Between categories and continua: growth-form organization in global leaf economics spectrum space

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Abstract

The leaf economics spectrum (LES) describes a globally coordinated trade-off between acquisitive and conservative plant resource-use strategies, yet how major plant growth forms are organized within multidimensional LES space, and the extent to which observed patterns reflect phylogenetic history, remains incompletely resolved. Using species-level trait data from the TRY Plant Trait Database, we examined multidimensional trait organization across 3,206 vascular plant species representing trees, shrubs, herbs, graminoids, and climbers using four core functional traits: specific leaf area, leaf nitrogen content, leaf dry matter content, and vegetative height.

Principal component analysis identified a dominant acquisitive-conservative LES axis explaining 50.3% of total trait variation, while a secondary height-associated axis explained an additional 25.2%. Major growth forms occupied significantly differentiated yet strongly overlapping regions of multidimensional trait space, with herbs and graminoids generally associated with more acquisitive strategies than woody growth forms. Growth-form differentiation remained significant across multivariate and phylogenetically informed analyses despite strong phylogenetic structure in LES positioning. Extensive overlap among growth forms and repeated occupation of similar trait regions across distantly related lineages indicated that similar ecological strategies are not restricted to particular evolutionary lineages.. Together, these findings suggest that global plant ecological strategies are continuous, multidimensional, and evolutionarily structured, with major growth forms representing overlapping regions of trait space rather than discrete functional categories.

Keywords: leaf economics spectrum; plant functional traits; growth forms; phylogenetic comparative analysis; multidimensional trait space; vascular plants.

1. Introduction

Plant functional traits play a central role in shaping ecological strategies, species interactions, and ecosystem functioning across terrestrial ecosystems. Traits associated with resource acquisition, tissue construction, growth, and stress tolerance influence how plants respond to environmental gradients and contribute to large-scale patterns of vegetation dynamics (Díaz et al., 2016; Mcgill et al., 2006). Consequently, trait-based ecology has increasingly emphasized continuous axes of functional variation rather than strictly discrete ecological categories (Laughlin, 2014; Mcgill et al., 2006). Among these frameworks, the leaf economics spectrum (LES) describes a globally coordinated trade-off between acquisitive and conservative resource-use strategies, linking traits such as specific leaf area, leaf nutrient concentrations, and tissue density across vascular plants worldwide (Wright et al., 2004). Species positioned toward the acquisitive end of the spectrum typically exhibit rapid resource acquisition and growth, whereas conservative species invest in structurally robust tissues associated with slower growth and greater persistence (Reich, 2014; Wright et al., 2004). The remarkable global consistency of the LES has established it as one of the foundational frameworks in contemporary plant functional ecology (Díaz et al., 2016; Wright et al., 2004).

While the LES captures a dominant axis of plant functional variation, increasing evidence suggests that plant ecological strategies are multidimensional rather than reducible to a single universal continuum (Díaz et al., 2016; Reich, 2014). Recent global syntheses of plant form and function have demonstrated that traits associated with plant stature, structural investment, hydraulics, and biomass allocation may vary semi-independently from classical leaf-level economic traits (Li and He, 2024; Weigelt et al., 2021). In particular, dimensions related to plant size and architecture often occupy orthogonal axes relative to core LES traits, implying that whole-plant ecological strategies cannot always be represented adequately by a single acquisitive–conservative spectrum (Díaz et al., 2016; Li and Prentice, 2024; Ma et al., 2024). Consequently, modern trait-based ecology has increasingly emphasized multidimensional phenotypic spaces and continuous ecological variation rather than rigid functional classifications (Laughlin, 2014; Li and He, 2024; Mcgill et al., 2006). These frameworks suggest that substantial trait overlap, partial decoupling among trait syndromes, and multidimensional ecological trade-offs may represent fundamental features of plant strategy organization across vascular plants (Adler et al., 2014; Weigelt et al., 2021).

Major plant growth forms represent broad ecological and structural strategies that differ in lifespan, architecture, biomass allocation, competitive dynamics, and resource-use patterns (Díaz et al., 1999). Woody and herbaceous taxa, for example, often exhibit contrasting investment strategies associated with tissue longevity, hydraulic architecture, and growth rates, potentially influencing their positioning within global trait spectra (Díaz et al., 2016; Reich, 2014). Increasing empirical evidence suggests that plant economic strategies may therefore exhibit structured variation among growth forms and functional groups (Li et al., 2025; Zhao et al., 2016), despite substantial overlap in multidimensional trait space (Weigelt et al., 2021). Studies integrating leaf, wood, and whole-plant traits have shown that growth forms and plant functional types can influence the organization of economic spectra across regional and biome-specific systems (Díaz et al., 2016; Reich, 2014; Zhao et al., 2016). At the same time, considerable functional overlap among growth forms indicates that ecological strategies are unlikely to form discrete categories, but instead occupy partially overlapping regions within broader continuous trait continua (Adler et al., 2014; Laughlin, 2014). Together, these findings suggest that major growth forms may retain ecological significance within global trait spectra while remaining embedded within fundamentally continuous and multidimensional patterns of plant strategy variation (Díaz et al., 2016; Weigelt et al., 2021).

Plant functional traits are also strongly influenced by evolutionary history (Donovan et al., 2011; Flores et al., 2014; Sanchez‑Martinez et al., 2025). Numerous studies have demonstrated that LES-associated traits exhibit significant phylogenetic signal, indicating that closely related species frequently resemble one another in resource-use strategies and functional syndromes (Akram et al., 2022; Flores et al., 2014; Mason and Donovan, 2015). This phylogenetic conservatism suggests that broad patterns of trait variation may partly reflect shared ancestry rather than independent ecological adaptation (Ackerly, 2003). At the same time, similar ecological pressures may repeatedly drive unrelated lineages toward comparable acquisitive or conservative strategies, potentially generating functional convergence across distantly related taxa (Losos, 2011; Mason and Donovan, 2015). Consequently, distinguishing ecological differentiation from phylogenetic structure has become a central challenge in comparative functional ecology (Ackerly, 2003). Understanding whether growth-form differentiation within LES space persists after accounting for phylogenetic relatedness, therefore, requires explicit phylogenetic comparative approaches capable of separating evolutionary history from broader ecological patterning.

Although the LES has been extensively characterized across vascular plants, comparatively fewer studies have explicitly quantified how major plant growth forms are distributed within global LES space while simultaneously accounting for phylogenetic relatedness. Previous work has often focused on regional systems, restricted taxonomic groups, or limited sets of growth forms, leaving uncertainty regarding the extent to which broad plant growth forms occupy structured but overlapping regions within global trait continua (Mason and Donovan, 2015; Zhao et al., 2016). The degree to which observed growth-form differentiation reflects phylogenetic conservatism versus broader ecological structuring remains poorly resolved at macroecological scales (Ackerly, 2003; Donovan et al., 2011). Addressing these questions is important for understanding how ecological strategies are organized across vascular plants and how evolutionary history interacts with functional differentiation in shaping global trait distributions (Díaz et al., 2016; Reich, 2014). Here, we compiled a global species-level trait dataset derived from the TRY Plant Trait Database (Kattge et al., 2020) to examine how major plant growth forms are distributed within leaf economics spectrum space across vascular plants. Using principal component analysis, multivariate permutation approaches, mixed-effects models, and phylogenetic comparative analyses, we evaluated whether growth forms occupy structured regions within multidimensional trait space and whether these patterns persist after accounting for shared evolutionary history. Specifically, we asked: (1) Do major plant growth forms exhibit non-random positioning within global LES space? (2) To what extent are observed patterns associated with phylogenetic conservatism? and (3) Do growth-form differences remain detectable after accounting for phylogenetic relatedness? By integrating large-scale trait synthesis with comparative evolutionary approaches, this study aims to clarify how broad ecological strategies are organized across vascular plants within a globally conserved but multidimensional trait framework.

2. Methods

2.1 Trait dataset assembly

Plant functional trait data were obtained from the TRY Plant Trait Database (Kattge et al., 2020). Four traits associated with the leaf economics spectrum (LES) and broader plant ecological strategy were selected for analysis: specific leaf area (SLA; TraitID 3117), leaf nitrogen content per dry mass (TraitID 14), leaf dry matter content (LDMC; TraitID 3106), and vegetative plant height (TraitID 47). The original TRY extraction contained approximately 30.8 million records representing 336,774 vascular plant species. Trait measurements were aggregated to species-level median values to reduce the influence of extreme observations and heterogeneous sampling intensity among species. Trait data were reshaped into a species-by-trait matrix, and species lacking complete information for one or more focal traits were excluded from downstream analyses. Species names were subsequently cleaned and standardized by removing malformed or unresolved taxonomic entries. This filtering procedure resulted in a complete multivariate trait dataset containing 3,206 species. Major plant growth forms were assigned using categorical growth-form records available within the TRY dataset. Original categorical descriptions were standardized and harmonized into five major growth-form categories: trees, shrubs, herbs, graminoids, and climbers. Ferns and fern allies were excluded from subsequent analyses because of limited representation and their distinct evolutionary history relative to seed plants. Because trait distributions were strongly right-skewed, SLA, leaf nitrogen content, LDMC, and vegetative height were log10-transformed prior to analysis. All transformed variables were subsequently centered and scaled before multivariate ordination and comparative analyses.

2.2 Principal component analysis and multivariate trait structure

Principal component analysis (PCA) was performed using the log-transformed and standardized trait matrix to characterize major axes of multivariate variation associated with the LES and multivariate plant strategy space. PCA was conducted using the prcomp function in R with variable scaling enabled. Principal component scores were extracted for downstream analyses, and trait loadings were examined to interpret ecological gradients represented by each axis. Growth-form differentiation along the primary LES axis (PC1) was initially evaluated using one-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) tests for pairwise comparisons among growth forms. Effect sizes were quantified using η^2 calculated from ANOVA sums of squares. To evaluate multivariate differentiation across the full trait space, permutational multivariate analysis of variance (PERMANOVA) was conducted using the adonis2 function in the vegan package with Euclidean distance matrices and 999 permutations.

2.3 Robustness analyses

To evaluate whether observed growth-form differentiation was sensitive to unequal sample sizes among growth forms, repeated balanced subsampling analyses were performed. For each iteration, equal numbers of species were randomly sampled from each growth form ($n = 99$ per group), followed by recalculation of PCA and ANOVA on the balanced dataset. This procedure was repeated 100 times, and distributions of ANOVA effect sizes (η^2), F-statistics, and associated significance values were summarized to assess robustness of observed patterns across repeated balanced draws.

2.4 Phylogenetic reconstruction and comparative analyses

Phylogenetic relationships among species were assembled using V.PhyloMaker2 based on the GBOTB.extended megaphylogeny under scenario 3 (Jin and Qian, 2022). Species names were matched to phylogenetic tip labels, and unmatched taxa were excluded from phylogenetically informed analyses. The resulting pruned phylogeny contained 3,079 species. This reduction from the original 3,206-species trait dataset reflected exclusion of taxa that could not be matched confidently to phylogenetic tip labels within the GBOTB.extended megaphylogeny. Phylogenetic signal in LES positioning was quantified for PC1 scores using both Blomberg's K and Pagel's λ implemented in the `phytools` package. To test whether growth-form differentiation persisted after accounting for phylogenetic relatedness, phylogenetic ANOVA (`phylANOVA`) and phylogenetic generalized least squares (PGLS) models were conducted. PGLS analyses were implemented using the `caper` package with Pagel's λ estimated by maximum likelihood. To further account for potential taxonomic non-independence, linear mixed-effects models were fitted using genus as a random intercept term. Mixed-effects analyses were implemented using the `lme4` and `lmerTest` packages.

2.5 Data visualisation

Ordination plots, violin plots, coefficient plots, robustness distributions, and phylogenetic visualizations were generated using `ggplot2`, `phytools`, and associated visualization packages in R. For visualization purposes, phylomorphospace analyses were displayed using a balanced subset of 125 species (25 species per growth form) to improve interpretability of phylogenetic relationships within ordination space. Trait loading vectors were visualized using PCA loading biplots, and phylogenetic trait distributions were examined using continuous trait mapping (`contMap`) and phylomorphospace approaches. All statistical analyses and visualizations were conducted in R version 4.5.2 (R Core Team, 2025).

3. Results

3.1 Global structure of the LES

Principal component analysis (PCA) identified a dominant primary axis of multivariate trait variation corresponding to the canonical leaf economics spectrum (LES). PC1 primarily represented coordinated variation in SLA, leaf nitrogen content, LDMC, and vegetative height consistent with the canonical acquisitive–conservative LES gradient. The first principal component (PC1) explained 50.3% of total trait variation, whereas the second principal component (PC2) explained an additional 25.2%, together accounting for 75.5% of total variation across species trait space (Figure 1; Table 1).

PC1 was positively associated with specific leaf area (loading = 0.53) and leaf nitrogen content (0.48), and negatively associated with leaf dry matter content (-0.59) and vegetative height (-0.37), indicating a major gradient from acquisitive to conservative ecological strategies. In contrast, PC2 was strongly associated with vegetative height (0.78), suggesting an additional axis related to plant stature and structural differentiation.

Major plant growth forms occupied structured but overlapping regions of multidimensional LES space (Figure 1). Growth-form differentiation was evident along both the primary LES axis (PC1) and the secondary stature-associated axis (PC2). Herbs and graminoids were generally positioned toward acquisitive regions of trait space characterized by high SLA and leaf nitrogen content, whereas shrubs and trees occupied comparatively conservative regions associated with higher tissue investment and lower resource-acquisition traits. Climbers occupied intermediate regions of ordination space and overlapped partially with multiple growth forms.

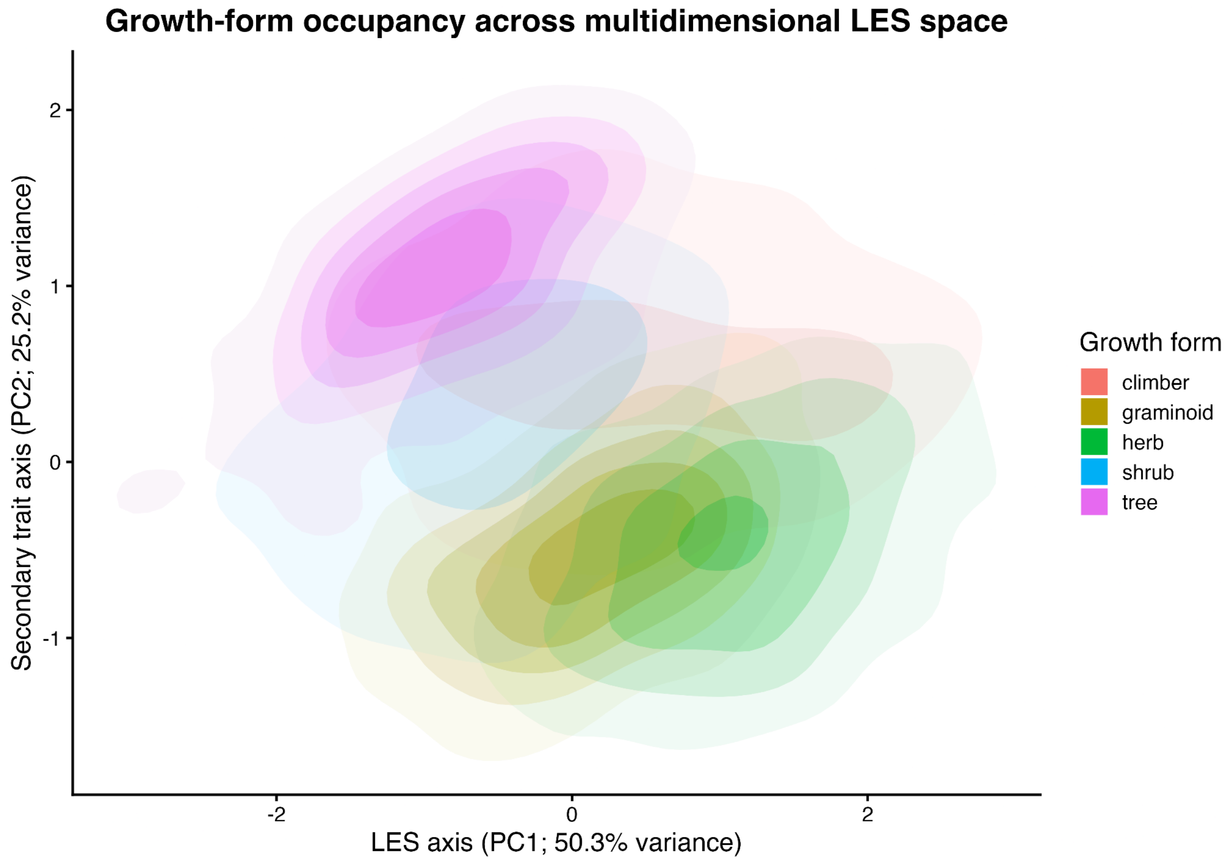

Figure 1. Growth-form occupancy across multidimensional leaf economics spectrum (LES) space. Density contours represent the distribution of five major plant growth forms (trees, shrubs, herbs, graminoids, and climbers) within principal component trait space. PC1 explained 50.3% of total trait variation and corresponded primarily to the acquisitive–conservative LES gradient, whereas PC2 explained 25.2% of variation and was associated mainly with vegetative height. Growth forms occupied structured but strongly overlapping regions of multidimensional trait space, indicating substantial ecological differentiation despite continuous functional variation across vascular plants.

3.2 Growth-form differentiation along the LES

Growth forms differed significantly along the primary LES axis (PC1). One-way analysis of variance (ANOVA) revealed strong overall growth-form effects on PC1 positioning ($F_{4,3200}$ = 536.5, $p < 0.001$), with growth form explaining approximately 40.1% of total variation in LES positioning ($\eta^2 = 0.401$; Table 1).

Pairwise Tukey post hoc comparisons indicated significant differentiation among nearly all growth-form contrasts (all adjusted $p < 0.05$). Herbs occupied significantly more acquisitive regions of LES space than all other growth forms, whereas trees and shrubs were associated with comparatively conservative strategies. Trees and shrubs remained more similar to one another than to herbaceous growth forms, although their differences also remained statistically significant (adjusted $p = 0.002$). Graminoids occupied intermediate positions within LES space but differed significantly from both woody and herbaceous groups.

Despite these significant differences, substantial overlap among growth forms remained evident throughout multidimensional trait space (Figure 1), suggesting that growth forms occupy partially overlapping regions along continuous ecological gradients rather than entirely discrete ecological categories.

Figure 2 further illustrates variation in PC1 distributions among growth forms. Herbs exhibited the highest PC1 values overall, whereas trees and shrubs occupied lower regions of the LES axis associated with greater structural investment and conservative resource-use strategies. Climbers and graminoids occupied intermediate but variable regions of trait space.

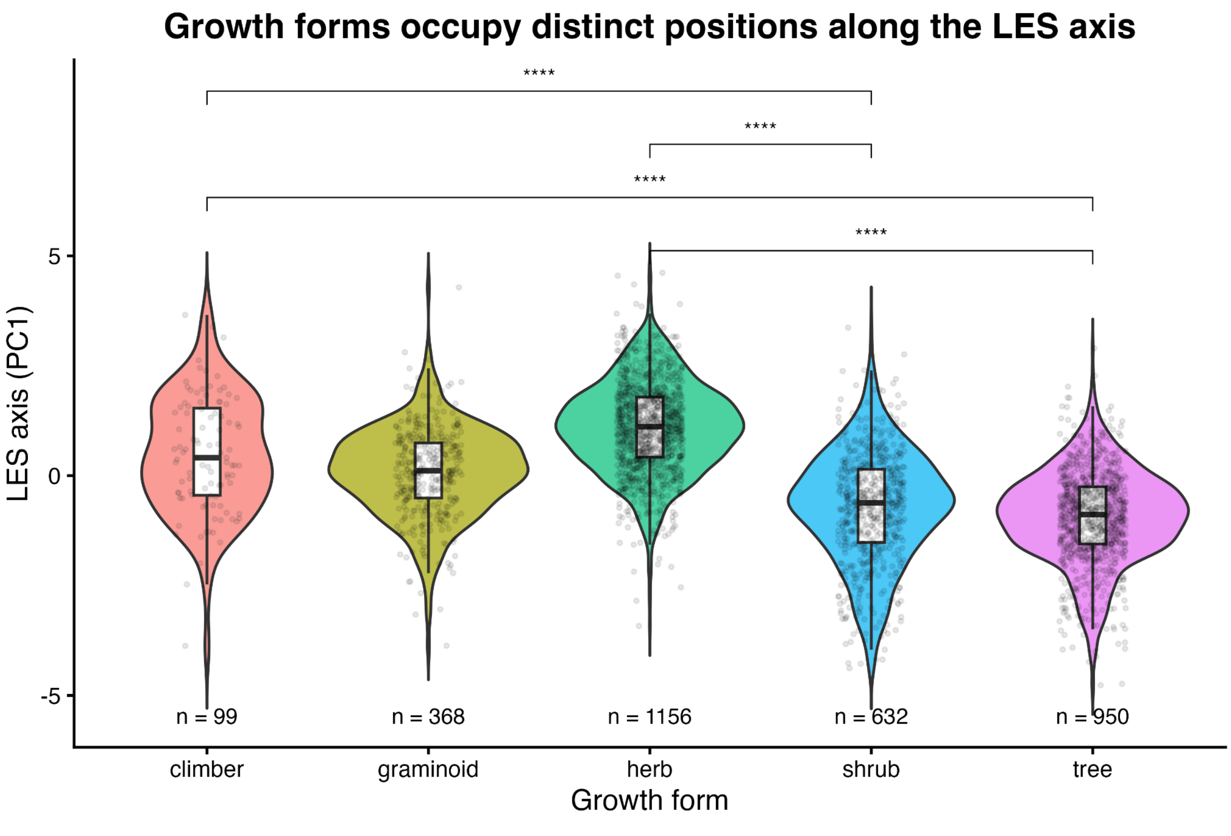

Figure 2. Distribution of leaf economics spectrum (LES) positioning (PC1 scores) among major plant growth forms. Violin plots represent the density distribution of species along the primary LES axis, with embedded boxplots indicating medians and interquartile ranges. Higher PC1 values correspond to more acquisitive ecological strategies characterized by high specific

leaf area and leaf nitrogen content, whereas lower values indicate more conservative strategies associated with greater tissue investment and higher leaf dry matter content.

Significant differences among growth forms were detected using ANOVA followed by Tukey's HSD tests (all major pairwise contrasts $p < 0.05$). Herbs occupied the most acquisitive regions of LES space, whereas shrubs and trees were associated with comparatively conservative strategies.

3.3 Multivariate differentiation and robustness analyses

Permutational multivariate analysis of variance (PERMANOVA) further supported strong differentiation among growth forms across the full four-trait space. Growth form was associated with strong multivariate differentiation across the full four-trait space ($F_{4,3074} = 1118.6$, $R^2 = 0.593$, $p = 0.001$, Table 1), indicating strong multivariate differentiation among growth forms within multidimensional LES space despite broad overlap among species distributions.

Repeated balanced subsampling analyses demonstrated that observed growth-form differentiation was robust to unequal sample sizes among growth forms. Across 100 independent balanced resampling iterations, effect sizes remained highly stable (mean $\eta^2 = 0.310 \pm 0.023$ SD), while all iterations retained highly significant growth-form effects (mean $F = 55.3$; all $p < 0.001$). These results indicate that observed differentiation among growth forms was not driven solely by imbalanced representation across functional groups.

The distribution of η^2 values across repeated balanced subsampling analyses remained consistently centered around moderate effect sizes (Figure S1), further supporting the robustness of growth-form differentiation within LES space across vascular plants. Tests for homogeneity of multivariate dispersion indicated significant differences in within-group trait dispersion among growth forms (PERMDISP: $F_{4,3200} = 54.45$, $p = 0.001$; Table 1), suggesting that observed multivariate differentiation reflects both centroid separation and differences in ecological breadth among groups.

3.4 Phylogenetic structure of LES variation

Phylogenetic analyses revealed strong evolutionary structure underlying LES positioning across vascular plants. Pagel's λ for PC1 scores was high ($\lambda = 0.918$; likelihood ratio test $p < 0.001$), indicating strong phylogenetic structure in global LES organization. In contrast, Blomberg's K values were comparatively low but statistically significant ($K = 0.012$, $p = 0.001$), suggesting that although closely related taxa tended to resemble one another functionally, trait evolution deviated from expectations under a simple Brownian-motion model (Table 1).

Phylogenetic ANOVA further demonstrated that growth-form differentiation along the LES remained significant after accounting for shared evolutionary history ($F = 524.3$, $p = 0.005$).

Pairwise phylogenetic contrasts indicated especially strong differentiation between herbaceous and woody growth forms, whereas some contrasts involving graminoids and climbers were reduced after phylogenetic correction, suggesting partial phylogenetic overlap among these groups.

Phylomorphospace analyses showed that major growth forms occupied broadly overlapping regions of multidimensional LES space despite underlying phylogenetic structure (Figure 3). Similar positions within LES space frequently occurred across multiple evolutionary lineages, whereas related taxa often remained partially clustered within ordination space. Collectively, ecological and phylogenetic analyses supported a model of structured but overlapping organization of vascular plant strategies across global LES space (Table 1).

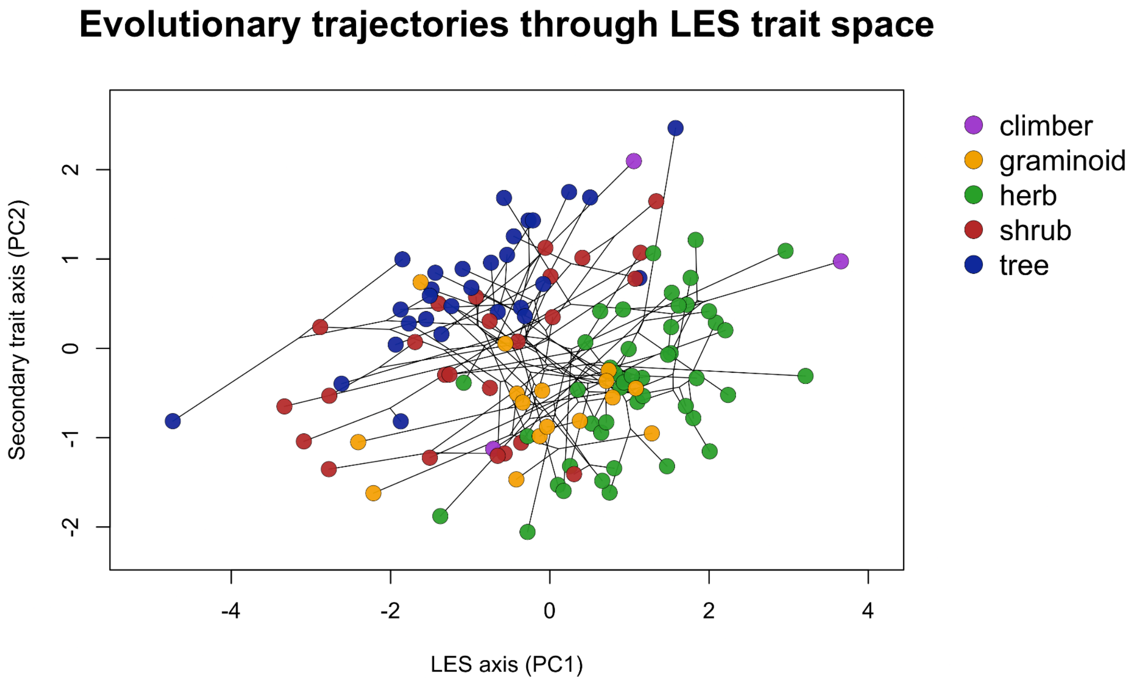

Figure 3. Evolutionary trajectories through multidimensional leaf economics spectrum (LES) space across vascular plants. Phylomorphospace representation of phylogenetic relationships projected into principal component trait space for a balanced visualization subset of 125 vascular plant species (25 species per growth form). Colored points represent major plant growth forms (trees, shrubs, herbs, graminoids, and climbers), while connecting lineages indicate phylogenetic relationships among taxa. Major growth forms occupied partially overlapping regions of LES space, while related taxa often remained locally clustered within ordination space, indicating simultaneous ecological overlap and phylogenetic structure in global plant functional strategies.

Table 1. Summary of major statistical analyses examining ecological and phylogenetic structure of the global leaf economics spectrum across vascular plant growth forms.

Analysis	Metric	Value	P-value	Interpretation
How is global LES variation structured?	PC1 variance explained	50.3%	NA	Canonical LES axis
How multidimensional is global trait space?	PC2 variance explained	25.2%	NA	Semi-independent axis associated with plant height and structural strategy
Do major growth forms differ along the LES?	ANOVA F statistic	536.5	<2e-16	Strong differentiation among growth forms
How much LES variation is explained by growth form? (ANOVA)	Effect size (η^2)	0.401	NA	Growth form explains substantial variation in LES positioning
Do growth forms differ across multidimensional trait space?	PERMANOVA R^2	0.593	0.001	Strong multivariate differentiation across global trait space
Do growth forms differ in ecological breadth and dispersion?	PERMDISP F statistic	54.45	<2e-16	Differences in within-group trait dispersion among growth forms

Are growth-form patterns robust to unequal sample sizes?	Mean η² ± SD	0.31 ± 0.023	All iterations <0.001	Differentiation remains stable after balanced subsampling
Is LES positioning phylogenetically structured?	Pagel's λ	0.918	<0.001	Strong phylogenetic structure in global LES organization
Does LES evolution follow Brownian expectations?	Blomberg's K	0.012	0.001	Phylogenetic signal significantly weaker than expected under Brownian motion
Does growth-form differentiation persist after phylogenetic correction?	Phylogenetic ANOVA	F = 524.3	0.005	Growth-form differentiation remains significant after accounting for shared ancestry

4. Discussion

4.1 Growth forms retain structured but overlapping ecological distributions within LES space

Major plant growth forms occupied significantly differentiated yet strongly overlapping regions of global LES space, indicating that broad structural categories retain substantial ecological organization while remaining embedded within fundamentally continuous trait variation (Díaz et al., 2016; Zhao et al., 2016). Herbs exhibited the most acquisitive ecological strategies overall, whereas trees and shrubs occupied comparatively conservative regions of trait space associated with greater structural investment and lower resource-acquisition capacity (Reich, 2014; Wright et al., 2004). Graminoids and climbers occupied intermediate but highly variable positions within multidimensional LES space, indicating that major growth forms are not discretely segregated within global LES organization (Adler et al., 2014; Ren et al., 2022). These broad patterns are consistent with classical interpretations of the leaf economics spectrum, in which acquisitive strategies are associated with rapid resource acquisition and short tissue lifespans, whereas conservative strategies emphasize persistence, tissue durability, and long-term resource retention (Reich, 2014; Wright et al., 2004).

Despite strong statistical differentiation among growth forms, substantial overlap remained evident throughout ordination space and PC1 distributions. In particular, the broad trait ranges observed within graminoids, climbers, and shrubs indicate that species belonging to distinct architectural categories frequently occupied similar regions of LES space. Such overlap suggests that major growth forms do not represent discrete ecological syndromes, but instead correspond to shifted probability distributions within a continuous multidimensional trait landscape (Adler et al., 2014; Mcgill et al., 2006). This interpretation aligns with emerging trait-based frameworks proposing that plant ecological strategies are organized along continuous phenotypic gradients rather than rigid categorical functional types (Laughlin, 2023, 2014). The persistence of overlap across all major growth forms further indicates that common ecological trade-offs constrain functional trait combinations across broad evolutionary and structural contexts (Reich, 2014; Wright et al., 2004).

At the same time, the magnitude of growth-form differentiation observed here remained substantial. Growth form explained approximately 40% of variation along the primary LES axis and nearly 60% of total multivariate trait variation, indicating that broad structural strategies retain considerable ecological significance at global scales (Table 1). These findings suggest that growth forms continue to capture biologically meaningful differences in resource-use strategy, tissue investment, and ecological organization despite extensive overlap among species (Cornelissen et al., 2003; Díaz et al., 2016). Rather than functioning as discrete ecological categories, major plant growth forms may therefore be better interpreted as probabilistic centers within multidimensional trait space. Such an interpretation reconciles traditional growth-form classifications with increasingly continuous frameworks in trait-based ecology by suggesting that broad structural categories capture central tendencies in ecological strategy without imposing strict functional boundaries (Laughlin, 2014; Li and He, 2024).

The extensive overlap observed among growth forms also has broader implications for understanding plant functional organization across vascular plants. Similar LES-associated strategies occurred across multiple structural forms, indicating that acquisitive and conservative ecological strategies are not uniquely associated with particular architectures or life histories (Donovan et al., 2011; Mason and Donovan, 2015). Instead, comparable positions within LES space appear achievable across diverse structural and evolutionary contexts, likely reflecting shared ecological constraints associated with resource acquisition, tissue persistence, and growth–survival trade-offs (Díaz et al., 2016; Reich, 2014). Together, these results support the view that global plant ecological strategy is simultaneously structured and continuous, with growth forms retaining ecological meaning while remaining embedded within broader multidimensional trait continua (Li and He, 2024; Weigelt et al., 2021).

4.2 Multidimensional ecological organization extends beyond the canonical LES axis

Although the primary principal component recovered the canonical acquisitive–conservative leaf economics spectrum, the substantial contribution of the second principal component indicates that global plant ecological strategy cannot be fully represented along a single universal economic axis. While PC1 explained approximately half of total trait variation, PC2 accounted for an additional 25% of variation and was strongly associated with vegetative height and structural differentiation. These results suggest that multidimensional ecological organization remains a fundamental feature of global plant trait structure even within a relatively constrained LES-focused trait dataset. Rather than collapsing into a single acquisitive–conservative continuum, vascular plant strategies appear distributed across multiple partially decoupled dimensions of ecological variation (Díaz et al., 2016; Laughlin, 2014; Li and He, 2024; Weigelt et al., 2021).

The relatively weak correlations between vegetative height and core LES traits (Figure S3) further support the interpretation that structural and size-related variation is only partially integrated with classical leaf economic trade-offs. Specific leaf area and leaf nitrogen content remained strongly associated with acquisitive ecological strategies, whereas vegetative height loaded predominantly onto a separate ordination axis. This pattern suggests that variation associated with plant height and structural strategy may represent a semi-independent dimension of ecological organization rather than a simple extension of canonical LES structure. Similar partial decoupling between size-related traits and leaf economic traits has been reported in recent global syntheses emphasizing multidimensional plant form and function, including work demonstrating that plant size, architecture, and structural investment often occupy orthogonal or weakly integrated axes relative to classical LES traits (Li and Prentice, 2024; Li and He, 2024; Ma et al., 2024; Weigelt et al., 2021). Together, these findings support the growing view that plant ecological strategies emerge from interacting but non-identical trait syndromes distributed across broader multidimensional phenotypic spaces.

Importantly, multidimensionality did not eliminate broader growth-form organization within LES space. Major growth forms remained strongly differentiated despite extensive overlap and dispersion throughout ordination space, indicating that broad structural strategies continue to organize ecological variation even under continuous multidimensional trait distributions. These results suggest that global plant ecological organization is neither fully partitioned into discrete functional types nor completely unconstrained along continuous spectra. Instead, major growth forms may occupy probabilistic centers within broader multidimensional trait landscapes shaped by overlapping ecological trade-offs, structural constraints, and evolutionary history. Such an interpretation helps reconcile classical growth-form classifications with increasingly continuous frameworks in trait-based ecology by suggesting that broad ecological categories capture central tendencies in strategy space without imposing rigid functional boundaries (Adler et al., 2014; Laughlin, 2014; Li and He, 2024).

4.3 Phylogenetic structure and ecological differentiation in global LES positioning

Phylogenetic analyses revealed that positioning along the primary LES axis retained substantial evolutionary structure across vascular plants. The high Pagel's λ observed for PC1 scores indicates that closely related taxa frequently occupied similar regions of LES space, consistent with previous studies demonstrating significant phylogenetic organization in plant functional traits and leaf economic strategies (Donovan et al., 2011; Flores et al., 2014; Mason and Donovan, 2015). At broad macroevolutionary scales, these results suggest that major dimensions of ecological strategy remain strongly influenced by shared evolutionary history and lineage-specific constraints on resource-use syndromes (Ackerly, 2009, 2003; Akram et al., 2022). Similar phylogenetic organization in LES-associated traits has been reported across both regional and global syntheses, indicating that coordinated trait syndromes are frequently conserved across evolutionary lineages despite substantial ecological diversification(Flores et al., 2014; Sanchez‐Martinez et al., 2025).

At the same time, the comparatively weak but significant Blomberg's K values suggest that phylogenetic organization within LES space deviates substantially from expectations under a simple Brownian-motion model of trait evolution. Although related taxa tended to resemble one another functionally, ecological strategies were not tightly clustered within evolutionary lineages. Instead, phylogenetic structure appeared diffuse across multidimensional trait space, implying that ecological differentiation and repeated trait reorganization have occurred extensively throughout vascular plant evolution. Such patterns are consistent with studies suggesting that plant functional evolution frequently reflects combinations of phylogenetic constraint, adaptive divergence, and repeated occupation of similar ecological strategies across distantly related clades (Donovan et al., 2011; Losos, 2011; Mason and Donovan, 2015). Together, these findings indicate that positioning along the primary LES axis is simultaneously structured by shared ancestry and shaped by substantial ecological redistribution across evolutionary lineages.

Importantly, growth-form differentiation remained highly significant even after accounting for phylogenetic relatedness through phylogenetic ANOVA, mixed-effects models, and phylogenetic generalized least squares analyses. These results indicate that broad ecological differentiation among trees, shrubs, herbs, graminoids, and climbers cannot be fully explained solely by common ancestry. Instead, major growth forms appear to retain partially independent ecological organization beyond phylogenetic inertia alone. Similar persistence of functional differentiation after phylogenetic correction has been reported in studies examining variation in plant economic spectra across functional groups and environmental gradients (Ackerly, 2003; Ren et al., 2022; Zhao et al., 2016). The continued separation of herbaceous and woody growth forms following phylogenetic correction particularly suggests that contrasting structural and resource-allocation strategies represent recurring ecological solutions that extend across multiple evolutionary lineages.

Phylomorphospace analyses further demonstrated that similar regions of LES space were repeatedly occupied across distantly related taxa, while related species often remained partially clustered within local regions of trait space. This combination of overlap and localized clustering indicates that global plant ecological organization reflects simultaneous phylogenetic structure and repeated occupation of similar regions of trait space. Comparable acquisitive and conservative strategies were observed across multiple evolutionary contexts, likely reflecting common ecological constraints associated with resource acquisition, tissue persistence, competition, and growth–survival trade-offs (Donovan et al., 2011; Losos, 2011; Reich, 2014). Consequently, the present results support a macroevolutionary framework in which global plant ecological strategies are neither strictly lineage-bound nor evolutionarily unconstrained, but instead emerge through the interaction of phylogenetic history, ecological filtering, and repeated occupation of similar regions of multidimensional trait space.

4.4 Implications for functional classification and global vegetation ecology

The present results have broader implications for how plant ecological strategies are conceptualized and classified across vascular plants. Traditional ecological frameworks have often relied on discrete plant functional types or broad growth-form categories to simplify ecological complexity and predict vegetation dynamics at regional and global scales (Mcgill et al., 2006). While such classifications remain ecologically useful, the extensive overlap observed among growth forms in the present study indicates that plant ecological strategies cannot be fully partitioned into rigid categorical groups. Instead, major growth forms appear embedded within broader continuous and multidimensional trait distributions, consistent with increasingly trait-centered approaches to functional ecology (Adler et al., 2014; Laughlin, 2023; Li and Prentice, 2024; Ma et al., 2024).

At the same time, the strong differentiation detected among growth forms demonstrates that broad structural categories continue to capture substantial ecological organization despite extensive overlap in trait space. Growth forms therefore remain informative descriptors of broad ecological strategy, resource-use syndromes, and structural investment patterns, even though they do not correspond to discrete functional entities. This distinction is important because it suggests that classical growth-form classifications and continuous trait-based frameworks should not necessarily be viewed as competing ecological paradigms. Rather, the present results support an integrative perspective in which broad growth forms represent probabilistic regions within multidimensional ecological landscapes shaped by overlapping trade-offs, environmental filtering, and evolutionary history(Cornelissen et al., 2003; Díaz et al., 2016; Li and He, 2024).

The substantial multidimensional overlap observed across vascular plants also has implications for predicting vegetation responses to environmental change. Similar ecological strategies occurred repeatedly across distinct growth forms and evolutionary lineages, suggesting that comparable functional responses to environmental stress, climate variability, or disturbance may emerge across structurally different taxa (Li and Prentice, 2024; Ma et al., 2024; Sanchez‑Martinez et al., 2025). Such flexibility may contribute to the resilience and reorganization of plant communities under changing environmental conditions by allowing multiple structural strategies to occupy similar regions of functional trait space (Adler et al., 2014; Reich, 2014). At the same time, the persistence of broad growth-form differentiation indicates that shifts in vegetation composition may still influence ecosystem processes through coordinated differences in tissue investment, plant stature, and resource economics.

More broadly, these findings reinforce the growing importance of multidimensional trait-based approaches in macroecology and global vegetation science. Increasing evidence suggests that ecosystem functioning, biodiversity patterns, and vegetation responses to environmental change are influenced not only by single dominant trait axes, but also by interactions among partially decoupled dimensions of plant form, function, and evolutionary history (Díaz et al., 2016; Laughlin, 2023; Li and Prentice, 2024; Li and He, 2024). By integrating large-scale trait synthesis with phylogenetic comparative analyses, the present study supports a conceptual framework in which global plant ecological organization is simultaneously continuous, multidimensional, and evolutionarily structured, while still retaining recognizable growth-form organization across vascular plants.

4.5 Limitations and future directions

Several limitations should be considered when interpreting the present results. First, the analyses were based on a relatively restricted set of four functional traits associated primarily with the leaf economics spectrum and broader structural strategy. Although these traits captured major dimensions of global ecological variation, they do not encompass the full complexity of plant functional organization. Important axes related to hydraulics, wood density, rooting strategies, reproductive allocation, defense traits, and belowground resource acquisition were not included and may contribute additional dimensions of ecological differentiation across vascular plants (Díaz et al., 2016; Weigelt et al., 2021). Nevertheless, substantial multidimensional structure emerged even within this relatively constrained trait set, suggesting that broader whole-plant trait datasets may reveal even greater complexity in global ecological organization.

Second, the inclusion of vegetative height as both a functional trait and a characteristic closely associated with broad growth-form classification may partially contribute to observed separation among major plant groups. Trees, shrubs, and herbaceous taxa differ intrinsically in stature and structural architecture, and therefore some component of multivariate differentiation likely reflects this inherent association between plant form and height-related ecological strategy. However, the persistence of substantial overlap among growth forms, together with continued differentiation after phylogenetic correction and balanced subsampling analyses, suggests that observed patterns cannot be attributed solely to categorical growth-form definitions. Rather, broad structural strategies appear embedded within more continuous multidimensional trait distributions shaped by both ecological and evolutionary processes.

Additional limitations arise from the use of species-level median trait values derived from global database syntheses. Aggregation to species-level median values necessarily reduces intraspecific variability, phenotypic plasticity, and environmentally contingent trait expression, all of which can contribute substantially to ecological differentiation within species and across environmental gradients (Siefert et al., 2015). Furthermore, although the TRY database represents the most comprehensive global plant trait resource currently available, geographic and taxonomic sampling biases remain unavoidable in large-scale syntheses (Kattge et al., 2020). Phylogenetic signal analyses were also conducted specifically on PC1 scores representing LES positioning rather than across full multidimensional trait space, and therefore should be interpreted as reflecting evolutionary structure along the primary LES axis rather than complete multivariate trait evolution.

Future work integrating broader whole-plant trait datasets, environmental gradients, and additional phylogenetic comparative approaches could further clarify how multidimensional ecological strategies are organized across vascular plants. In particular, incorporating traits associated with hydraulics, rooting depth, wood economics, reproductive allocation, and stress tolerance may help resolve how different dimensions of plant strategy interact across environmental and evolutionary contexts. Expanding trait-based analyses toward dynamic multidimensional trait networks and environmental response frameworks may also improve predictions of vegetation reorganization under ongoing climate and biodiversity change.

5. Conclusion

Using a global species-level trait dataset derived from the TRY Plant Trait Database, this study examined how major plant growth forms are distributed within multidimensional leaf economics spectrum (LES) space while accounting for phylogenetic relatedness across vascular plants. The analyses revealed that major growth forms occupy significantly differentiated but strongly overlapping regions of global trait space. Herbs and graminoids were generally associated with more acquisitive ecological strategies, whereas trees and shrubs occupied comparatively conservative regions characterized by greater structural investment. Despite this differentiation, extensive overlap among growth forms remained evident throughout multidimensional ordination space, indicating that plant ecological strategies are not organized into rigid functional categories but instead occur along continuous ecological gradients.

The results further demonstrated that global plant ecological organization extends beyond a single canonical LES axis. Although the primary principal component captured the dominant acquisitive–conservative spectrum, substantial additional variation was associated with plant height and structural differentiation, supporting increasingly multidimensional perspectives in trait-based ecology. Phylogenetic analyses additionally revealed strong evolutionary structure in LES positioning while indicating repeated occupation of similar regions of trait space across distantly related lineages. Importantly, growth-form differentiation persisted even after accounting for phylogenetic relatedness, suggesting that broad ecological strategies cannot be explained solely by shared ancestry.

Together, these findings support a conceptual framework in which global plant ecological strategies are simultaneously continuous, multidimensional, and evolutionarily structured, while still retaining recognizable growth-form organization across vascular plants. Rather than representing discrete ecological entities, major growth forms appear to occupy probabilistic regions within broader multidimensional trait landscapes shaped by interacting ecological trade-offs and evolutionary processes. By integrating large-scale trait synthesis with phylogenetic comparative approaches, this study contributes to a more nuanced understanding of how ecological strategies are organized across vascular plants within global trait space.

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