very rare. However, it is unclear how the whole plant's function and form are restricted. The SSD considers the trade-off between mortality risk and the growth potential caused by the hydraulic failure. The Leaf area (LA) directly affects water and leaf energy balance LN and the LMA are the conversation strategies and the many features of leaf resource achievement. Leaf Mass Area reflects the trade-off between carbon gaining and longevity. Similarly, Nmass indicates the trade-off between the benefits of the photosynthetic capability and the expense of collecting nitrogen and suffering herbivory (Díaz et al., 2016; Yaseen et al., 2022).

In contrast to low-altitude tropical forests, tropical cloud forests (TCF) experience an unusual interaction of abiotic variables (Long et al., 2011). Individuals, species, and communities are affected by abiotic influences, species distribution, and the basic composition of communities (Gao et al., 2023). For instance, research has demonstrated that, despite severe abiotic constraints such as insufficient availability of soil nutrients and strong winds, facilitative interactions in tropical cloud forests facilitate the assembly and coexistence of tree species (Long et al., 2013). Similar abiotic factors will probably influence systems for allocating resources to individual species, interspecies relationships, and communities. Phosphate and nitrogen are key factors affecting species richness, Evenness, and community composition in soil. According to Augusto et al. (2017), the amount of soil N is positively correlated with the plant Simpson index, and according to Medvigy et al. (2019), soil P is crucial for plant diversity production and maintenance. Insufficient soil nutrients may generally be a limiting factor for species diversity reduction (Liu et al., 2020). For example, soil qualities are mechanistically linked to plant biomass (Fayolle et al., 2012). In contrast, Plant growth has been limited in Neotropical forests due to differences in soil P (John et al., 2007).

Above-ground productivity of a forest community is positively connected to soil formation, air purification, and the entire ecosystem where tree species predominated (Baró et al., 2014; Grace et al., 2016; Pesola et al., 2017). Tropical forests are well-known for their higher biodiversity and above-ground biomass and the fact that they grow on strongly weathered soils. A diverse range of plant species and soil types exist even in a tropical region (Fujii et al., 2018). Tree biomass is influenced by abiotic factors, such as water availability, although other factors also play a role in tropical regions (Poorter et al., 2016). Abiotic factors affecting tree biomass include soil nutrients and management history (Lohbeck et al., 2015; Poorter et al., 2016; Ali and Yan, 2017; Van Der Sande et al., 2017). Studying leaf morphological and physiological plasticity in response to altering soil properties such as soil nitrogen (N) and phosphorus (P) availability is significant and necessary for predicting carbon (C) dynamics in tropical forests worldwide (Mo et al., 2020). However, there are several studies on above-ground biomass worldwide, but very little research has been focused on the factors or drivers of biomass in tropical cloud forests, Hainan Island.

Most early community-building research focused on changes in species diversity, where all species are viewed as ecological equivalents of autonomous evolution. However, they cannot describe species' evolutionary history and functional characteristic information and adequately expose the roots of community development (Webb et al., 2002; Swenson et al., 2012). Besides, there is limited knowledge about the construction mechanism of tropical cloud forest communities

and different variations and correlations in FTs of plants in tropical cloud forests. We studied 12 functional traits and five soil nutrients of 73 tree species in Bawangling Nature Reserve (BNR), in the Hainan Island tropical cloud forest situation, and conducted multivariate analyses to examine their relationships and variations. In particular, the elevation is founded on the leaf and the stem functional traits associated with resource gain plus protection (Wright et al., 2004; Agrawal and Fishbein, 2006). Preserving the species (community building) is often regarded as the most challenging ecological concern to address.

The multivariate relationships among functional traits reflect how plants adjust to environments through limited resource allocation. These relationships are well studied across species, but whether the nature of these trait relationships changes across soil abiotic factors is rarely explored in the tropical cloud forest of Bawangling, Hainan Island. We hypothesized that plant functional traits and above-ground biomass would be strongly associated with soil abiotic factors given their direct relationship to soil resource acquisition and use. We also aim (a) how soil abiotic factors influence species diversity that allocate resources based on functional traits and soil nutrients in the tropical cloud forests of Bawangling and (b) whether morphological traits were linked with leaf nutrient concentration.

## Materials and methods

### Site conditions

Bawangling Nature Reserve (18°50′–19°05′N, 109°05′–109°25′ E) is one of the tropical cloud forests of Hainan Island. The terrain is high in the middle and low in the surroundings, with higher rainfall in the east. The west is less, and the south is warmer than the north; the southwest and west are affected by the southwestern season Wind influences; the dry season, which runs from November until April the following year, is accentuated by the wind; the central mountainous region has more clouds and fog and lower temperatures. While the average daily relative humidity ranges from 87.88 to 100% during the rainy season (May to October), the average daily air temperature ranges from 17.6 to 24.8°C. Notably, during the rainy season (May–October), the average daily temperature varies between 17.6 and 24.8°C, while relative humidity averages between 87.88 and 100%. The soils are montane meadow soils made from sandstone parent material, and the terrain may be steep with slopes ranging from 3° to 65° (Hu and Li, 1992; Long et al., 2011). In the cloud forests at BNR, the average tree height was 4.79 ± 2.80 m, with 9,633 stems per hectare of trees. Despite significant variations in tree density, all sites shared a similar species composition, with *Exbucklandia tonkinensis*, *Osmanthus hainanensis*, *Polyspora axillaris*, *Machilus velutina*, *Illicium ternstroemioides*, *Rhododendron moulmianense*, *Syzygium odoratum*, *Osmanthus didymopetalus*, *Podocarpus neriifolius*, and *Michelia mediocris*.

### Data collection

In the Bawangling Nature Reserve, we collected data from randomly located 20 m × 20 m plots in tropical cloud forests (BNR: 21 plots). Each 400 m<sup>2</sup> field was divided into four subplots of 10 × 10 m and 16 quadrats of 5 × 5 m using the neighbor grid method. The

spacing across plots was kept higher than 50 meters. Flora Reipublicae Popularis Sinicae was used for taxonomic identification (Editorial Committee of Flora China, 2004). The forest where the sample plot is located consists of primitive old forest (undisturbed), mainly distributed at an altitude of 1,250 m above the summit or ridge. The DBH information was collected using the measuring tape for all the sampled trees, and the tree height was measured using a laser rangefinder (Long et al., 2022). Overall, we investigated 118 species having 9,728 individuals in the Bawangling tropical cloud forest of Hainan Island. The height of all trees with a dbh ≥ 1 was recorded using a clinometer.

The research area's trees are relatively mature in stature, which allowed us to precisely measure the H, DBH, LA, LSA, LC, LT, LDW, SSD, LMA, LP, LN, and LSS for each of the tree species occurring plots. Response characteristics and impact traits were selected as functional features to illustrate how plants develop, endure, adjust to interference, and use environmental resources (Chave et al., 2009; Manek, 2023) (Table 1). Taking the one-sided area of a fresh leaf as an example, LMA is the dry mass divided by the one-sided area. It is believed that variations in LMA reflect the number of resources each species allocates to leaf development (Poorter et al., 2009). A plant's capacity to receive nutrients and alter its pace of development is also influenced by LMA (Castro-Díez, 2012). As a measure of a plant's capacity to strive for space and light (Long et al., 2015a), H measures the shortest distance from the plant stem base to the tallest sucker or shoot in the canopy. As a result, H is associated with acquiring carbon (Falster and Westoby, 2003).

Five newly sprouted leaves from each species were collected from each plot 400 m<sup>2</sup> plot. To measure leaf thickness, a Vernier caliper with digital displays was used. Similarly, the leaf area (LA) was also measured using a leaf area meter. For each tree, a digital balance was used to weigh the leaves. The leaf is weighed on an Ohaus Adventurer AR2140 Analytical Balance, Hayward, CA, U.S.A. after it has been dried for at least 72 h at 70 degrees Celsius to a constant weight to determine the leaf Mass Area (mg mm<sup>2</sup>) and SLA (Specific Leaf Area) (mm<sup>2</sup> mg<sup>-1</sup>).

Plant central stem portion oven-dry mass is measured over by the portion of the volume of the same plant when it is still fresh to determine SSD it is shown as (mg mm<sup>-3</sup>). The same type of plants should be indicated for both leaf quality and height, i.e., mature, healthy plants with leaves exposed to full sunshine. A small sample size of five individuals per species was taken with thinner main stems (diameter < 6 cm) and a 10 cm long section at least cut out at the height or length of one-third of the stems (Reyes et al., 1992; Cornelissen et al., 2003).

Kjeldahl technique was used to measure nitrogen concentration. After samples were broken down using the HClO<sub>4</sub>-H<sub>2</sub>SO<sub>4</sub> digestion procedure, the phosphorus level was assessed using the molybdenum blue colorimetric method (Yang et al., 2021) and the anthrone colorimetric technique was used to determine the amount of soluble sugar (Cheng et al., 2019).

### Soil analysis

Each 5 m × 5 m takes off all of the soil's surface litter in the tiny sample square, 20 cm from top to bottom. We collected soil samples from different study sites, mixed them thoroughly, and marked them

TABLE 1 List of the functional traits, as well as their ecological strategies.

Functional traits	Abbreviation	Unit	Strategy	Reference
Height	H	M	Used to estimate individual tree biomass	Phalla et al. (2017)
Diameter at breast height	DBH	Cm	DBH helps make management and planning decisions	Morgenroth et al. (2020)
Specific leaf area	SLA	mm <sup>2</sup> g <sup>-1</sup>	Resource acquisition and defense	Yang et al. (2021)
Leaf chlorophyll	LC	mg g <sup>-1</sup>	Resource capture and defense are directly related to the photosynthetic rate of plants.	Coste et al. (2010)
Leaf thickness	LT	Cm	Resource gain and defense	Yaseen et al. (2022)
Stem specific density	SSD	mg mm <sup>-3</sup>	Transport, structure and defense	Yaseen et al. (2022)
Leaf nitrogen content	LN	%	Resource capture and defense	Yang et al. (2021)
Leaf phosphorus content	LP	%	Resource capture Transport	Yang et al. (2021)
Leaf soluble sugar content	LS	%	Important energy source for plants	Quentin et al. (2015)

for further analysis such as to determine the soil's organic matter (OM), total nitrogen (TN), total phosphorus (TP), available nitrogen (AN), and adequate phosphorus (AP) contents after it dries naturally. The ability of potassium dichromate to measure the amount of organic matter in soil. The material is first broken down using the HClO<sub>4</sub>-H<sub>2</sub>SO<sub>4</sub> digestion process before being measured using the molybdenum antimony colorimetric method, which is a quantitative procedure. Use the hydrochloric acid-ammonium technique to calculate the effective phosphorus content. Alkaline solution diffusion was used to calculate the available nitrogen concentration (China Professional Council of Agricultural Chemistry, 1983).

## Statistical analysis

The mean values of functional traits (H, DBH, SLA, LA, LDM, LC, LT, LMA, SSD, LP, LN, and LSS) were determined in Bawangling Nature Reserve (BNR) present in 21 plots of 20 × 20 m (400 m<sup>2</sup>) (Long et al., 2020). A multivariate correlation analysis was performed by using “psych” package and “pairs.panels” function. Furthermore, the *p*-value, *t*-value, standard error (SE) and correlation (R-values) were quantified by using corr.test function in RStudio 4.3.1. A multivariate principal component analysis (PCA) was performed to evaluate correlations between soil nutrients and dominant species using OriginPro 2021 software. After that, we also quantified the polynomial bivariate regression to determine the non-linear relationship between above-ground biomass and soil nutrients. We chose polynomial regression because the distribution of the data was not significantly linear. To calculate the above-ground biomass (AGB), we used the equation of Kenzo et al. (2009) developed for the tropical cloud forest with tree DBH >5cm.

$$AGB = 0.1083 \left( dbh^2 \times H \right)^{0.08} \quad (1)$$

Whereas dbh represents the diameter at breast height and H represents the plant height (Equation 1).

To calculate the importance value (IVI) of each tree species we first calculated the relative frequency, relative density and relative dominance of each species in the study area (Equations 2–5).

$$\text{Relative dominance} = \frac{\text{dominance for a species}}{\text{total dominance for all species}} \times 100 \quad (2)$$

$$\text{Relative frequency} = \frac{\text{frequency for a species}}{\text{total frequency for all species}} \times 100 \quad (3)$$

$$\text{Relative density} = \frac{\text{density for a species}}{\text{total density for all species}} \times 100 \quad (4)$$

$$IVI = \text{Relative frequency} + \text{Relative density} + \text{Relative dominance} \quad (5)$$

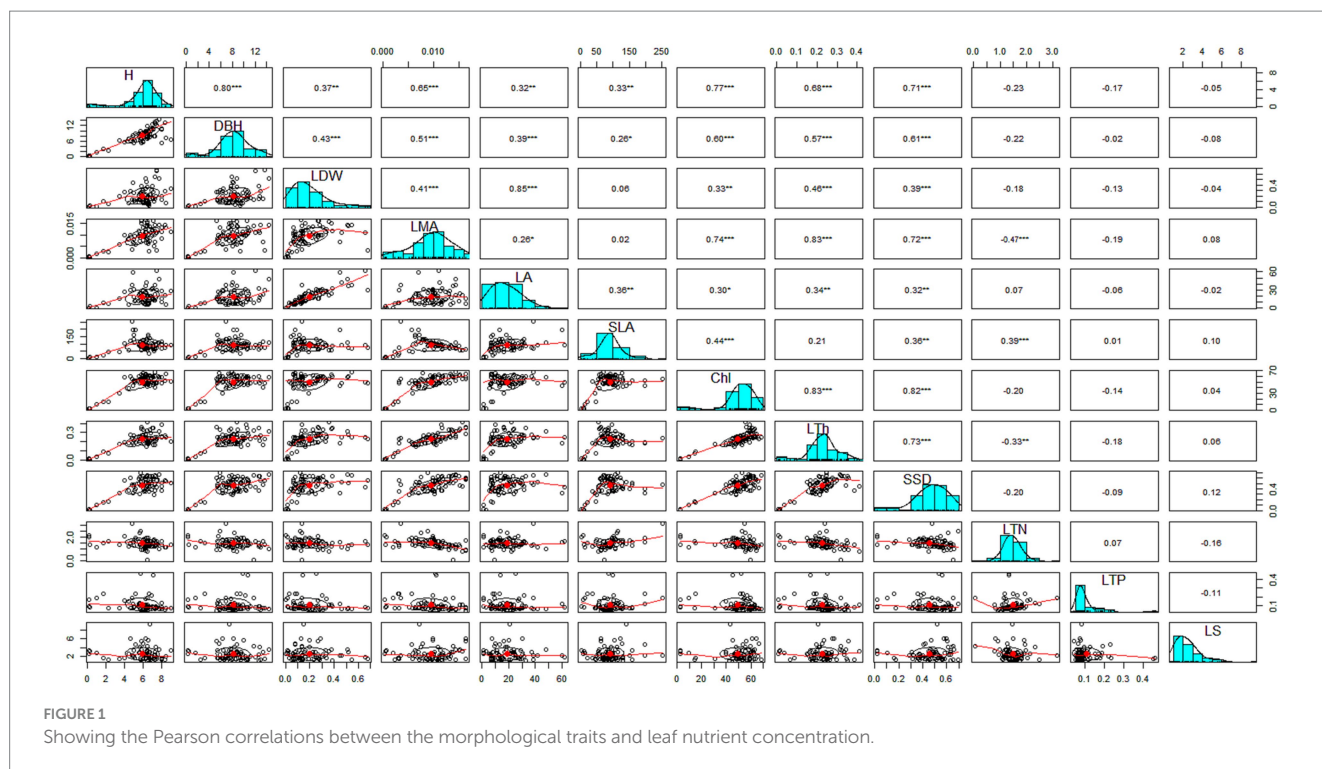
Moreover, the common diversity indices such as Pielou's evenness index (E) (Pielou, 1966) Shannon–Wiener index (H), (Shannon and Weaver, 1963), Simpson's diversity (D1), Simpson's dominance (D2), (Simpson, 1949) were used to describe the general properties of the species diversity in the tropical cloud forest of Bawangling.

## Results

### Relationship between morphological and leaf nutrient concentration

The multivariate analysis was performed to show the correlation between the morphological and leaf physiological functional traits (Figure 1). The leaf chlorophyll contents (chl) were significantly positively correlated with the morphological functional traits such as plant height ( $r = 0.77$ ), dbh ( $r = 0.60$ ), LMA (0.74), SLA ( $r = 0.44$ ), LA ( $r = 0.30$ ) and LDW ( $r = 0.33$ ). This association confirms that leaf structure modulates leaf chlorophyll and leaf morphological traits association. Secondly, the leaf total nitrogen (LTN) was significantly positively correlated with SLA ( $r = 0.39$ ) and significantly negatively with LMA ( $r = -0.47$ ), and LTh ( $r = -0.33$ ). However, no significant association was found with the rest of the morphological traits. The correlation of leaf total phosphorus (LTP) and leaf soluble sugar (LS) with morphological functional traits was found non-significant,





indicating that both LTP and LS were less defined by the morphological functional traits. Moreover, morphological functional traits were highly correlated with one another. Together, this set of leaf traits has been called the ‘worldwide leaf economics spectrum’ (LES) because this correlated suite of traits reflects the trade-off between the rapid acquisition of resources and the conservation of captured resources. The results of the correlation test such as standard error, correlation value and probability value for each trait were provided in (Supplementary Tables S2–S4).

### Functional traits determined by soil nutrients

The multivariate analysis was performed to identify the correlation between the functional traits and soil nutrients (Figure 2). We found that OM was significantly positively correlated with SLA ( $r = 0.26$ ,  $p = 0.05$ ), but negatively associated with LTP ( $r = -0.02$ ), SSD ( $r = -0.01$ ), LA ( $r = -0.02$ ), LDW ( $r = -0.13$ ) and H ( $r = -0.3$ ). The soil total phosphorus (TP) was significantly correlated with SLA ( $r = 0.25$ ,  $p = 0.05$ ), but negatively associated with LDW ( $r = -0.01$ ). However, it was positively but weakly associated with the rest of the functional traits. The soil available nitrogen (AN) was significantly positively correlated with LTN ( $r = 0.25$ ,  $p = 0.5$ ), and SLA ( $r = 0.38$ ,  $p = 0.005$ ), while significantly negatively associated with LDW ( $r = -0.23$ ,  $p = 0.5$ ). Similarly, the soil available (AP) was significantly correlated with SLA ( $r = 0.23$ ,  $p = 0.5$ ) but negatively with LTP ( $r = -0.12$ ), LA ( $r = -0.05$ ), LDW ( $r = -0.15$ ), dbh ( $r = -0.02$ ), and H ( $r = -0.02$ ). Moreover, we found that the soil total nitrogen (TN) was not significantly related to any of the functional traits indicating that plant functional traits were affected by soil TN. The results of the multiple correlation tests such as standard error, correlation value and

probability value for each functional trait and soil nutrient were provided in (Supplementary Tables S5–S7).

### Association between soil nutrients and dominant species

The principal component analysis was performed to show the visual relationship and dimensionality between the soil abiotic factors and dominant species. The two axes of PCA accounted for 87.3% of the variance in the soil nutrients and dominant species. The first PC showed 77.95% variation and is dominated by *Distylium racemosum* (IVI = 14.32), *Michelia mediocris* (IVI = 5.4), *Hypserpa nitida* (IVI = 5.92), *Rhododendron moulmianense* (IVI = 6.03), *Tabernaemontana bovina* (IVI = 7.55), *Psychotria asiatica* (IVI = 11.39), *Symplocos poilanei* (IVI = 7.54) and *Symplocos lancifolia* (IVI = 7.2). In comparison, the second PC showed 9.35% variation and is dominated by *Cyclobalanopsis disciformis* (IVI = 5.73), *Illicium ternstroemioides* (IVI = 4.43), *Elaeocarpus howii* (IVI = 4.68), *Polyspora axillariss* (IVI = 5.03), *Machilus velutina* (IVI = 3.63) (Figure 3).

### Relationship between above-ground biomass and soil abiotic factors

The polynomial regression fit was used to identify a nonlinear relationship between AGB and soil nutrients. A non-significant ( $p > 0.05$ ) relationship existed between soil abiotic factors and above-ground biomass. In tropical cloud forests of Bawangling, we found a relatively high and positive correlation of AGB with soil AN ( $r^2 = 0.031$ ) followed by TP ( $r^2 = 0.014$ ) and TN ( $r^2 = 0.013$ ), but a positively weak relationship of AGB with OM ( $r^2 = 0.008$ ), and AP ( $r^2 = 0.006$ ) (Figure 4).

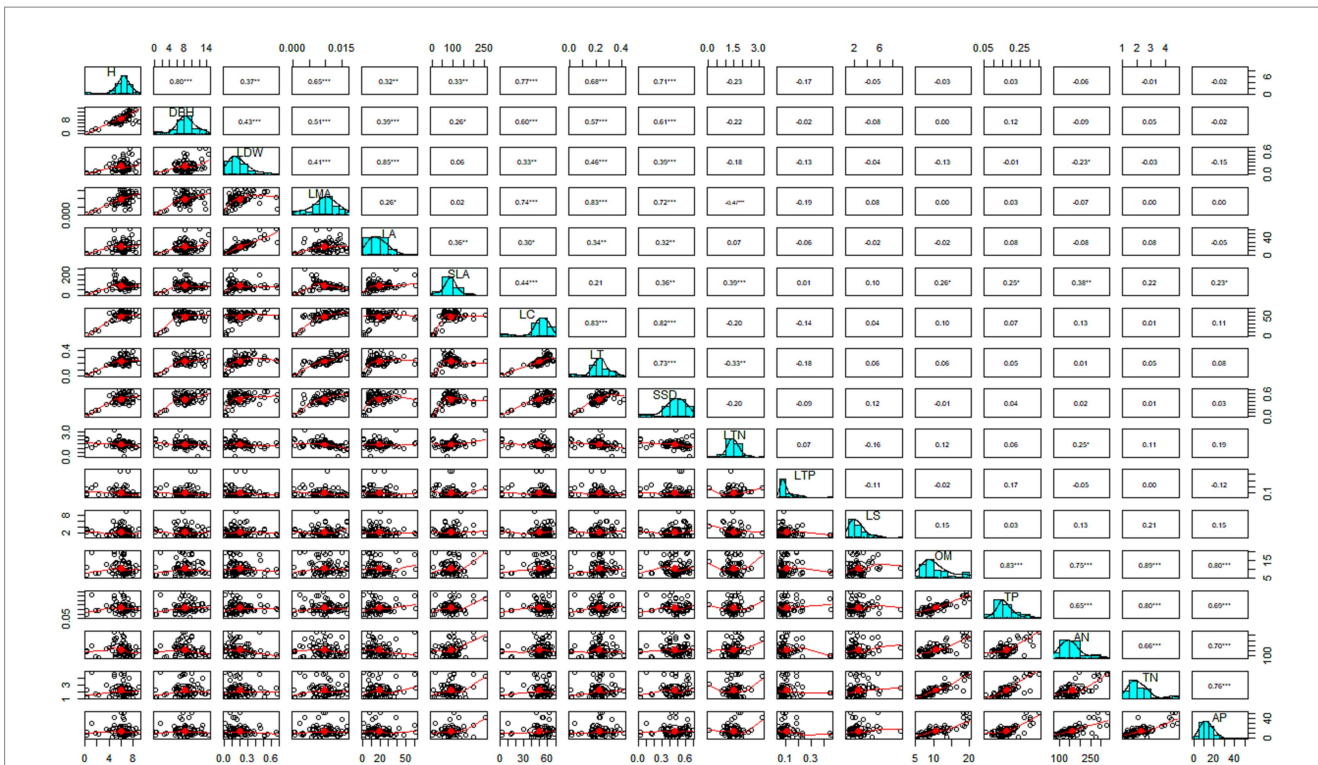


FIGURE 2 Showing the Pearson correlations between the functional traits and soil nutrients.

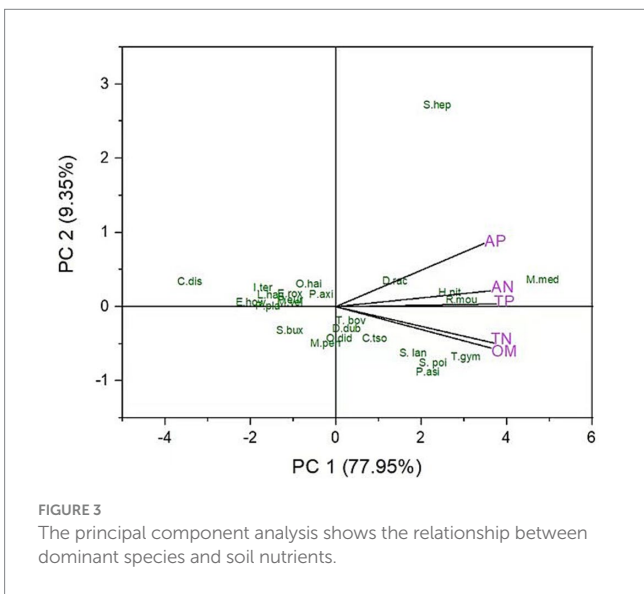


FIGURE 3 The principal component analysis shows the relationship between dominant species and soil nutrients.

*Exbucklandia tonkinensis* (4.84), *Ilex hainanensis* (3.58), *Illicium ternstroemioides* (4.43), *Lithocarpus hancei* (3.98), *Melastoma penicillatum* (6.37), *Syzygium buxifolium* (10.08), *Tabernaemontana bovina* (7.74) and *Psydrax dicoccos* (2.75). The phytosociological investigation would help us understand the vegetation dynamics of BWL forest vegetation and indicate the status of various species in the respective study sites. Diversity indices are the indicators of the species richness and health of vegetation in a particular area at a particular time. The diversity indices of the analyzed species showed higher values of Simpson diversity index (0.9581), Shannon<sub>H</sub>, Shannon diversity index ( $H'_c$ ) (3.649), Evenness (0.3257) and the Fisher alpha diversity (18.89) was recorded in the tropical cloud forest of Bawangling (Figure 5).

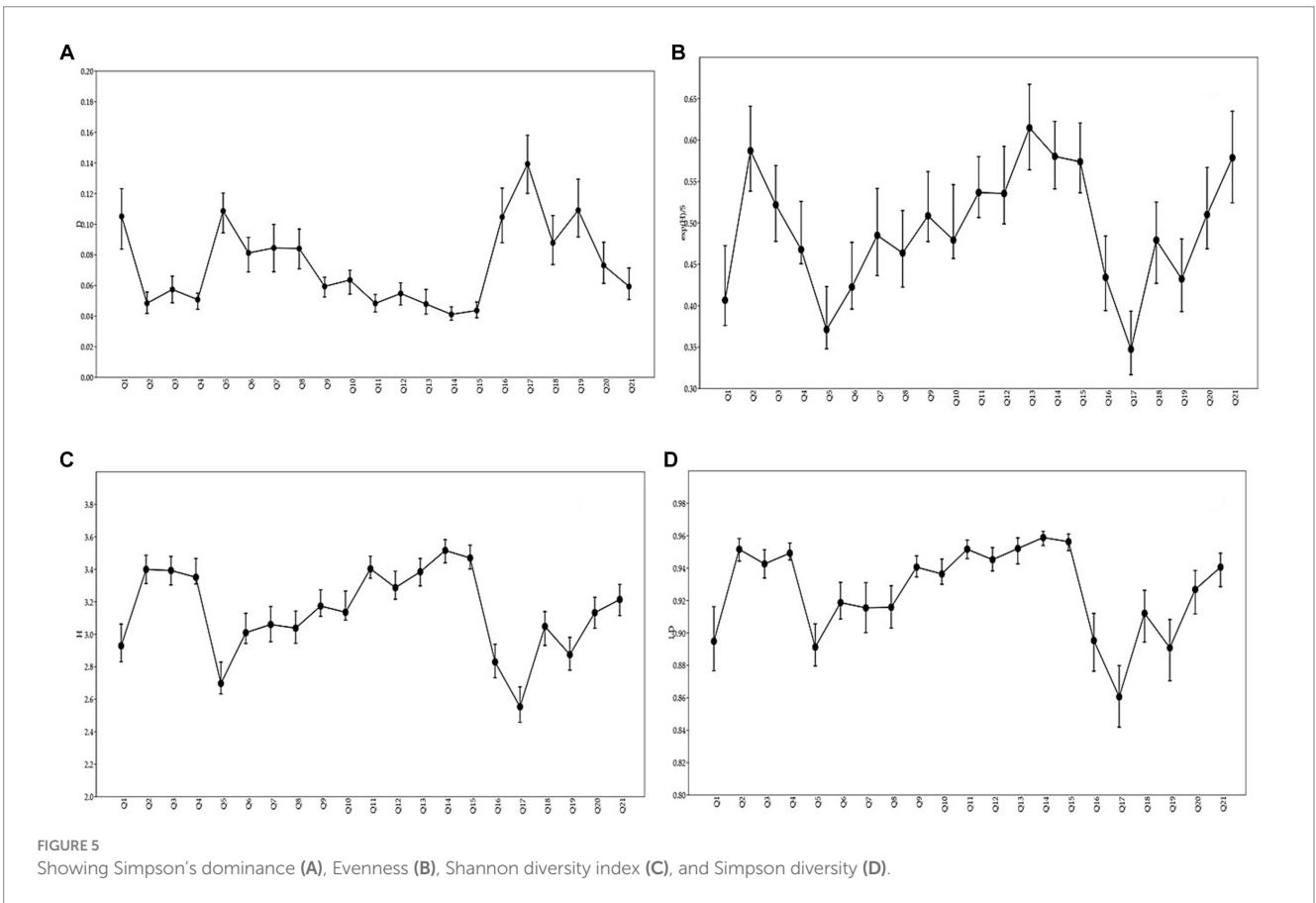
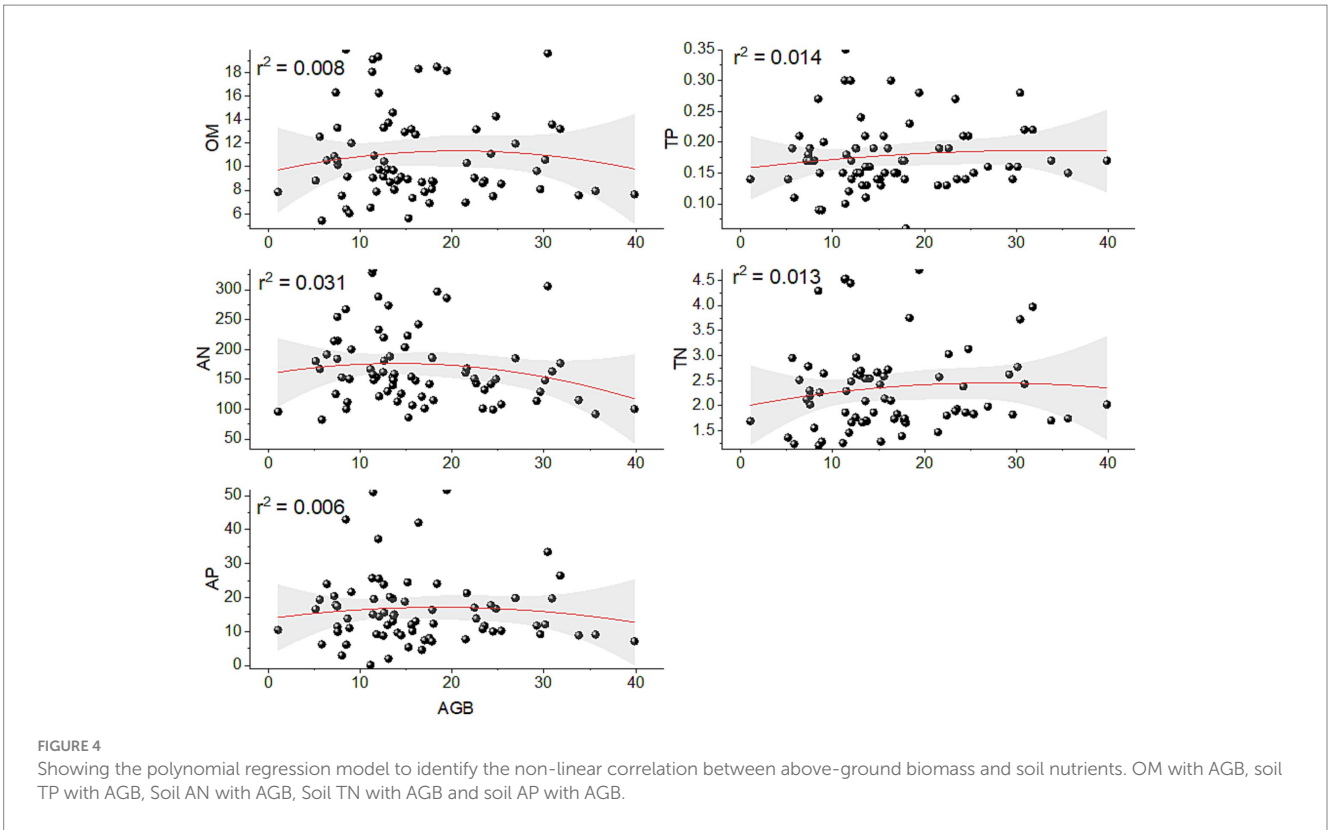
## Discussion

### Relationship between morphological and leaf physiological traits

Results of the multivariate analysis of morphological and physiological functional traits indicated a significant interaction. The observed functional traits were first categorized into two groups, morphological (H, DBH, LT, LA, SLA) and leaf physiological functional traits (LTN, LS, LC, LTP). These functional traits were chosen because they are recognized as reflecting important plant growth and survival strategies (Chave et al., 2009). The trees in the tropical cloud forest of Bawangling showed a disproportionate scaling relationship between morphological functional and leaf physiological traits. In our data set, LT showed a clear pattern of weak positive

### Phytosociological attributes and diversity indices

In BWL, tropical cloud forest structure and composition were quantified using various phytosociological indices such as frequency, density, and basal area analysis. The relative frequency, density, and basal area values were also determined. The species with a high importance value index (IVI) were called the dominant species. The maximum IVI was reported for *Cyclobalanopsis disciformis* (7.53), *Cyclobalanopsis poilanei* (8.83), *Dacrydium pectinatum* (4.94),



association with SLA indicating that low-SLA plants, with differential allocation to storage and defense, and more typical of resource-poor habitats tended to have thicker leaves than high-SLA plants with preferential allocation to photosynthesis and growth, more typical of resource-rich habitats. This is in agreement with Roderick et al. (2000). However, in the case of the Argentine dataset, LT could be as useful as SLA as an indicator of plant resource-use strategy. However, Wilson et al. (1999) have suggested a non-monotonic relationship between LT and plant resource-use strategy in the Northern European flora. The LT can vary for reasons related more to light availability than the use of soil resources (Roderick et al., 2000). This suggests that the usefulness of LT as an indicator of resource use can vary from region to region, and for different ecological reasons. Some other studies also showed that LT reflects the mechanical strength of leaves and is related to nutrient storage and resistance to adverse environmental conditions (Witkowski and Lamont, 1991; Onoda et al., 2011). Plants living in conditions of intense light and drought or in infertile soil conditions tend to have leaves with a greater thickness (Grady et al., 2013). Moreover, SLA is one of the fundamental functional characteristics that reflect trade-offs between resource acquisition and conservation (Conti et al., 2018). The SLA appears as a trait with more direct ecological interpretation in comparative studies. Therefore, among the leaf traits analyzed in this study, SLA appears to be the best candidate for inclusion in large screening programs oriented to regional to global-scale comparisons. The plant height (H) and diameter at breast height (dbh) are important traits describing the tropical forest stand. In our data set, we found significantly positive relations between height (H) and diameter at breast height (DBH). This is an agreement with Mugasha et al. (2013). The trees with large DBH were taller and had more expansive canopies. Moreover, tree dbh and height had a great significance in forest inventory, management, as well as forest carbon-stock and biomass estimation (Liu et al., 2018).

We also found a positive correlation of leaf chlorophyll contents (Chl) with leaf thickness (LT) and SLA. It is well known, that water stress causes greater thickness of outer walls of the leaf epidermis and cuticle, and leaf thickness has been shown to affect leaf chlorophyll contents (Wood et al., 1993). As a way of resource allocation within leaves, SLA profoundly influences the efficiency of assimilating photosynthetic active radiation and ultimately plant photosynthetic capacity (Green et al., 2003). Moreover, exposed leaves in the canopy are thicker, more vertically inclined, and have lower chlorophyll content per unit weight and a higher chlorophyll a/b ratio compared to understory leaves (Poorter et al., 1995). Some other studies documented the relationship between LMA-LTh and LMA-Chl relationships, indicating that these relationships clarify plant strategies that balance responses to stress with maximizing growth in tropical cloud forests. In addition, a positive relation between LMA-WD and LDW-LMA was observed in the present study that corroborated with the previous findings of Long et al. (2020). The positive relationship between LMA and WD indicates that plants augment the accumulation of carbon-rich chemicals in leaves and stems, increasing the lignin and carbon density of the cell wall, and contributing to the thickening and hardening of those walls. According to Hanley et al. (2007), some functional traits, such as WD, are universally regarded as essential functional features responsible for plant growth rates. A high WD reflects a highly competitive tolerance and a strong competitive impact associated with a slow prospective development

rate. The LMA is the dry mass divided by the one-sided area of a fresh leaf and can reflect the investment strategy of carbon and other nutrients in leaves (Wright et al., 2004; Poorter et al., 2009). The LMA is also related to a plant's ability to obtain nutrients and change growth rate (Castro-Díez, 2012).

Some previous studies reported a positive correlation between morphological (SLA) and leaf physiological traits (LN and LP) for a wide range of species richness and biomes (Wright and Westoby, 2001; Lamont and Wiens, 2003; Yang et al., 2021; Yaseen et al., 2022) which supports our findings. Several factors affect the distribution and variation of nutrients between organs of the plant. For example, it depends upon plant functional groups, environmental control, and evolutionary history (Han et al., 2011; Song et al., 2016; Yang et al., 2018). Soil nutrients and climate are the main factors controlling the change of LPC and LNC and their proportion. In addition, SLA is closely associated with other important traits including leaf nitrogen concentration, lifespan and plant relative growth rate (Wright et al., 2004), representing one of the main ecological strategies of plants (Westoby, 1998; Wright et al., 2004) that are in line with our study. Some other studies showed a significantly positive correlation between TN and LPC (Zhang et al., 2020). This is because the phosphorus cycle is mainly influenced by climate and soil (Elser et al., 2010). Moreover, phosphorus is produced by rock weathering. It is, therefore, more dependent on climate change. The primary component of nucleic acid, ATP, sugar phosphate, and phospholipids in plants is phosphorus since these processes are directly tied to photosynthesis (Rao and Terry, 1995). Phosphorus-rich plants generally have increased stomatal conductance Thomas et al. (2006), while stomata function as a control interface for regulating plant water loss. Approximately 40% of the precipitation that falls on land surfaces is returned to the atmosphere via transpiration. The increase in soil temperature benefits the available nitrogen (AN) because it positively impacts the decomposition of litter and nutrient circulation. Under high AN conditions, plants may take more nitrogen, increasing the LN contents, as there is no inhibition from the soil components. With increased LN contents, photosynthesis and respiratory enzymes are activated, resulting in a greater CO<sub>2</sub> exchange in leaves (Noguchi and Terashima, 2006).

In our data set, we found a positive correlation between morphological traits (SLA, LA, LT) and nonstructural carbohydrates (NSCs). The nonstructural carbohydrates (NSCs) are stored primarily as soluble sugars and starch in tree species and play important roles in the metabolic processes (photosynthesis, respiration, production) of plants and represent important physiological functional traits in plant's adaptation to external environment (Fischer and Höll, 1991; Quentin et al., 2015). According to Dietze et al. (2014), soluble sugar can be used as a direct carbon source for transportation and plant use. Thus, soluble sugar indicates the plant's ability to buffer environmental fluctuations (Zhang et al., 2021) by reflecting the balance between carbon intake and consumption (Würth et al., 2005). In the same way, soluble sugars influence the growth and development of plant tissue, both generative and vegetative. The leaf sugar content increased as the plants were flowering (Yang et al., 2022). Some other studies reported that SLA, NCS and LN concentrations were important predictors of leaf respiration across species and populations (Lee et al., 2005). The content of NSCs and their composition reflects the balance between carbon sources and sinks in plants (Li et al., 2016), while their allocation ratios in leaves, roots, and stems are considered as an



eco-physiological attribute to evaluate the carbon budgets and adaptive strategies of plant species. Hence, these morpho-physiological traits suggest that these type trait relationships in tropical cloud forests could directly affect the growth, reproduction, and survival of the species in the tropical cloud forest.

## Association between functional traits and soil nutrients

In this attempt to quantify relationships between functional traits and soil nutrients for the tropical cloud forest of Bawangling, we found several consistent, significant relationships. For example, OM was significantly positively correlated with SLA, but negatively associated with LTP, SSD, LA, LDW and H. Contrary to this, the relationship between SLA and soil organic carbon (TOC) displays an opposite pattern. This is probably because more nitrogen was locked up in relatively recalcitrant soil OM and therefore less available for uptake by plants, and also because of stoichiometric constraints (Ordoñez et al., 2009). The soil total phosphorus (TP) was significantly correlated with SLA and LTP. These findings were in agreement with the previous study of Ordoñez et al. (2009). Similarly, the soil available (AP) was also significantly correlated with SLA and is considered to be a limiting nutrient for plant growth and development all over the world (Vance et al., 2003). However, some other studies found an opposite trend indicating that the SLA and soil AP were not related (He et al., 2018). Although soil total P is not directly associated with actual P availability (Hinsinger, 2001), it still seemed to be a robust indicator of phosphorus fertility and was related to both leaf N and leaf P. Similarly, the soil available nitrogen (AN) was significantly positively correlated with LTN. The leaf nitrogen was the only leaf trait related to indicators of both N and P. This effect of soil P on leaf N seems determined by a tight coupling of leaf N and leaf P (Güsewell, 2004). Moreover, we found that the soil total nitrogen (TN) was positively related to SLA. Some previous studies revealed that nitrogen fertilization can increase SLA (Al Haj Khaled et al., 2005), while high nitrogen availability favors the dominance of high-SLA species (Craine et al., 2001). Likewise, other reports also indicated that SLA was positively related and responsive to soil nitrogen concentration (Niklas et al., 2005; He et al., 2018). Moreover, Ordoñez et al., (2009) revealed that the relations of soil total N with SLA, LP were not significant and those with LNC were in the opposite direction which supports our finding. Overall, the soil nitrogen and phosphorus were significantly correlated with leaf traits, while leaf traits such as SLA, LN, and LP are positively related to plant relative growth rates, leaf carbon assimilation rates, and energy supply.

## Association between soil nutrients and dominant species

In tropical coastal forests in southern China, species richness is strongly correlated with soil nutrients, TP, TN, and OM. By increasing the concentration of OM and TN in soil, species diversity and dominant species richness can be maintained (Whittaker et al., 1989; Long et al., 2018). Our findings also showed that soil nutrients significantly influenced dominant species, corroborated by previous studies (Neri et al., 2012). For example, *Distylium racemosum*

(14.32), *Hypserpa nitida* (5.92), *Rhododendron moulmainsense* (6.03), *Tabernaemontana bovina* (7.55), *Psychotria asiatica* (11.39), *Symplocos poilanei* (7.54) and *Symplocos lancifolia* (7.2) is positively and closely associated with AN, TP, TN, and OM. Furthermore, in the deciduous forests of western India, the data showed a clear correlation between soil nitrogen and phosphorus concentrations as well as soil carbon concentrations and tree species richness (Kumar et al., 2010). Thus, dominant species and their impacts on their environments are key to predicting ecosystem diversity patterns.

## Association between above-ground biomass and soil abiotic factors

The relationship between above-ground biomass and soil nutrients is fundamental to ecosystem functioning. Nutrients such as nitrogen (N), phosphorus (P), and organic matter (OM) are essential for plant growth and development, and their availability in the soil directly influences the productivity and composition of above-ground biomass. Additionally, organic matter in the soil plays a crucial role in nutrient cycling and availability. Above-ground biomass and productivity in forest ecosystems are influenced by changes in functional attributes as well as tree sizes, and by environmental factors (such as soils and topography) (Paquette et al., 2015; Zhang and Chen, 2015; Prado-Junior et al., 2016; Yuan et al., 2016). Our findings showed that TP was weakly but positively correlated with AGB, while soil phosphorus is an important growth-limiting resource and a vital driver of AGB in tropical forests (Cleveland et al., 2011). Some other studies indicated that soil phosphorus cannot be the significant determinant of AGB in tropical cloud forests, these findings were approximately support our findings (Lavorel and Gamier, 2002). It is very likely that many other soil nutrients are also essential and may be co-limiting tree growth. Contrary to our findings, a significantly positive association was found between soil TP and plant biomass (Fayiah et al., 2019). Soil P is the primary nutrient balancing plant productivity and better development in the forest ecosystem (Chen et al., 2000). We also found that TN was positively correlated with AGB, which corroborates with the study of Fayiah et al. (2019). A strong positive correlation between available nitrogen and above-ground biomass, indicating that higher availability of N promotes increased biomass production (Lambers et al., 2008). Soil properties are essential in determining plant relationships because soil nitrogen availability can predict plant biomass across different ecosystems (Dingaan et al., 2016). According to Tiessen et al. (1994), organic matter content in the soil was positively correlated with above-ground biomass. A strong positive relationship between AGB and OM was found in the study of Zhao et al. (2023). In line with this, we also found the same results for AGB and OM. In terms of organic matter, it serves as a source of nutrients and plays a vital role in nutrient cycling within ecosystems. In conclusion, we found a positive but weak relationship between above-ground biomass and soil nutrients, including total N, total P, available N, available P, and organic matter. The availability of nutrients in the soil directly influences above-ground biomass production and composition. These findings underscore the importance of nutrient management and preserving organic matter to ensure sustainable ecosystem functioning and productivity.

## Phytosociological attributes and species diversity

Various phytosociological attributes were evaluated and quantified for Bawangling vegetation stands, and it was found that most of the species were distributed contagiously ( $>0.025$ ). In contrast, few species were distributed randomly, such as *Casearia membranacea*, *Elaeocarpus sylvestris*, *Exbucklandia tonkinensis* and *Ficus variolosa*. In Riparian vegetation, the structure and composition of the forest were also investigated through density frequency and abundance analysis (Curtis and McIntosh, 1950; Kujur et al., 2022) and abundance to frequency ratio (A/F ratio). This ratio represents both random (0.025–0.05) and contagious ( $>0.05$ ) distributions (Curtis and Cottam, 1962; Kujur et al., 2022). Furthermore, species distribution patterns can be inferred from the A/F ratio. In optimal conditions, there may not be enough opportunities for seed dispersal or survival of saplings and such distributions are caused by phytogeographical restrictions (Long et al., 2015b; Kumar et al., 2017). In some cases, there was a clumping pattern of the species. Alternatively, this clumping may result from insufficient species seed dispersal (Richards, 1996) or the loss of trees allowing for the growth of several saplings simultaneously. Nevertheless, in Bawangling, the high tree density is responsible for the clumping of species distribution. Bawangling trees were dispersed in different directions and had different densities, indicating significant effects of disturbance regimes (Jhariya et al., 2019; Khan et al., 2020). Lyon and Gross (2005) suggest that disturbance regimes can regulate species composition and diversity patterns. Heterogeneity is likely the result of site conditions and geomorphological processes, which significantly determine species diversity, distribution, and abundance. The species (*Distylium racemosum*, *Pinus fenzeliana*, *Psychotria asiatica*) having IVI value  $>10$  reflect their dominance in the form of frequency and density value of the species in Bawangling TCF. Moreover, in the tropical cloud forests of Yunnan Province, the Lauraceae and Fagaceae (Shi and Zhu, 2009) and in Costa Rica, the Lauraceae (Nadkarni et al., 1995) are dominant families. Moreover, in Mexico's tropical cloud forests, *Symphytum* species are the dominant species; the other dominant genera are variable (Alcántara and Luna, 2002). In addition, over time, species diversity has increased; it may be possible to identify what tree species will be most suitable for restoring coastal windbreaks in the area (Yaseen et al., 2022). Moreover, the appearance and structure of communities are significantly different due to different environments and climates. As for the species with the lowest IVI values, they are fragile and may threaten biodiversity. In the study site, fragmentation is responsible for degenerating indigenous species, which alters their structure, composition and diversity (Ramakrishnan et al., 2000). The diversity indices are indicators of species richness and vegetation health in particular areas at certain times. The diversity indices of the analyzed species indicated higher values of Simpson diversity index (0.9581), Shannon diversity index ( $H'$ ) (3.649), Evenness (0.3257) and the Fisher alpha diversity (18.89) were recorded in the TCF of Bawangling. There are several ways of expressing plant diversity, but the most intuitive way is through species diversity. It represents the number and distribution of species within a community, a reflection of the resource-based coexistence (Jung, 2014; Wang et al., 2016).

Many ecological complexities within a plant community evolve in a specific location over time from different plant species. According to Wang et al. (2001), it is formed by the long-term interactions and relationships between plants and other species before moving on to

the environment. Community species' structure and composition are the basis for ecosystem activities and functions. The composition and structure of the community can be analyzed to learn more about coexistence guidelines and mechanisms that lead to species formation (Loreau et al., 2001). Our study confirms the significant role of soil abiotic factors in helping plant species assemble into communities in tropical cloud forests (TCF). The leaf economic spectrum (LES) of the Bawangling tropical cloud forest produces resource acquisition methods with distinct trade-offs between morphological and nutritional traits.

## Conclusion

The soil nutrients that determine species diversity and above-ground biomass in the Bawangling tropical cloud forest of Hainan Island have been investigated. The functional traits were categorized into two groups such as morphological (H, DBH, LT, LA, SLA) and leaf physiological functional traits (LTN, LS, LC, LTP) showing a trade-off between conservative and acquisitive resource usage. These morpho-physiological traits suggest the inter-trait relationships in tropical cloud forests that directly affect the growth, reproduction, and survival of the species. This study highlights the critical role of local variation in soil nutrients primarily soil nitrogen and phosphorus for regulating trait selection and species distributions that support our hypothesis. However, the above-ground biomass (AGB) was not significantly influenced by soil abiotic factors that partially support our hypothesis. Our research also revealed that soil nutrients significantly affect several dominant species such as *Distylium racemosum*, *Hypserpa nitida* individuals, *Rhododendron moulmainense*, *Tabernaemontana bovina*, *Psychotria asiatica*, *Symplocos poilanei* and *Symplocos lancifolia* in which soil phosphorus and available nitrogen shared the highest. Based on these findings, plants in this forest may use various developmental strategies connected to functional qualities and soil characteristics to adapt to local environmental conditions equally. Using several phytosociological attributes such as frequency density and basal area, the tropical forest showed more heterogeneity regarding species composition and community structure. Hence, these morpho-physiological traits and ABG associated with soil nutrients suggest that these trait relationships in tropical cloud forests can directly affect growth performance, reproduction, and survival of the species in the tropical cloud forest and contribute to a better understanding of plant ecological services, species co-existence, maintenance of the biodiversity and functioning of the tropical cloud forests.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

## Author contributions

FB: Formal analysis, Methodology, Writing – original draft. SB: Formal analysis, Methodology, Software, Writing – review &

editing, WL: Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

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## Conflict of interest

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## Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2024.1342135/full#supplementary-material>



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