Leaf economics spectrum in different ecological contexts: an evolutionary refinement

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Abstract. The leaf economics spectrum (LES) has long served as a central paradigm in plant functional ecology, describing coordinated variation in leaf traits along a continuum from resource-acquisitive to resource-conservative strategies. Despite its broad empirical support across taxa and biomes, accumulating evidence suggests that the LES may oversimplify the multidimensional nature of plant adaptation. This study re-evaluates the LES from an integrative perspective, emphasizing its context dependency across biogeographic regions, taxonomic scales, and environmental gradients. We examine how evolutionary processes, including selection and phylogenetic conservatism, interact with abiotic stressors to shape trait covariation, and highlight the limitations of interpreting LES relationships as universally fixed. Furthermore, we explore the utility of network-based approaches in capturing system-level trait integration, revealing modular structures and shifting functional hubs that underlie similar ecological strategies. The analysis also incorporates alternative and orthogonal trait dimensions, such as root, wood, and hydraulic traits, which intersect with but are not fully captured by the canonical LES. Finally, we address the temporal dynamics of leaf traits, demonstrating how ontogenetic and phenological variation introduce additional complexity into trait expression. Collectively, these findings support a reconceptualization of the LES as an emergent, scale-dependent property embedded within a multidimensional and dynamic trait space, thereby advancing our understanding of plant ecological strategies and improving predictive models under changing environmental conditions.

Keywords: leaf economics spectrum, plant functional traits, trait covariation networks, ecological strategies, phenotypic plasticity, evolutionary ecology, trait integration, environmental gradients, plant adaptation, multidimensional trait space.

Introduction. The leaf economics spectrum (LES) has emerged as one of the most influential conceptual frameworks in plant functional ecology, providing a unifying axis along which leaf traits covary from resource-acquisitive to resource-conservative strategies (Díaz et al., 2015; Reich, 2014; Pan et al., 2020). While its empirical robustness across global datasets has been widely demonstrated, the continued reliance on LES as a primary interpretative tool risks oversimplifying the multidimensional nature of plant functional adaptation (Joswig et al., 2021; Maynard et al., 2022; Vleminckx et al., 2021). In particular, the increasing availability of high-resolution trait data across environmental gradients, phylogenetic lineages, and organizational scales calls for a more nuanced understanding of how leaf-level strategies integrate within broader ecological and evolutionary systems (Joswig et al., 2021; Maynard et al., 2022; He et al., 2020).

Rather than viewing the LES as a static or universal descriptor, it is more appropriately interpreted as an emergent property arising from the interaction between physiological constraints, developmental pathways, and environmental filtering (Reich, 2014; Díaz et al., 2015; Gomarasca et al., 2023). Leaf traits are not optimized in isolation but are embedded within whole-plant economic strategies that involve trade-offs among carbon gain, water use, structural investment, and survival under stress (Reich, 2014; Li et al., 2021; Mueller et al., 2024; Liu et al., 2022). Consequently, the apparent coherence of the LES at global scales may mask underlying heterogeneity in the mechanisms generating similar trait syndromes (Anderegg et al., 2018; Vleminckx et al., 2021; Weemstra et al., 2016; De La Riva et al., 2021).

Recent research has increasingly emphasized the context dependency of trait relationships, highlighting that similar positions along the LES can be achieved through distinct anatomical, biochemical, or developmental routes (Anderegg et al., 2018; Vleminckx et al., 2021; Weemstra et al., 2016; Jian-Guo et al., 2024; He et al., 2020). This raises fundamental questions regarding the degree to which LES reflects convergent evolution (in the sense of Tripathi et al., 2026) versus multiple alternative adaptive solutions (Doležal & Mudrák, 2026; Hjertaas et al., 2023; Assis, 2023; Pandey et al., 2026). Moreover, the integration of leaf traits with belowground processes, hydraulic architecture, and phenological strategies suggests that leaf economics cannot be fully understood without considering cross-organ coordination and whole-plant functioning (Reich, 2014; Vleminckx et al., 2021; Li et al., 2021; Mueller et al., 2024; Weemstra et al., 2016; Jian-Guo et al., 2024; De La Riva et al., 2021; Liu et al., 2022).

In this context, revisiting the LES from an explicitly integrative perspective becomes essential (Reich, 2014; Joswig et al., 2021; Gomarasca et al., 2023; Maynard et al., 2022; He et al., 2020; Díaz et al., 2015). Such an approach not only refines our understanding of plant ecological strategies but also improves the predictive power of trait-based models under scenarios of environmental change (Joswig et al., 2021; Gomarasca et al., 2023; Maynard et al., 2022; He et al., 2020). By moving beyond a strictly one-dimensional framework, it becomes possible to reconcile global generalities with local complexity and to identify the processes that generate both convergence and divergence in plant functional traits (Vleminckx et al., 2021; Anderegg et al., 2018; Weemstra et al., 2016; Liese et al., 2017; Maynard et al., 2022; Doležal & Mudrák, 2026; Liu et al., 2022; Díaz et al., 2015).

Aim of the Study. The present study aims to critically reassess the conceptual and empirical foundations of the leaf economics spectrum (LES) by situating it within a broader, integrative framework of plant functional ecology. Specifically, it seeks to evaluate the extent to which the LES represents a universal axis of trait coordination versus an emergent, context-dependent pattern shaped by environmental filtering, phylogenetic constraints, and whole-plant integration. By synthesizing evidence across spatial scales, organizational levels, and ecological contexts, the study further aims to identify the mechanisms underlying both convergence and divergence in leaf trait syndromes, with particular emphasis on multidimensional trait networks, alternative functional axes, and temporal dynamics. Ultimately, the work aspires to refine the predictive capacity of trait-based ecological models under conditions of environmental variability and global change.

Universality versus Biome and Biogeographic Dependence. Globally, a single LES captures coordinated variation in leaf structure, chemistry and physiology across 2548 species and 175 sites, largely independent of growth form, plant functional type or biome (Wright et al., 2004; Reich, 2014; Díaz et al., 2015). LES relationships also hold across major floras, supporting a broad "fast–slow" plant spectrum (Reich, 2014; Díaz et al., 2015). However, biogeographic history modifies trait allometries: floras from different regions show distinct slopes and intercepts in key LES relationships (e.g. Amass–Nmass, LL–LMA), even after controlling for climate (Heberling & Fridley, 2012). Within species, much trait variation occurs at high taxonomic levels, but trait covariation often shifts sign at small scales and LES traits respond independently to environment, challenging simple resource-strategy inference from LES within communities (Anderegg et al., 2018). Within a dominant Mediterranean evergreen oak, a strong intraspecific LES exists, yet trait–climate relationships deviate partially from the global pattern, including atypically high N and photosynthetic capacity at high robustness (Niinemets, 2014) (Table 1, Figure 1).

Evolutionary Mechanisms and the Role of Abiotic Stress. Fundamental trade-offs between investment in structural tissue versus liquid-phase processes, and between photosynthetic rate, construction cost and leaf lifespan, can generate the global LES (Shipley et al., 2006). Phylogenetic analyses of leaf mass per area (LMA) show weak but significant conservatism and evolution under weak stabilizing selection toward clade-specific optima, with stronger constraint in woody than herbaceous taxa (Flores et al., 2014). A synthesis of selection and quantitative genetics indicates substantial genetic variation and selection on both ends of the LES, and variable genetic correlations among traits, implying selection—not genetic constraint—has dominated LES evolution (Donovan et al., 2011). In *Helianthus*, more acquisitive LES strategies repeatedly evolved in cooler, drier, more fertile environments, but key LES trade-offs (LMA vs lifespan) break down, suggesting whole-plant processes and habitat-specific selection restructure trait covariation at small evolutionary scales (Mason & Donovan, 2015). Experimental drought and nutrient stress studies show conservative shifts (reduced SLA, increased root allocation) consistent with a move toward "slow" strategies, but root traits and belowground responses often decouple from aboveground LES axes and are strongly context-dependent (Vleminckx et al., 2021; Jiang et al., 2023; Wang et al., 2024; Asefa et al., 2022).

Table 1

Axes of variation and local selection pressures:
trait–environment dependence of LES across scales

Scale / context	*Pattern in LES-related traits*	*References*
Global, cross-biome	Single, tight LES; modest climatic modulation	Wright et al., 2004; Díaz et al., 2015
Biogeographic regions	Different trait allometries; historical constraints	Heberling & Fridley, 2012
Within genera / species	Partial or reversed trait correlations; scale-dependent plasticity	Anderegg et al., 2018; Niinemets, 2014; Mason & Donovan, 2015.

Trait Covariation Networks and System-Level Integration. Beyond pairwise trait correlations, plant functional strategies can be more accurately described using network-based approaches that capture the structure and strength of multidimensional trait covariation (Rao et al., 2023; Flores-Moreno et al., 2019; Kleyer et al., 2018). In this framework, leaf traits are not treated as isolated variables but as components of an interconnected system, where the topology of trait relationships reflects underlying biological constraints and adaptive coordination (Luo et al., 2026; Medeiros et al., 2025; Flores-Moreno et al., 2019).

Trait covariation networks allow the identification of modules—clusters of tightly linked traits—that may correspond to specific functional domains such as carbon acquisition, structural reinforcement, or hydraulic regulation (Medeiros et al., 2025; Flores-Moreno et al., 2019; Kleyer et al., 2018). Importantly, these modules are not fixed but can reorganize in response to environmental conditions, leading to shifts in network architecture without necessarily altering the overall position of a species along the LES (Rao et al., 2023; Medeiros et al., 2025; Anderegg et al., 2018; Yang et al., 2018). This perspective provides a mechanistic explanation for why similar LES patterns can emerge from different internal trait configurations (Blonder et al., 2011; Vleminckx et al., 2021; Li & Prentice, 2024; Reich, 2014).

Network approaches also reveal that some traits act as hubs with disproportionately high connectivity, exerting strong influence over system behavior (Luo et al., 2026; Rao et al., 2023; Medeiros et al., 2025; Kleyer et al., 2018). Traits such as leaf mass per area, nitrogen content, and vein density often occupy central positions, linking physiological performance with structural investment (Medeiros et al., 2025; Blonder et al., 2011; Dong et al., 2020; Li et al., 2025). However, the identity and importance of these hubs can vary across ecosystems, suggesting that functional integration is context-dependent (Luo et al., 2026; Medeiros et al., 2025; Flores-Moreno et al., 2019; Anderegg et al., 2018).

By incorporating network theory into plant ecology, it becomes possible to move beyond linear trait spectra and towards a systems-level understanding of plant strategies (Rao et al., 2023; Medeiros et al., 2025; Flores-Moreno et al., 2019; Kleyer et al., 2018). This shift is particularly relevant for predicting responses to environmental perturbations, as network resilience and reorganization may determine the capacity of plants to maintain functional performance under stress (Rao et al., 2023; Medeiros et al., 2025; Anderegg et al., 2018; Lei et al., 2025).

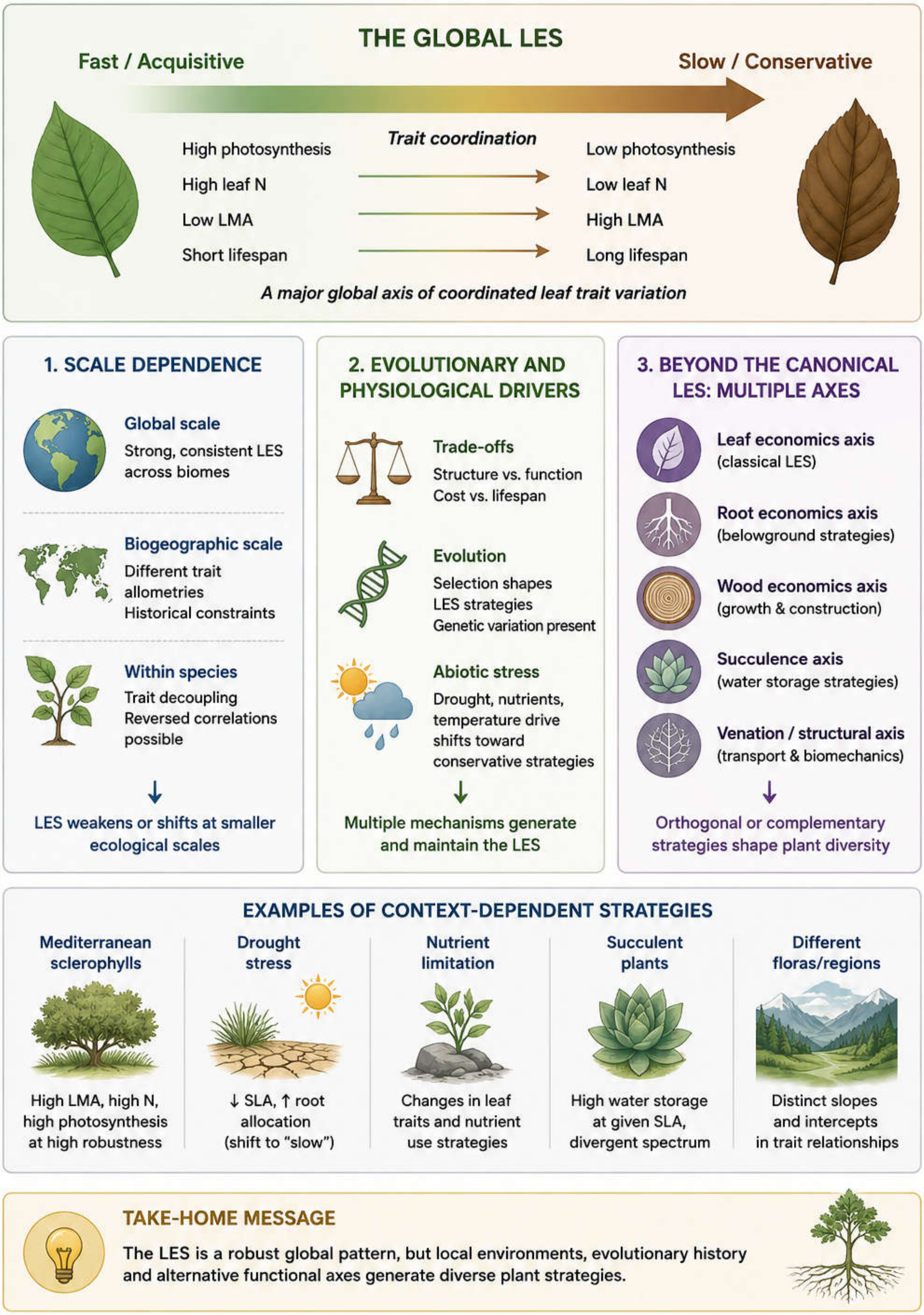

Figure 1. Leaf Economics Spectrum (LES) across ecological and evolutionary contexts.

Alternative or Orthogonal Strategies Beyond the Canonical LES. Evidence increasingly points to multiple functional dimensions rather than a single whole-plant economics axis. In Amazonian trees, nearly half of trait heterogeneity is captured by four orthogonal axes: a fine-root axis, two distinct leaf economics axes and a wood economics axis; these dimensions respond differently to soil fertility and climate (Vleminckx et al., 2021). A global spectrum of plant form and function shows that LES is only one of two major axes, the other reflecting plant and organ size (Díaz et al., 2015). Within oaks, sclerophylly has evolved repeatedly under combined constraints (nutrient scarcity, drought, cold, herbivory) and its ecological implications are strongly modulated by leaf habit, implying "different roads" to similar positions along or adjacent to the LES (Alonso-Forn et al., 2020). In sclerophyll *Eurya japonica*, trait correlation networks reorganize between dry P-rich and wet P-poor habitats, preserving an overall trade-off but shifting the trait pathways that implement it (He, 2021). Succulent taxa define a distinct structural leaf trait spectrum: at any given SLA, water storage traits are an order of magnitude higher, and coordination among SLA, water mass and saturated water content diverges sharply from non-succulent leaves, only weakly related to aridity (Mozzi et al., 2024). Venation geometry provides another mechanistic axis: variation in vein density, distance and loopiness can reproduce global LES scaling, and deviations highlight additional biomechanical or developmental constraints (Blonder et al., 2011). Together, these studies indicate that succulence, sclerophylly, venation architecture, root strategies and thermal tolerance axes represent alternative or orthogonal strategies that intersect with, but are not fully captured by, the classical LES.

Temporal Dynamics and Phenological Modulation of Leaf Traits. The majority of studies on the leaf economics spectrum rely on static trait measurements, implicitly assuming that trait values represent stable species-level characteristics (Wright et al., 2004; Reich, 2014). However, leaf traits are inherently dynamic, varying over time in response to developmental stage, seasonal changes, and episodic environmental events (Mason et al., 2013). Incorporating temporal dynamics into LES research provides critical insights into how plant strategies are expressed and modulated under real-world conditions (Hikosaka et al., 2025; Reich, 2014).

Leaf ontogeny plays a central role in shaping functional traits. Young leaves typically exhibit higher nutrient concentrations and photosynthetic capacities, which decline as structural components accumulate and senescence processes begin (Mason et al., 2013; Ji et al., 2021; Long et al., 2024). This ontogenetic trajectory implies that a single species may traverse different positions along the LES over the lifespan of a leaf, challenging the notion of fixed trait syndromes (Ji et al., 2021; Onoda et al., 2017).

Seasonal variation further complicates this picture, particularly in environments with pronounced climatic fluctuations. Changes in temperature, water availability, and light conditions can induce reversible adjustments in leaf physiology, such as shifts in stomatal conductance, pigment composition, and metabolic activity (Joshi et al., 2024; Singh et al., 2023; Buss et al., 2024; Burnett et al., 2021). These adjustments may occur without corresponding changes in structural traits, leading to partial decoupling between morphology and function over time (Liu et al., 2019; Buss et al., 2024; Rawat et al., 2021).

In addition, phenological strategies—such as leaf flushing, retention, and shedding—interact with environmental variability to influence the temporal deployment of leaf traits (Krishna & Garkoti, 2022; Chakrabarty et al., 2021; Park et al., 2025; Ongole et al., 2021). Evergreen and deciduous species, for instance, may occupy similar positions in trait space at a given moment but differ substantially in the duration and timing of trait expression (Hikosaka et al., 2025; Krishna & Garkoti, 2022; Chakrabarty et al., 2021; Tameirão, 2025).

Recognizing the temporal dimension of leaf traits thus adds a critical layer of complexity to the LES framework (Long et al., 2024). It highlights that plant strategies are not only defined by trait values but also by when and for how long these traits are expressed, offering a more dynamic and realistic view of plant ecological adaptation (Hikosaka et al., 2025; Krishna & Garkoti, 2022; Reich, 2014).

Conclusions. The analysis presented in this study demonstrates that, while the leaf economics spectrum remains a powerful and unifying framework, its interpretation as a singular and universal axis of plant functional variation is increasingly untenable. Instead, the LES should be understood as an emergent pattern arising from the interaction of multiple biological and environmental processes operating across scales. Evidence from biogeographic comparisons, intraspecific variability, and experimental manipulations underscores the context dependency of trait relationships, challenging the assumption of fixed coordination among key leaf traits.

Moreover, the incorporation of network-based approaches reveals that plant functional strategies are structured by complex systems of trait interdependence rather than simple pairwise correlations. This systems-level perspective provides a mechanistic basis for the coexistence of convergent ecological outcomes with divergent underlying trait configurations. The identification of alternative and orthogonal axes of variation further highlights that leaf-level traits capture only a subset of the broader functional diversity of plants, necessitating a whole-plant perspective that integrates above- and belowground processes.

The recognition of temporal dynamics adds an additional dimension, indicating that plant strategies are not static but vary across developmental and phenological timescales. This temporal variability complicates the use of static trait measurements and calls for more dynamic approaches in trait-based ecology.

In light of these considerations, future research should move beyond the reductionist application of the LES and adopt integrative, multidimensional frameworks that better reflect the complexity of plant ecological strategies. Such an approach will enhance the robustness of ecological inference and improve the predictive capacity of models addressing plant responses to environmental change.

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