



Functional Plant Traits and Their Role in Adaptation to Resource-Limited Forest Environments

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ABSTRACT

Functional traits provide an ecological basis for understanding how forest communities respond to variation in environmental resources. This study examined functional trait composition, functional diversity, resource gradients, and aboveground biomass (AGB) across 200 forest plots comprising deciduous, evergreen, and mixed forests. Community-weighted leaf and structural traits were evaluated alongside functional diversity indices, edaphic variables, and climatic conditions. Forest types differed significantly in LDMC, SLA, maximum height, maximum DBH, functional dispersion, functional richness, and AGB ($p < 0.001$). Evergreen forests showed greater structural trait values, whereas mixed forests exhibited higher SLA and functional diversity. Trait–environment analysis revealed strong associations between soil nitrogen and maximum height ($r = 0.704$) and DBH ($r = 0.674$), while SLA was positively associated with relative humidity ($r = 0.659$). Functional traits explained 79.5% of AGB variation, exceeding the explanatory contribution of environmental variables or functional diversity alone. The integrated model combining trait, environmental, and diversity predictors achieved the highest explanatory performance ($R^2 = 0.849$; adjusted $R^2 = 0.829$). DBHmax, soil nitrogen, and Hmax emerged as prominent biomass predictors. These findings demonstrate that integrating functional traits with environmental resource gradients can clarify community-level ecological strategies and forest biomass patterns under resource constraints.

Keywords: Functional traits, Environmental filtering, Resource limitation, Functional diversity, Aboveground biomass

1. Introduction

Forest is a system that operates in a highly dynamic temporal and spatial environment in terms of water, nutrients, temperature and other environmental resources. This heterogeneity affects establishment and growth of plants, as well as the composition of communities and productivity of the ecosystem, because it favours those species which have the necessary traits in order to adapt to the conditions. Responses can be understood using plant functional traits, which bridge the gap between morphology, function and resource acquisition, conservation and competition. Consider actions of the soil–plant–atmosphere interface are especially important, as belowground resources and the atmosphere interact to drive plant function and ecosystem response to environmental change (Silva & Lambers, 2021). The soil biological processes could also change the availability of resources and the carbon cycle, which would provide a further layer of environmental regulation of forest function (Anthony et al., 2020).

Functional traits represent two opposing ecological strategies, in which plants gain and hold scarce resources. Specific leaf area (SLA) and leaf dry matter content (LDMC) are leaf traits that reveal much about a plant's ability to acquire resources rapidly or use them conservatively, while plant height, stem diameter and crown dimensions are traits that reflect structural investment and competitive ability. Leaf traits of evergreen broad-leaved forests have been shown to vary considerably among different ecological strategies (Wang et al., 2024). Likewise, the research in tropical dry forests has highlighted the importance of functional traits on the understanding of plant response to environmental constraints and resource limiting conditions (Yadav et al., 2022). Moreover, traits can be sensitive to the abiotic and biotic context in which they are expressed (e.g., neighbourhood interactions), suggesting that functional strategies can be a product of environmental and community processes (Bandow, 2022). These relationships render the trait-based approaches especially pertinent in understanding the forest responses to resource limitation (Kumar et al., 2025).

One of the key mechanisms that connects resource conditions to forest functional composition is called environmental filtering. In restrictive environments environmental factors may select for specific combinations of traits and against those strategies that are not well adapted to the available resources. A strong filtering according to hydraulic traits has been reported, for example, in temperate forest communities where water availability is reduced (Zhao et al., 2022). Meanwhile, there can be differentiation at multiple functional dimensions, such as in the use of resources, to support coexistence, where species occupy distinct ecological niches. Therefore, the analysis of single community-weighted traits might not necessarily give a full picture of ecological organisation. Measures of functional richness, dispersion, divergence, evenness and dominance can be used in addition to trait means, to describe the extent and distribution of functional strategies within communities.

Forest biomass and productivity are also important ecological aspects of functional traits. Functional trait trade-offs can interact with soil resources to regulate biomass stocks and productivity of species at the ecosystem scale, showing that ecosystem performance is dependent on soil resources and plant strategies (Caleño-Ruiz et al., 2023). At the larger forest gradients, climate, stand properties, and environment factors influence aboveground biomass (Ding & Zang, 2021). The diversity effects can also vary between different stand structures and different local environmental contexts, and different aspects of diversity can have opposing associations with biomass in tropical forests (Abbasi et al., 2023). Results of studies from other bioclimatic systems also show that functional diversity and functional composition are responsible for aboveground biomass (Feizabadi et al., 2021).

Climate, soil resources are not independent of each other but work in tandem. Above- and belowground biomass allocation can be altered due to climatic effects on soil nutrient conditions (Zhang et al., 2023). New synthesis further suggests that the functional traits affect the quantified extent and sign of plant biomass responses to global environmental shifts, thereby highlighting the need of taking functional traits into account for ecosystem functioning. The results indicate that using an integrated approach of climatic conditions, edaphic resources, functional composition and functional diversity in the analysis might offer a higher ecological value than analysing each component alone.

Despite the increase in trait-based studies, it is still unclear how several components of functional composition change simultaneously between the different forest types and how biomass is related to this in resource-limited settings. Few studies focus on multiple functional dimensions of diversity, many highlight specific traits, environmental drivers or aspects of diversity, and few combine community-weighted leaf traits, structural traits, multidimensional functional diversity, edaphic resources, climatic gradients and aboveground biomass in a single analytical framework. Combining these components can help to quantify if there is a link between resource gradients and different ecological strategies at the community level and if there are particular dimensions of traits that are most strongly associated with forest biomass. This study,

therefore, focuses on the variation in functional traits and ecological strategies in response to resource in deciduous, evergreen and mixed forest environments. There are three objectives of the study:

- Quantify functional trait and diversity variation across contrasting forest types.
- Determine associations between environmental resources and community-level functional traits.
- Assess functional and environmental contributions to variation in aboveground biomass.

2. Materials and Methods

2.1 Study Design and Data Structure

A plot-level observational design with quantitative approach was employed for the study on functional plant traits in the resource-limited forest environment (ALI, 2026). A total of 200 forest plots (90 deciduous, 70 evergreen and 40 mixed) were analyzed. Forest plots were analysed as independent units.

2.2 Functional Plant Traits

Community-weighted mean (CWM) traits were used to characterize the plant functional composition including leaf dry matter content (LDMC), specific leaf area (SLA), maximum height (Hmax), maximum diameter at breast height (DBHmax) and maximum crown dimension. These variables were chosen as leaf-resource and structural strategies of forest communities.

2.3 Functional Diversity Assessment

Functional dispersion (FDis), functional richness (FRic), functional divergence (FDiv), functional evenness (FEve) and functional dominance (FDomin) were used to assess functional diversity. The difference in distribution and dominance of functional strategies among forest communities was characterized by these indices.

2.4 Environmental Resource Assessment

Soil N, Ca, Mg, Na, Cu, Mn, Ni, Co and Cr and climatic factors such as temperature, precipitation, relative humidity and MWP were used to represent environmental conditions. These variables were analysed as a possible environmental correlate of functional trait variation.

2.5 Aboveground Biomass Modeling

Ecosystem level response variable was aboveground biomass (AGB). The environmental, functional-trait and functional-diversity models were tested in isolation and then integrated. The R^2 , adjusted R^2 , RMSE and AIC were used to assess the model performance.

2.6 Statistical Analysis

Forest type differences and trait–environment relationships were characterized using descriptive statistics, one-way ANOVA, Pearson correlation and principal component analysis (PCA). Multiple regression and random forest regression were used on AGB data, and five-fold cross validation and permutation importance were used to evaluate the predictive power and the contribution of the predictors. Data analysis was done using Python, pandas, NumPy, SciPy, statsmodels and scikit-learn and figures were created in Matplotlib. A p value of < 0.05 was considered statistically significant.

3. Results

3.1 Functional Trait Variation Across Forest Types

There is variation in functional traits according to forest types. There were significant variation in the functional traits between the three forest types. As seen in Table 1, evergreen forests showed higher value of LDMC, Hmax, MDBH while mixed forests showed higher value of SLA, FDis and FRic. There were significant differences in LDMC, SLA, Hmax, DBHmax, FDis, FRic and aboveground biomass (AGB) ($p < 0.001$) but not for crown size ($p = 0.095$). The multivariate differentiation in functional-trait composition (figure 1) is clear, with the first two principal components explaining 72.1% of the total variation.

Table 1. Functional Trait, Functional Diversity, and Biomass Variation Across Forest Types

Variable	Deciduous (n=90)	Evergreen (n=70)	Mixed (n=40)	F	p
CWM LDMC	-0.137 ± 1.239	0.399 ± 0.668	-0.391 ± 0.567	10.38	<0.001
CWM SLA	-0.010 ± 0.817	-0.554 ± 0.777	0.991 ± 0.976	43.30	<0.001
CWM Hmax	-0.441 ± 0.211	0.741 ± 1.383	-0.305 ± 0.300	42.12	<0.001
CWM DBHmax	-0.458 ± 0.467	0.473 ± 1.360	0.204 ± 0.635	21.90	<0.001
FDis	-0.195 ± 0.739	-0.364 ± 0.958	1.076 ± 0.849	41.49	<0.001
FRic	-0.066 ± 0.839	-0.568 ± 0.277	1.143 ± 1.197	59.82	<0.001
AGB	-0.449 ± 0.090	0.208 ± 0.835	0.018 ± 0.401	32.22	<0.001

Values are mean $\pm$ SD; variables are standardized.

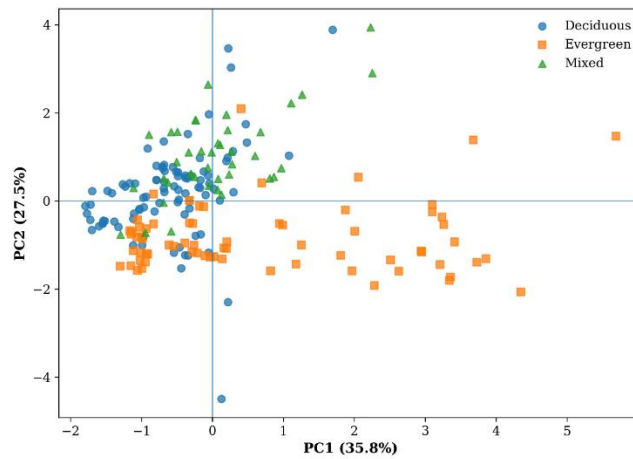


Figure 1. Principal Component Ordination of Functional Traits Across Deciduous, Evergreen, and Mixed Forests

3.2 Trait–Environment Relationships

There were clear functional trait–environmental relationships. As revealed by table 2, SLA had a strong positive correlation with the relative humidity with the value of $r = 0.659$ and had a strong negative correlation with the MWP with the value of $r = -0.513$. Soil N was highly correlated with structural characteristics, notably, Hmax ($r = 0.704$) and DBHmax ($r = 0.674$). Both traits decreased in response to increasing levels of chromium. The general correlation structure, as shown in Figure 2, suggests that there are differential responses of leaf and structural traits to resource gradients.

Table 2. Major Relationships Between Functional Traits and Environmental Resources

Functional trait	Environmental variable	<i>r</i>	<i>p</i>
CWM_LDMC	Precipitation	0.344	<0.001
CWM_SLA	Relative humidity	0.659	<0.001
CWM_SLA	MWP	−0.513	<0.001
CWM_Hmax	Nitrogen	0.704	<0.001
CWM_Hmax	Chromium	−0.460	<0.001
CWM_DBHmax	Nitrogen	0.674	<0.001
CWM_DBHmax	Chromium	−0.448	<0.001

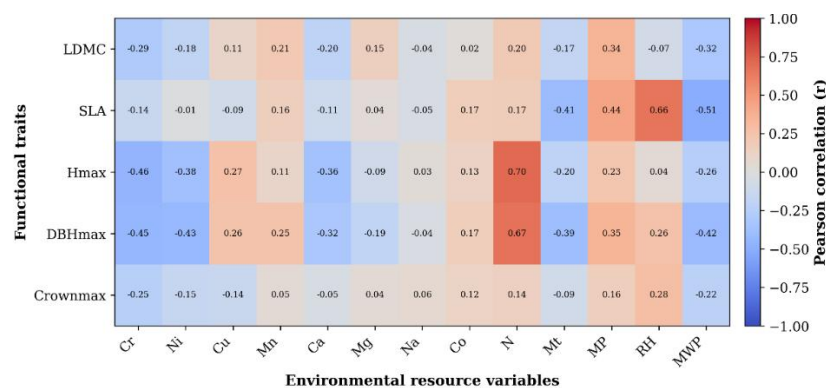


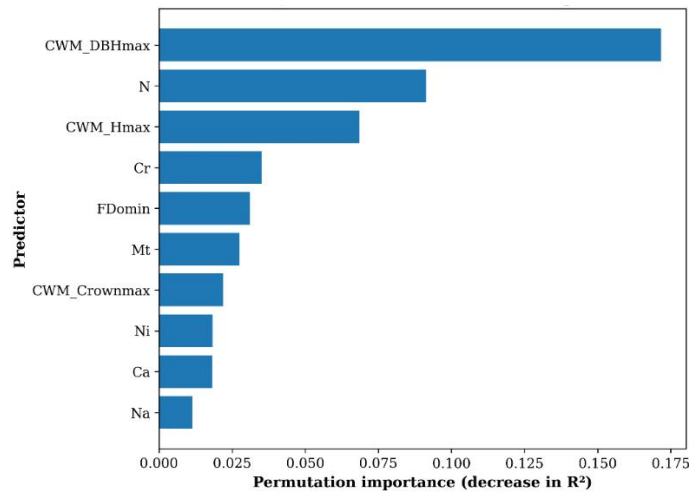
Figure 2. Correlation Heatmap of Functional Traits and Environmental Resource Variables

3.3 Functional Traits and Aboveground Biomass

Functional traits were more effective in explaining AGB than environmental resources and/or functional diversity alone. The trait model explained 79.5% of the AGB variation, whereas the environmental predictors and functional diversity explained 64.9% and 50.9% of the AGB variation, respectively (Table 3). The integrated model performed best ($R^2 = 0.849$; adjusted $R^2 = 0.829$; RMSE = 0.235). Important positive predictors were DBHmax, Hmax, functional dominance and soil nitrogen. Based on Figure 3, the highest permutation importance was obtained for DBHmax which was 0.165 followed by nitrogen (0.092) and Hmax (0.082).

Table 3. Model Performance for Aboveground Biomass

Model	R ²	Adjusted R ²	RMSE	AIC
Environmental	0.649	0.625	0.358	184.77
Functional traits	0.795	0.790	0.274	61.53
Functional diversity	0.509	0.496	0.424	236.24
Integrated	0.849	0.829	0.235	36.63

**Figure 3. Permutation Importance of Functional and Environmental Predictors of Aboveground Biomass**

The results across all types of forests show high functional differentiation and high relationships between the composition of traits and the gradients of forest resources. Forest biomass varied significantly with structural traits; especially with DBHmax and Hmax and soil nitrogen.

4. Discussion

Functional traits show significant variation among the deciduous, evergreen and mixed forests, suggesting different ecological strategies in different forest environments. Evergreen forests had higher values of LDMC, maximum height and DBH while mixed forests had higher values of SLA, functional dispersion and functional richness. Differentiation in this way is in line with the idea that the combination of functional traits is different ways of acquiring and conserving resources, growing and persisting in the face of environmental change (Laughlin, 2023). The influence of the environment on plant traits can also vary across life forms and ecological contexts, highlighting the need to take into account several functional dimensions at the same time (Cheng et al., 2022).

The results of the observed trait–environment relationships also suggest systematic change in functional composition with resource gradient. Relative humidity was positively associated with SLA, while MWP had a negative association, and particularly strong associations between soil nitrogen and structural traits. Nmax, Hmax, and DBHmax were positively correlated with nitrogen, implying that higher levels of nutrient availability occurred with communities with higher degrees of structural development. Similar research has found that environmental conditions can favor specific functional strategies and thus have an impact on community structure (Yang et al., 2022). Functional traits thus may offer an important connection between the ecological strategies of the species of the communities, and the local environment in which they develop in resource-limited environments.

These patterns are more generally in accordance with the 'environmental filtering' in which abiotic conditions limit what functional strategies are able to persist in a community. Functional traits have also been linked to species coexistence in unfavourable environments where abiotic factors are imposing strong constraints on ecological strategies (Tameirão et al., 2021). But environmental associations cannot be the only means of community assembly for filtering. The environmental filtering paradigm must be interpreted carefully as environmental changes may influence community composition, for example, through competition, dispersal, historical processes and stochastic effects (Baecher, 2024). Recent studies have suggested that environmental filtering and dispersal limitation can both play a role in shaping taxonomic, functional and phylogenetic diversity (Long et al., 2025).

The apparent importance of the different assembly processes may be further mediated by the spatial scale.

The relative importance of environmental filtering and dispersal limitation on plant diversity along multiple dimensions has been demonstrated to change depending on sampling scale (Hu et al., 2023). Thus, the variations among forest types in this case are better viewed as functional trends along an environmental gradient than as proof of one kind of assembly. The importance of environmental heterogeneity in the organization of communities has been demonstrated in other systems beyond plant communities. Biological response to environmental variation is also a threshold-dependent phenomena, meaning that biological response is not necessarily equal over all levels of environmental variation (Norris, 2020).

Forest biomass also was strongly correlated with functional composition. The functional-trait model accounted for 79.5% of the AGB variation, the functional-diversity model for 50.9%, and the integrated model that included environmental variables, functional traits as well as functional diversity for 84.9%. Soil nitrogen and Hmax were the next most important permutations followed by DBHmax. These results suggest that certain structural properties of the dominant vegetation were especially useful for the understanding of the variation in forest biomass. This aligns with the trait-based theory, which posits that plant size and other functional traits affect growth, survival, competitive ability and demography (Laughlin, 2023).

Soil N further illustrates the need to view functional attributes and environmental resources in conjunction with each other. How much more structure and biomass will come from specific combinations of traits may depend on the availability of resources. However, the high functional dispersion and richness of mixed forests suggest that under certain environmental conditions, communities are able to tolerate a wider spectrum of ecological strategies. The results highlight the importance of accounting for community-weighted traits, in addition to multidimensional functional diversity, in the analysis of forest responses to resource constraints.

However, there are some problems with the study. It is cross sectional and thus does not allow causal relationships to be drawn between resource availability, functional traits and biomass, and community-weighted traits cannot be differentiated from evolutionary adaptation. In addition, dispersal, demographic parameters, physiological responses and temporal environmental variability were not taken into account. The limitations are relevant as environmental filtering can interact with non-filtering processes in determining the composition of the community (Baecher, 2024; Long et al., 2025). Long-term forest monitoring combined with species-level traits, experimental manipulation of nutrient and water availability and demographic measurements is needed in future research. This would give more evidence to differentiate whether they are short-term ecological responses or long-term adaptive strategies, and to better understand the relationships between functional traits and forest resilience in the face of a changing and more variable environment (Laughlin, 2023).

5. Conclusion

The results of this study show that functional traits of plants serve as a good foundation for understanding plant community responses to different resource conditions in forest ecosystems. Each forest type (deciduous, evergreen and mixed) exhibited different functional strategies, where evergreen forests were more structurally dominated and mixed forests were more functionally diverse and had higher SLA. These patterns were strongly related to environmental gradients, mainly in terms of soil nitrogen, relative humidity and climatic conditions. For forest structure, strong positive relationships between nitrogen and maximum height and DBH were found, emphasizing the importance of resource availability for forest structure development. There was also high explanatory power for aboveground biomass for functional traits. The trait-based model accounted for 79.5% of the biomass variation and the integrated model (functional traits, diversity and environmental variables) accounted for 84.9%. DBHmax, nitrogen and Hmax were the most influential predictors. These results suggest that forest biomass structure is the result of an integration of vegetation structure and environmental resources. In summary, the use of functional composition, diversity and resource gradients is a valuable framework in which to assess forest ecological strategies, but there is a need to investigate the causal and adaptive processes through longitudinal and experimental studies.

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