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A BACKGROUND ABOUT LEAF ECONOMIC SPECTRUM IN TROPICAL VEGETATION

UM PANORAMA SOBRE O ESPECTRO ECONÔMICO DAS FOLHAS NA VEGETAÇÃO TROPICAL

UN PANORAMA SOBRE EL ESPECTRO ECONÓMICO DE LAS HOJAS EN LA VEGETACIÓN TROPICAL

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ABSTRACT

The Leaf Economic Spectrum (LES) describes the different strategies of leaves in capturing and using resources, ranging from fast-growing species with short-lived leaves to those that adopt a more conservative approach, investing in durable and efficient leaves in the use of resources. The objective of this systematic review is to quantify and investigate studies on the Leaf Economic Spectrum (LES) in tropical vegetation, analyzing the association with functional traits, their geographic distribution, vegetation types, plant life habits and the main biotic and abiotic factors that shape these characteristics. The current study performed a systematic review of the indexed databases (Web of Science, Scopus) in the last 20 years (2004-2024). We identified 160 publications. The discovery of articles investigating leaf functional properties and the leaf economic spectrum in the tropics, the topic of our systematic review, has grown considerably over the past eight years. We identified a dominant association of studies published with the Neotropical region. The most common functional leaf attributes studied in the framework of LES (e.g. specific leaf area, leaf nitrogen concentration and photosynthetic capacity) were all found to be associated with the plant growth rate in our research. The distribution of LES research shows that LES studies of tropical vegetation cover a relatively higher amount of sampling for tropical and subtropical dry and moist broadleaf forests than others. Despite the advances, significant knowledge gaps remain, particularly regarding physiological traits and understudied plant groups such as lianas, epiphytes, and bryophytes. Future research efforts must prioritize a broader range of life forms and functional traits, integrating eco-physiological and biogeochemical approaches to better predict the responses of tropical vegetation to environmental changes and to support more effective conservation and restoration strategies.

Keywords: Environmental Filters. Functional Traits. Nitrogen. Phosphorus. Specific Leaf Area. Systematic Review. Tropical Forests.

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RESUMO
O Espectro Econômico das Folhas (Leaf Economic Spectrum – LES) descreve as diferentes estratégias das folhas na captura e no uso de recursos, variando desde espécies de crescimento rápido, com folhas de curta duração, até aquelas que adotam uma abordagem mais conservadora, investindo em folhas duráveis e eficientes no uso de recursos. O objetivo desta revisão sistemática é quantificar e investigar estudos sobre o Espectro Econômico das Folhas (LES) na vegetação tropical, analisando sua associação com atributos funcionais, a distribuição geográfica, os tipos de vegetação, os hábitos de vida das plantas e os principais fatores bióticos e abióticos que moldam essas características. O presente estudo realizou uma revisão sistemática em bases de dados indexadas (Web of Science, Scopus) nos últimos 20 anos (2004–2024). Foram identificadas 160 publicações. A produção de artigos que investigam propriedades funcionais das folhas e o espectro econômico das folhas nos trópicos, tema desta revisão sistemática, cresceu consideravelmente nos últimos oito anos. Identificou-se uma associação dominante de estudos publicados com a região Neotropical. Os atributos funcionais foliares mais comumente estudados no âmbito do LES (por exemplo, área foliar específica, concentração de nitrogênio foliar e capacidade fotossintética) mostraram-se associados à taxa de crescimento das plantas em nossa análise. A distribuição das pesquisas sobre o LES indica que os estudos em vegetação tropical apresentam maior esforço amostral em florestas tropicais e subtropicais secas e úmidas de folhas largas em comparação com outros tipos de vegetação. Apesar dos avanços, permanecem lacunas significativas de conhecimento, especialmente no que se refere a atributos fisiológicos e a grupos vegetais pouco estudados, como lianas, epífitas e briófitas. Pesquisas futuras devem priorizar uma gama mais ampla de formas de vida e atributos funcionais, integrando abordagens ecofisiológicas e biogeoquímicas para melhor prever as respostas da vegetação tropical às mudanças ambientais e apoiar estratégias mais eficazes de conservação e restauração.

Palavras-chave: Filtros Ambientais. Atributos Funcionais. Nitrogênio. Fósforo. Área Foliar Específica. Revisão Sistemática. Florestas Tropicais.

RESUMEN
El Espectro Económico de las Hojas (Leaf Economic Spectrum – LES) describe las diferentes estrategias de las hojas para capturar y utilizar recursos, que van desde especies de rápido crecimiento con hojas de corta vida hasta aquellas que adoptan un enfoque más conservador, invirtiendo en hojas duraderas y eficientes en el uso de recursos. El objetivo de esta revisión sistemática es cuantificar e investigar los estudios sobre el Espectro Económico de las Hojas (LES) en la vegetación tropical, analizando su asociación con rasgos funcionales, la distribución geográfica, los tipos de vegetación, los hábitos de vida de las plantas y los principales factores bióticos y abióticos que configuran estas características. El presente estudio realizó una revisión sistemática de bases de datos indexadas (Web of Science, Scopus) de los últimos 20 años (2004–2024). Se identificaron 160 publicaciones. La producción de artículos que investigan las propiedades funcionales de las hojas y el espectro económico de las hojas en los trópicos, tema de esta revisión sistemática, ha crecido considerablemente en los últimos ocho años. Se identificó una asociación dominante de los estudios publicados con la región Neotropical. Los atributos funcionales foliares más comúnmente estudiados en el marco del LES (por ejemplo, área foliar específica, concentración de nitrógeno foliar y capacidad fotosintética) se encontraron asociados con la tasa de crecimiento de las plantas en nuestro análisis. La distribución de la investigación sobre el LES muestra que los estudios de vegetación tropical presentan un mayor esfuerzo de muestreo en bosques tropicales y subtropicales secos y húmedos de hojas anchas en

comparación con otros tipos de vegetación. A pesar de los avances, persisten importantes vacíos de conocimiento, especialmente en relación con los rasgos fisiológicos y con grupos vegetales poco estudiados, como lianas, epífitas y briófitas. Los esfuerzos de investigación futuros deben priorizar una gama más amplia de formas de vida y rasgos funcionales, integrando enfoques ecofisiológicos y biogeoquímicos para predecir mejor las respuestas de la vegetación tropical a los cambios ambientales y apoyar estrategias más eficaces de conservación y restauración.

Palabras clave: Filtros Ambientales. Rasgos Funcionales. Nitrógeno. Fósforo. Área Foliar Específica. Revisión Sistemática. Bosques Tropicales.

1 INTRODUCTION

Plants exhibit high phenotypic plasticity, developing effective adaptive strategies to tolerate environmental variations and unfavorable ecological interactions (Niijhout, 2003; Schneider, 2022). Within this context, the Leaf Economic Spectrum (LES) has emerged as a fundamental theoretical framework for understanding how leaf functional strategies mediate resource acquisition and conservation in response to environmental variations (Wright et al., 2004; Díaz et al., 2016). LES describes a continuous gradient of leaf attributes reflecting a trade-off between in obtaining resources, ranging from species with short-lived leaves, high photosynthesis rates, and fast growth that are less conservative to more conservative species with more durable leaves and greater efficiency in resource use over time (Wright et al., 2004).

In tropical ecosystems, where high environmental variability directly influences species' adaptation strategies, this concept is particularly relevant (Braga et al., 2016; Vlemincky et al., 2021; Ferrero et al., 2022). The diversity of tropical vegetation, including forests (dry and wet), savannas, and wetlands (Barlow et al., 2018), provides an ideal setting to investigate how biotic and abiotic factors shape plant functional traits (Malhi et al., 2014; Lapola et al., 2023). Functional traits associated across the LES continuum are influenced by environmental gradients such as temperature, water availability, soil fertility, and altitudinal elevation, which act as selective pressures on plant strategies (Götzenberger et al., 2011; Garnier et al., 2016; de Bello et al., 2021). In low-temperature, high-altitude environments, for example, plants typically have a low rate of photosynthesis, low nitrogen concentration, small specific leaf area, and slow growth to minimize water loss and merit resource use efficiency (van der Sande et al., 2016; Matesanz et al., 2021; Sanaphre-Villanueva et al., 2022). In hot and humid regions, plants present inverse characteristics, with more delicate leaves and higher photosynthetic rates, which promotes growth and light capture (Wright et al., 2004).

Functional traits of leaves can vary between individuals of different species (interspecific variation), reflecting distinct evolutionary adaptations, and between groups of individuals within the same species (intraspecific variation), reflecting changes in local conditions and/or ecological interactions (Araujo et al., 2021; Ferrero et al., 2022). Studies on the variation of functional traits in individuals of the same species have been widely studied, especially in tropical ecosystems, where competition for resources and microclimatic variations in the environment cause these individuals to develop different adaptive strategies to ensure the survival and perpetuation of their descendants (Albert et al., 2010; Hulshof &

Swenson, 2010). For example, individuals of the same species may have thicker leaves rich in secondary compounds in areas with high herbivory pressure, while in environments with greater availability of light and nutrients, they may develop thinner leaves with a high specific leaf area (Lambers et al., 2008; Aguilar-Peralta et al., 2022).

The objective of this systematic review is to quantify and investigate studies on the leaf economic spectrum (LES) in tropical vegetation. Specifically, we aim to identify studies that focus on LES and its associated functional traits, considering their geographic distribution, vegetation type, plant life habits, and key biotic and abiotic factors influencing these traits. By bringing together this information, we aim to provide a comprehensive overview of how LES-related traits have been studied in tropical ecosystems. Ultimately, we hope that this will contribute to a better understanding of plant ecological strategies and their potential responses to environmental change.

2 METHODOLOGY

2.1 SYSTEMATIC LITERATURE SEARCH

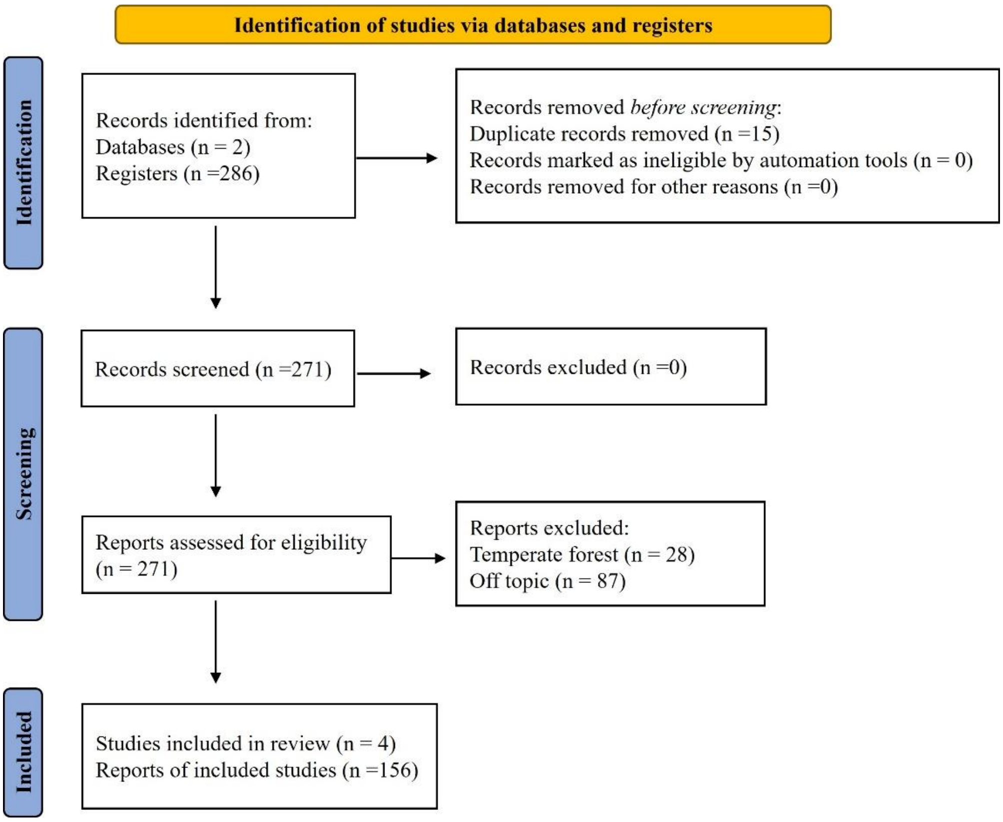
The bibliographic search was conducted in January 2025, targeting articles indexed in the Web of Science and Scopus databases. We employed the search terms: “Leaf economic* spectrum” AND “Tropical Forest” across titles, abstracts, and keywords. We did not limit the chronological period of the search. All selected articles were written in English and presented results that address the functional characteristics related to the leaf economic spectrum (both at the species and community levels) and community assembly in tropical forests. In the second stage, the retrieved articles were screened to ensure relevance. Duplicate records and studies that did not meet the pre-established inclusion criteria were removed using the Rayyan platform (Ouzzani et al., 2016) and the Mendeley reference manager. Articles that did not have LES as their central theme were excluded.

In total, 286 publications were collected, from which, after the screening process, a set of 160 articles were selected for analysis (Figure 1, Appendix S1). Data were extracted from these scientific articles, such as: year of publication, authors, the country where the study was conducted, area of knowledge, vegetation type, life form (wood or herbaceous), ecological group (tree, shrub, liana, fern) and results regarding the economic spectrum of the leaf (specific leaf area, leaf nitrogen concentration, leaf phosphorus concentration, leaf lifespan, photosynthetic capacity, and nocturnal respiration rate).

The annual publication growth rate was calculated based on the percentage change between the current number of publications and the previous number. The following formula was used: Publication growth rate=(current value- previous value)/(previous value)*100.

Figure 1

Flowchart of the research protocol and articles included in the systematic literature review on the economic spectrum of leaves in tropical forests (adapted from Haddaway et al., 2022), from 2009 to 2024



3 RESULTS AND DISCUSSION

3.1 CHRONOLOGICAL EVOLUTION OF STUDIES ON LES

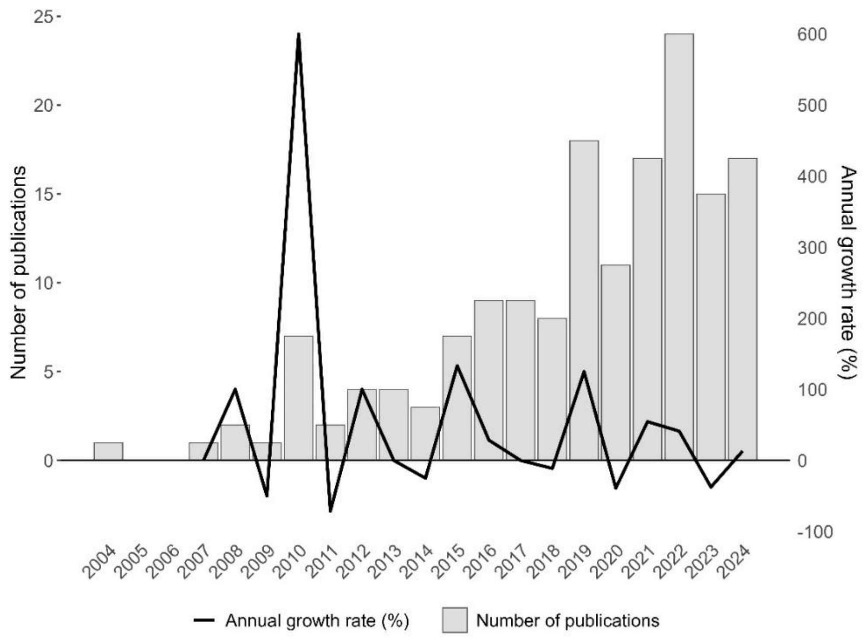
Over the last ten years (2014 – 2024), there has been a gradual increase in the number of scientific publications evaluating leaf functional traits through a multidimensional approach and their relationship with LES in tropical vegetation (Figure 2). This growth trend has intensified since 2015, with the highest number of publications recorded in 2022.

However, the annual growth rate for publications changes throughout the years explored, with alternating phases of exponential growth and sharp drops in the relative number of scientific publications. Notably, 2010 is the year with the greatest relative increase, while subsequent years show smaller differences, thereby indicating the gradual concentration of the research field.

Overall, the results suggest a progressive increase in scientific production, with occasional fluctuations, possibly associated with external factors, such as research funding, academic interest in the topic, and changes in research funding (Millones-Gómez et al., 2021; Ou et al., 2024). Although studies addressing different resource trade-off strategies have been ongoing since the 1970s - when Grime defined the competitive, stress-tolerant, ruderal (CSR) theory (Grime, 1974, 1977, 2001) (reviewed by Grime & Pierce, 2012). It was not until 2004 that Wright and collaborators related the functional characteristics of leaves and resource trade-off strategies to this central idea of "economy" for resource allocation, grouping the characteristics that are correlated into groups with different strategies for resource investment (Wright et al., 2004; Reich, 2014; Pierce et al., 2017). The growing volume of publications observed in recent years underscores the increasing relevance of the LES framework and suggests a continued expansion of research on plant resource-use strategies in tropical ecosystems.

Figure 2

Number of published scientific articles about the leaf economic spectrum in tropical vegetation from 2004 to 2024. The gray bars represent the absolute count of publications per year, while the black line indicates the percentage change from the previous year (N=160)



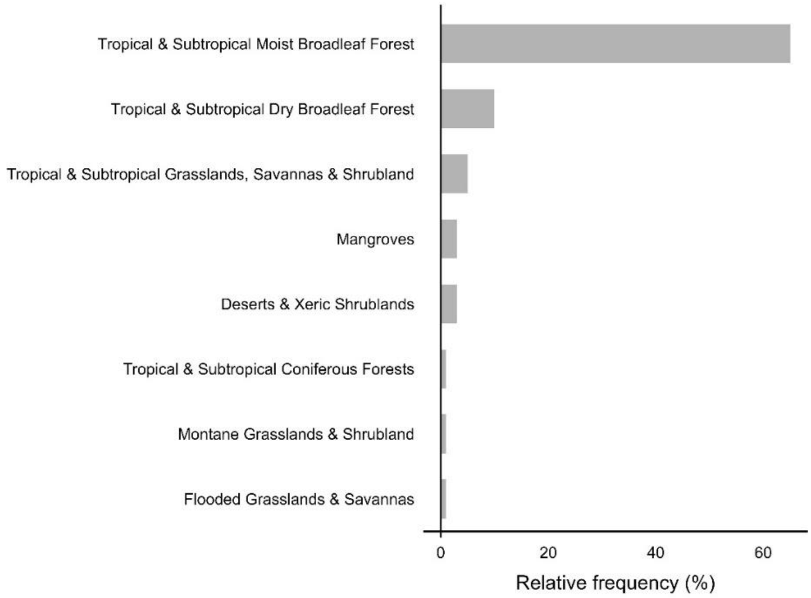
3.2 GLOBAL DISTRIBUTION OF STUDIES ON LES

On the global scale, scientific publications did not show a homogeneous distribution among countries with tropical vegetation. Research efforts were mainly focused on the tropical part of the Asian continent, which played a significant role, representing 33.5% of the total data, and in the Neotropical region, with substantial contributions from Brazil (15%), Panama (9.5%) and Mexico (7.7%). In contrast, the low occurrence of researched areas in the African continent and Oceania is notable, representing only 6% to 2.4% of the total. This imbalance in research coverage is not exclusive to studies on functional attributes. When analyzing the anthropogenic influence on tropical forests, Malhi et al. (2014) already highlighted this disparity in forest types and emphasized the need to expand study areas. Similarly, Loureiro et al. (2023), identified the same pattern in scientific research distribution when assessing the functional traits of plants in forest restoration areas, suggesting that this research gap extends beyond leaf economics studies to the broader spectrum of functional data.

When examining the distribution of studies across the different ecoregions, we observed that 68% of the scientific articles were conducted in tropical and subtropical moist broadleaf forests, while just over 23% occurred in dry, desert, and floodplain (Figure 3). The greater concentration of studies in humid ecoregions can be explained by two factors: the inhomogeneous distribution of research areas since more than 58% (n=68) of these studies were conducted in Brazil, China, and Panama; and/or the strong interest of the academic community in the high diversity, adaptation, and resilience of the species present in these environments (Malhi et al., 2014; Zhang et al., 2022).

Figure 3

Relative frequency of ecoregions (N= 173) reported in studies on the leaf economic spectrum in tropical vegetation published between the years 2004 and 2024



In monodominant forests, in which a single tree species represents more than 50% proportion of basal area and abundance (Hart et al., 1989; Peh et al., 2011), the factors that modulate leaf functional traits are not fully understood, but there is evidence that they are related to the absence of disturbance, shade tolerance, soil nutrient availability, as well as evolutionary and spatial characteristics (Connell & Lowman, 1989; Hart et al., 1989; Peh et al., 2011; Brookshire & Thomas, 2013; Nascimento et al., 2017; Araújo et al., 2022).

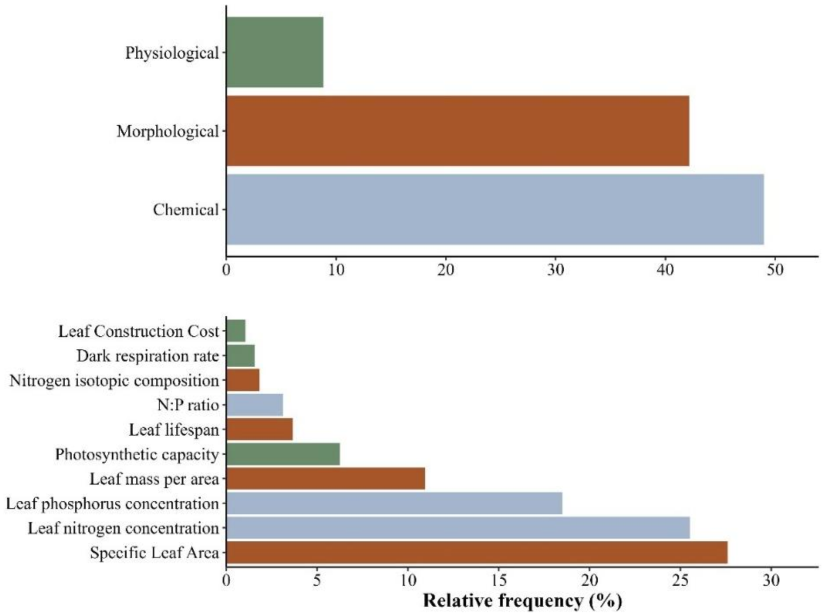
Despite the ecological importance of these forest formations, the literature on the subject remains limited. In our research, only one study appeared that explicitly examined the functional leaf characteristics related to LES in monodominant species. When evaluating the functional leaf characteristics of Brosimum rubescens Taub. (Moraceae), Araújo et al. (2022) observed that, in monodominant forests in the Amazon, this species presents functional characteristics that favor the acquisition of resources, such as larger specific leaf area, stomatal size, and maximum stomatal aperture. These attributes promote high photosynthetic rates and faster growth, favoring its dominance. On the other hand, in mixed forests, B. rubescens adopts an opposite strategy, characterized by functional traits associated with resource conservation, such as thicker adaxial cuticle, palisade and spongy parenchyma, and thicker leaves. These adaptations are often related to drought resistance and greater water use efficiency (Gratani et al. 2006). The ability of this species to adjust its functional traits according to the environment reflects its high phenotypic plasticity, allowing it to adapt to different ecological conditions and contributing to its persistence and dominance in certain areas (Araújo et al., 2022).

3.3 FUNCTIONAL TRAITS ASSOCIATED WITH LES

Our data indicates that studies on LES prioritize the evaluation of structural traits and nutritional composition, representing more than 90% of the attributes analyzed (Figure 4A). This discrepancy may be directly related to the specific objectives of each research or the difficulty and high experimental costs involved in providing physiological data. The predominance of chemicals and morphological traits - particularly specific leaf area and nitrogen and phosphorus concentrations (Figure 4B) in scientific literature can be explained by their strong relationship with plant productivity and resource use efficiency. These variables are widely used to assess plant growth strategies and adaptation to varying environmental conditions (Wright et al., 2004; Reich et al., 2014; Cheng et al., 2016) and are highly responsive to environmental gradients (Wright & Westoby, 2001; Wright et al., 2004; Reich & Oleksy, 2004).

Figure 4

Relative frequency of leaf functional traits (N=384) in studies on the leaf economic spectrum. The top graphic (A) shows the frequency of traits grouped into three categories: physiological (green), morphological (brown) and chemical (blue). The bottom graphic (B) details the frequency of specific traits within each of those categories



Although the key attributes proposed in the LES model (Wright et al., 2004) offer valuable insights into plant resource acquisition strategies, numerous other traits also contribute substantially to plant functioning. Of the total number of leaf attributes evaluated in the articles surveyed in this review, 54% (N=453) refer to attributes that are not directly linked to LES. Attributes such as leaf hardness and density, dark respiration rate, efficiency in the use of photosynthetic nitrogen and phosphorus, among others, are not part of the main axis of LES (Kikuzawa et al., 2006; Chen et al., 2020), but many studies add these variables to the methodology because they are important in adding biochemical, physiological and defense information as they play roles correlated with the main variables of the model (Loureiro et al., 2023; Freitas et al., 2024).

Notably, traits related to leaf construction cost, dark respiration, and nitrogen isotopic composition monitoring indicate a gap in the understanding of plant energy efficiency and metabolism. This knowledge gap is particularly relevant considering that several studies suggest that traits such as photosynthetic capacity, nitrogen and phosphorus concentrations, specific leaf area, and leaf lifespan are governed by LES and guide leaf trait combinations in an economic spectrum (Wright et al., 2004; Chen et al., 2020). Nutrient concentrations and photosynthetic rate are positively correlated with specific leaf areas and negatively related to leaf lifespan (Wright et al., 2004; Díaz et al., 2016). Thus, species with larger, thinner leaves tend to exhibit higher resource acquisition and growth rates over shorter lifespans, whereas species with conservative traits typically show slower growth rates and higher investment in leaf construction (Reich et al., 1997; Wright et al., 2004; Díaz et al., 2016).

Despite being less frequently studied, leaf construction cost is a fundamental functional trait, as it determines the energy spent by plants to synthesize carbon skeletons and nitrogen compounds (Eamus et al., 1999; Xiao et al., 2018). Fast-growing species tend to have a larger specific leaf area, thinner blades, and lower leaf construction costs compared to slower-growing plants (Li et al., 2011). Such characteristics can be good predictors for evaluating plant resistance to environmental stress (Suárez, 2003, 2005), growth, and survival (Baruch & Goldstein, 1999; Liao et al., 2007; Song et al., 2007; Feng et al., 2008).

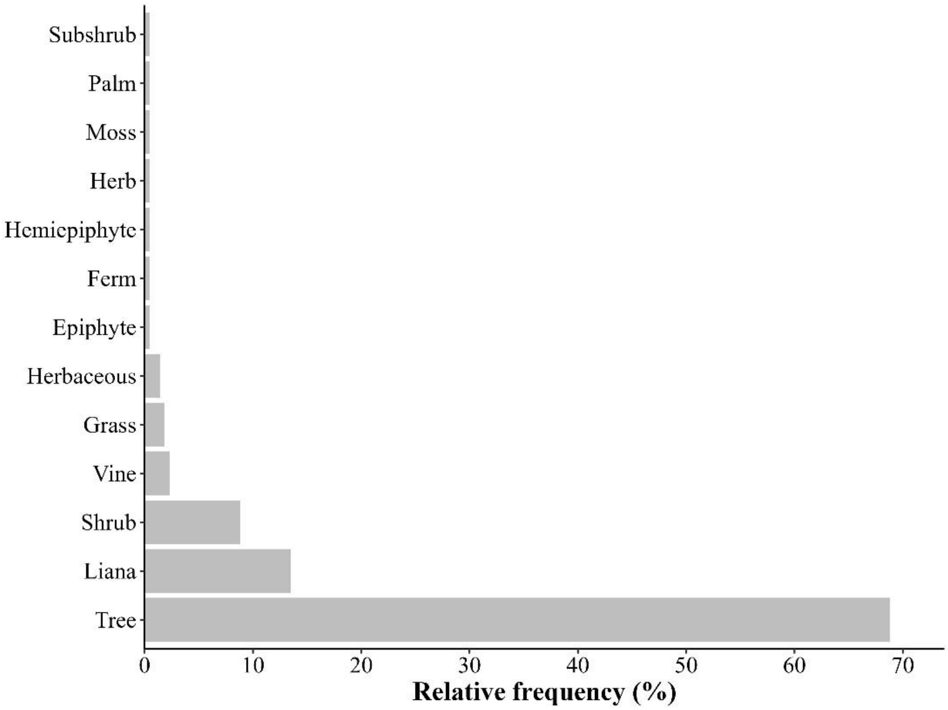
Nitrogen is strongly correlated with plant growth and photosynthetic processes, including carboxylation, bioenergetics, and light-harvesting components (Poorter & Evans, 1998), so it is positively related to photosynthetic capacity and photosynthetic nitrogen use efficiency (Feng et al., 2008; Hikosaka, 2014). Xiao et al. (2018) observed that in early successional forests, the cost of leaf construction is lower and inversely proportional to photosynthetic capacity, specific leaf area, and photosynthetic nitrogen use efficiency compared to late successional forests. This trend may be related to the change in floristic composition and, consequently, to changes in the functional characteristics of the community.

3.4 HOW PLANT LIFE HABIT CHANGES THE TRAITS OF THE LES

Sampling effort and data availability for LES vary considerably among different plant life habits. Arboreal individuals (n= 148) were recorded in approximately 70% of the total articles, wood lianas (climbers; n= 24) and shrubs (n= 19) (Figure 5) accounted for only 14% and 9% of the records, respectively. This discrepancy is mainly due to the greater abundance of trees and the facility of data collection, as the arboreal stratum of a community is widely studied in several fields of plant ecology and physiology.

Figure 5

Relative frequency of plant growth habit (N= 212) reported in studies on the leaf economic spectrum in tropical vegetation published between the years 2004 and 2024



In contrast, other life forms, such as subshrubs, palms, and non-wood species, were markedly underrepresented in datasets, with the last seven being recorded only once in the research. This low representation may be related to the difficulty in collecting data or to methodological limitations of leaf attributes in these life habits. Bryophytes have often been ignored in conservation actions because they are seen as plants of lesser relevance and complex to identify (Goffinet et al., 2009; Glime, 2017). In addition, groups such as mosses, hemiepiphytes and epiphytes have distinct ecological strategies, which may make it difficult for them to adapt to the traditional LES axes (Petter et al., 2015; Wuyun et al., 2024).

Among these underrepresented groups, wood lianas are particularly noteworthy. Their climbing growth form allows them to reach the forest canopy while bypassing the structural constraints faced by understory plants (Wyka et al., 2013; Smith-Martin et al., 2022). Although this group has low diversity and contributes relatively little to the wood biomass of the forest (van der Heijden et al., 2013; Gianoli, 2015; Slot & Winter, 2017), their ecological role is significant. Lianas are often dominant in more open habitats, such as clearings, forest edges, and human-disturbed areas, where their growth strategies give them competitive advantages (Laurence et al., 2001; Schnitzer & Bongers, 2002; Schnitzer, 2005). Understanding how their functional traits influence their growth strategies may help explain the recent increase in their abundance in tropical forests (Schnitzer & Bongers, 2011), especially in disturbed areas and in the process of succession. Regardless of forest type, lianas tend to adopt more acquisitive strategies for resource capture, positioning themselves at the fast end of the LES. (Zhu & Cao, 2010). Typically, lianas are characteristics such as high specific leaf area (low LMA), high nutrient concentrations, higher photosynthetic and respiration rates, lower leaf construction cost per unit area and useful lifespan (Paul & Yavitt, 2011; Zhu & Cao, 2010; Asner & Martin, 2012).

Differences in leaf economic strategies are also observed between plant species with distinct leaf habitats, such as decidual and evergreen trees. Plants with different growth forms exhibit distinct ecophysiological strategies even when coexisting in the same environment (Pimentel et al., 2004; Shi et al., 2015; Yan et al., 2016, Vitória et al., 2018). Regardless of the forest type or growth habit, plant species with deciduous or evergreen leaf habits that coexist have distinct leaf functional characteristics (Huang et al., 2015). Evergreen species generally display lower photosynthetic efficiency, reduced nutrient concentration, smaller specific leaf area, and longer useful lifespan (Reich et al., 1997; Tomlinson et al., 2013; Silva et al., 2019). In contrast, deciduous species are more efficient in capturing resources, with higher efficiency in the photosynthetic rate, larger specific leaf area, lower leaf construction cost, and shorter useful lifespan (Wright et al., 2004; Kröber et al., 2015; de Souza et al., 2020). According to Pandi et al. (2023), deciduous trees, by adopting acquisitive resource-use strategy, exhibit greater competitive advantage over evergreen species in environments without liana colonization (greater specific leaf area and mass-based nitrogen concentration), while evergreen species were more shade tolerant and acclimated better in shaded environments.

3.5 ENVIRONMENTAL FACTORS SHAPE FOLIAR STRATEGIES

Soil fertility results from the combined effects of physical, chemical, and biological factors that regulate nutrient mobilization and directly influence plant metabolism (Shen et al., 2019; Vitória et al. 2019; Delpiano et al. 2020). In tropical ecosystems, fertile soils favour species with rapid resource-acquisition strategies, while nutrient-poor soils select for species exhibiting more conservative functional traits (Freitas et al., 2024). A study conducted in a subtropical evergreen broadleaves forest in China demonstrated that soil fertility is one of the main factors that influenced the functional response of plants (Shen et al., 2019). The results showed that species adapted to rapid resource acquisition are more abundant in soils rich in phosphorus and potassium, but poor in nitrogen and organic matter. In contrast, species with conservative strategies predominate in soils with high nitrogen and organic matter contents, but low in phosphorus and potassium (Shen et al., 2019).

In addition to soil fertility, water availability is one of the main limiting factors for plant performance in natural ecosystems (Pinheiro & Chaves, 2011). In dry tropical forests, water availability acts as an environmental filter, selecting functional leaf traits that enhance species survival under drought conditions (Lebrija-Trejos et al., 2010). Under these conditions, plants adopt different strategies to minimize water loss through stomata and, at the same time, maintain efficient CO_2 assimilation (Falcão et al., 2017). In areas with greater water availability, a pattern characterized by larger specific leaf area, higher nitrogen and phosphorus concentrations, thinner leaves, and lower water-use efficiency is observed (Appendix S2). On the other hand, in environments with water restriction, thicker leaves and greater water use efficiency prevail, reflecting adaptations to drought conditions (Schönbeck et al., 2015; Ouédraogo et al., 2016; Wang et al., 2021).

Although Wright et al. (2004) demonstrated that mean annual precipitation is not a strong global predictor of measuring leaf characteristics related to LES. Martinelli et al. (2021) observed that, across evaluating the elemental and isotopic concentration of carbon and nitrogen, soil and climate conditions showed a strong relationship with leaf functional characteristics in different Brazilian biomes. Species sampled in the Caatinga, vegetation located in dry environments, presented more conservative characteristics, with higher values in leaf N concentration and $\delta^{15}N$, and lower C:N ratio, indicating a longer nitrogen residence time in the soil due to low leaching and lower absorption by plants (Martinelli et al., 2021). In contrast, species sampled in areas with higher average annual precipitation, such as evergreen forests of the Atlantic Forest and the Amazon Rainforest, present low levels of leaf nitrogen and a high C:N ratio, indicating a greater dependence on an acquisition strategy to obtain and use resources efficiently (Martinelli et al., 2021, Freitas et al., 2024).

Temperature and solar radiation intensity are two strongly correlated environmental variables within the LES that influence the adaptive leaf characteristics of plants. Most studies found in the literature relate leaf functional characteristics with the different adaptive ways of the plant to deal with thermal and light stress (Appendix S2). In general, plants in environments with high light intensity tend to present lower SLA, high photosynthetic rate and consequently, higher nitrogen concentrations, and lower leaf longevity (Wright et al., 2004; Gotsch et al., 2015; Falcão et al., 2017; Limberger et al., 2021).

Changes in temperature, climate and rainfall regime caused by climate change can negatively affect the fitness of acquisitive species, since these species are more dependent on resources and in conditions of drought and rising temperatures, these resources can become scarce, compromising the survival of these species (Wright et al., 2004; Lavergne et al., 2010; Reich, 2014; Anderegg et al., 2019). In addition, increased CO2 concentration in the atmosphere can affect the balance between carbon absorption and water loss, impacting the efficiency of photosynthesis and modifying the functional characteristics of leaves over time (Way & Oren, 2010; Dusenge et al., 2019).

These changes in LES parameters can directly impact on the dynamics of tropical forests, affecting ecological succession, plant biomass and the carbon cycle. Constant monitoring of leaf functional traits and LES in different ecosystems is essential to understand how plants react to climate change and the effects that these reactions will have on the resilience of tropical ecosystems.

Leaf functional adaptations associated with the les through ecological succession

At both local and regional scales, the distribution of plant communities is influenced by adaptations to variations in biotic conditions, such as competition and herbivory, and abiotic conditions, such as temperature and precipitation (Veenendaal et al., 1998; Webb & Peart, 2000; Harms et al., 2001; Ter Steege et al., 2003). These environmental filters play a central role in the selecting traits associated with plant adaptive strategies (Lavorel et al., 1997; Lavorel & Garnier, 2002; Zakharova et al., 2019; Baraloto et al., 2012). Understanding how these functional traits link physiological mechanisms to community assembly processes is fundamental to ecology. (McGill et al., 2006; Bernard-Verdier et al., 2012; Mason et al., 2012).

Among the studies reviewed leaf functional traits associated with LES, 55% (n=88) analyzed the influence of these traits on species success along successional gradients (Appendix S2). The drivers ecological successions vary across forest type, community structure, and composition. However, predictable patterns in leaf economic spectrum emerge along the LES continuum in response to changing environmental conditions and resource availability (Wright et al., 2004). This pattern reflects a fundamental ecological trade-off: in early successional stages, pioneer species tend to invest in thin, highly photosynthetic leaves to maximize light and nutrient capture, whereas later-successional species develop thicker, more durable leaves that enhance resource conservation and longevity (Reich, 2014).

Areas undergoing forest succession often reflect a history of disturbance or degradation, and their functional attributes indicate the current phase of the succession process (Reich et al., 2004). In areas where succession occurs without external influences that alter the structure of the vegetation, the community typically follows the theoretical model proposed by Grime's C-S-R strategy (Grime et al., 1974, 1997; 2001; Grime & Pierce, 2012; Cintra et al., 2024). In the initial stages, such as in pastures and early regeneration areas, species with acquisitive functional traits predominate, which favor rapid growth and reproduction in environments with highlight availability (Cintra et al., 2024). As regeneration progresses and the structure of the vegetation becomes more complex, the environment acts as a filter, favoring species adapted to resource limitations and more conservative strategies (Cintra et al., 2024).

Different approaches associated with LES have been used to explain species success along successional gradients (Lohbeck et al., 2015). Studies on LES in wet and dry vegetation have revealed contrasting patterns in species' leaf strategies (Wright et al., 2004; Díaz et al., 2016). Studies comparing moist and dry tropical vegetation reveal contrasting successional dynamics. In tropical moist forests, succession is primarily driven by decreasing light availability due to canopy closure, whereas in tropical dry forests, it is closely linked to progressive increases in water availability over time (Nicotra et al., 1999; Lebrija-Trejos et al., 2011; Pineda-García et al., 2013).

Direct variations in leaf functional traits and LES of species throughout ecological succession have implications for forest preservation and recovery strategies (Werden et al., 2018; Carlucci et al., 2020; Loureiro et al., 2023). The advancement of deforestation and climate change can significantly alter the expected patterns of forest succession, directly influencing the adaptive characteristics of the plant (Reich et al., 2003; Wallwork et al., 2023; Cintra et al., 2024). Furthermore, understanding the variation in functional traits throughout ecological succession can provide support for more effective restoration strategies, especially in degraded areas, where natural succession may be limited by resource availability (Loureiro et al., 2023).

4 FINAL CONSIDERATIONS AND PERSPECTIVE

This systematic review allowed us to quantify and investigate studies on the Leaf Economic Spectrum (LES) in tropical vegetation, providing an overview of the progress of research in this field. The increase in the growth rate of scientific publications in recent decades reinforces the relevance of the topic. However, the variation in the number of publications in different years, as shown in Figure 4, suggests that external factors, such as funding and academic interests, determine the total number of articles written on the subject, influencing the scientific pace.

The results suggest that most studies focus on the evaluation of chemical and morphological functional attributes, meaning that functional attributes related to plant physiological processes, such as leaf construction cost and respiration rates, remain little explored. This gap highlights the need to expand methodological approaches to obtain more comprehensive information on leaf functioning, particularly about energy efficiency and plant metabolism. Furthermore, some life forms, such as lianas, epiphytes and bryophytes, remain underrepresented in literature, which limits the understanding of the functional diversity of tropical plants. Future studies should focus on the inclusion of these groups to improve knowledge about the traits that structure the functional continuum of LES, particularly those that mediate the response of sensitive species to variations in environmental variables.

Environmental factors stand out as key elements in the configuration of foliar strategies. Variations in soil fertility, water availability, temperature and light intensity act as ecological filters, selecting species with more acquisitive or conservative strategies, depending on the supply of resources. In addition, changes throughout ecological succession directly influence the distribution of functional traits, reflecting predictable patterns of adaptation of species to environmental conditions and interactions with other plants.

The geographic distribution of LES studies reveals a significant bias, with most research concentrated on humid tropical forests in Asia and the Neotropics, while drier regions such as savannas and seasonal forests, as well as continents such as Africa and Oceania, remain underexplored. This inequality raises a critical point: much of the current knowledge may be limited to specific environmental conditions, hindering broader predictions about leaf functionality in different tropical ecosystems.

By bringing together and analyzing the current state of the art on LES, this review provides a solid foundation for future investigations, highlighting the need for integrated approaches that combine ecophysiology, biogeochemistry, and functional modeling. Progress in this field is essential to understanding the economic trade-offs of leaves, predicting how plants will respond to environmental changes, and improving conservation, management, and ecological restoration strategies in tropical ecosystems in a changing world.

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APPENDIX

Table 1

Selected articles addressing leaf functional diversity associated with the LES in tropical ecosystems

D	MAIN AUTHOR	CO-AUTHORS	YEAR	TITLE	DOI
1	Baraloto, C.	Marcon, E.; Morneau, F.; Pavoine, S.; Roggy, J.	2010	Integrating functional diversity into tropical forest plantation designs to study ecosystem processes	10.1051/forest/2009110
2	Liu, X.	Swenson, N. G.; Zhang, J.; Ma, K.	2013	The environment and space, not phylogeny, determine trait dispersion in a subtropical forest	10.1111/1365-2435.12018
3	Mirabel, A.	Ouédraogo, D.; Beeckman, H.; Delvaux, C.; Doucet, J.; Hérault, B.; Fayolle, A.	2019	A whole-plant functional scheme predicting the early growth of tropical tree species...	10.1007/s00468-018-1795-8
4	Limberger, O.	Homeier, J.; Farwig, N.; Pucha-Cofrep, F.; Fries, A.; Leuschner, C.; Trachte, K.; Bendix, J.	2021	Classification of Tree Functional Types in a Megadiverse Tropical Mountain Forest...	10.3390/f12050649
5	Liu, Q.	Sterck, F. J.; Zhang, J.; Scheire, A.; Konings, E.; Cao, M.; Sha, L.; Poorter, L.	2021	Traits, strategies, and niches of liana species in a tropical seasonal rainforest	10.1007/s00442-021-04937-4
6	Yi, R.	Xu, X.; Huang, Y.; Zhu, S.; Xu, C.; Zhang, Y.	2022	Tropical plant species living under P limitation show signs of greater resistance to drought	10.1029/2021GL096686
7	Li, Y.	Feng, Y.; Li, W.; Tomlinson, K.; Liao, Z.; Zheng, Y.; Zhang, J.	2022	Leaf trait association in relation to herbivore defense, drought resistance, and economics in a tropical invasive plant	10.1002/ajb2.1858
8	Wang, J.	Wen, X.; Lyu, S.; Guo, Q.	2021	Transition in multi-dimensional leaf traits and their controls on water use strategies of co-occurring species along a soil limiting-resource gradient	10.1016/j.ecolind.2021.107838
9	Vicente-Silva, J.	Bergamin, R. S.; Zanini, K. J.; Pillar, V. D.; Müller, S. C.	2016	Assembly patterns and functional diversity of tree species in a successional gradient of Araucaria Forest in Southern Brazil	10.1016/j.ncon.2016.09.006

10	He, N.	Li, Y.; Liu, C.; Xu, L.; Li, M.; Zhang, J.; He, J.; Tang, Z.; Han, X.; Ye, Q.; Xiao, C.; Yu, Q.; Liu, S.; Sun, W.; Niu, S.; Li, S.; Sack, L.; Yu, G.	2020	Plant Trait Networks: Improved Resolution of the Dimensionality of Adaptation	10.1016/j.tree.2020.06.003
11	Mo, Q.	Wang, W.; Chen, Y.; Peng, Z.; Zhou, Q.	2020	Response of foliar functional traits to experimental N and P addition among overstory and understory species in a tropical secondary forest	10.1016/j.gecco.2020.e01109
12	Asefa, M.	Worthy, S. J.; Cao, M.; Song, X.; Lozano, Y. M.; Yang, J.	2022	Above- and below-ground plant traits are not consistent in response to drought and competition treatments	10.1093/aob/mcac108
13	Yang, X.	Li, R.; Jablonski, A.; Stovall, A.; Kim, J.; Yi, K.; Ma, Y.; Beverly, D.; Phillips, R.; Novick, K.; Xu, X.; Lerdau, M.	2023	Leaf angle as a leaf and canopy trait: Rejuvenating its role in ecology with new technology	10.1111/ele.14215
14	Wallwork, A.	Castro-Trujillo, B.; Banin, L. F.; Dent, D. H.; Skiba, U.; Kerdraon, D.; Sayer, E. J.	2023	Soil carbon dynamics are linked to tree species growth strategy in a naturally regenerating tropical forest	10.3389/ffgc.2023.1232694
15	Wen, Y.	Chen, C.; Sun, T.; Yang, Y.; Han, X.; He, B.; Lu, X.	2023	The change pattern of CSR ecological strategy of trees and seedlings during different succession stages in tropical lowland rainforests	10.3389/ffgc.2023.1236933
16	Avalos, G.	Cambronero, M.; Alvarez-Vergnani, C.	2023	Divergence in functional traits in seven species of neotropical palms of different forest strata	10.1007/s00442-023-05466-y
17	Adams, R. E.	West, J. B.	2022	Functional Groups Mask Inter- and Intraspecific Variation in Water Use Strategies in a Seasonally Dry Tropical Forest	10.3389/frwa.2022.950346
18	Yan, Y.	Fan, Z.; Fu, P.; Zhang, Z.	2024	Drought tolerance traits explain differential stem growth rates of evergreen and deciduous trees in a tropical karst forest	10.1016/j.pld.2024.08.001
19	Wagner, K.	Wanek, W.; Zotz, G.	2021	Functional Traits of a Rainforest Vascular Epiphyte Community: Trait Covariation and Indications for Host Specificity	10.3390/d13020097
20	Karim, M. R.	Halim, M. A.; Thomas, S. C.	2024	Foliar methane and nitrous oxide fluxes in tropical tree species	10.1016/j.scitotenv.2024.176503

21	Fu, B.	Wu, Y.; Zhang, S.; Sun, W.; Jia, M.; Deng, T.; He, H.; Yuan, B.; Fan, D.; Wang, Y.	2024	Synergistic retrieval of mangrove vital functional traits using field hyperspectral and satellite data	10.1016/j.jag.2024.103963
22	Matsuo, T.	Sande, M. T. v. d.; Amissah, L.; Dabo, J.; Abdul, S. M.; Poorter, L.	2024	Herbaceous species and dry forest species have more acquisitive leaf traits than woody species and wet forest species	10.1111/1365-2435.14477
23	Chaturvedi, R. K.	Pandey, S. K.; Tripathi, A.; Goparaju, L.; Raghubanshi, A. S.; Singh, J. S.	2024	Variations in the plasticity of functional traits indicate the differential impacts of abiotic and biotic factors on the structure and growth of trees in tropical dry forest fragments	10.3389/fpls.2023.1181293
24	Wu, M.	Liu, Y.; He, Z.; Gu, X.; Yu, Y.; Tao, Y.; Zhou, Q.; Mo, Q.	2024	Inter- and Intra-Specific Variation in Leaf Functional Traits at Different Maturity Levels in a Tropical Monsoon Forest	10.3390/f15081383
25	Li, X.	Li, Z.; Xu, Z.; Lu, Z.; Fan, Z.; Chen, Y.; Zhang, S.	2024	Leaf trait networks shift toward high modularity during the succession of a subtropical forest, in southwest China	10.1016/j.ecolind.2024.112490
26	Ferreira, K. F.	Silva, J. O.; Cuevas-Reyes, P.; FalcÃ£o, L. A. D.; EspÃ-rito-Santo, M. M.	2024	Chronosequence and Temporal Changes in Soil Conditions, Vegetation Structure and Leaf Traits in a Tropical Dry Forest in Brazil	10.3390/f15101700
27	Jiang, D.	Nie, T.; He, Q.; Yan, J.; Feng, E.; Ye, Q.	2024	A Tradeâ€Off Between Leaf Carbon Economics and Plant Size Among Mangrove Species in Dongzhaigang, China	10.1002/ece3.70559
28	Bouchard, E.	Searle, E. B.; Drapeau, P.; Liang, J.; Gamarra, J. G. P.; Abegg, M.; Alberti, G.; al., e.	2024	Global patterns and environmental drivers of forest functional composition	10.1111/geb.13790
29	Ramirez, J. A.	Craven, D.; Herrera, D.; Posada, J. M.; Reu, B.; Sierra, C. A.; Hoch, G.; Handa, I. T.; Messier, C.	2024	Non-structural carbohydrate concentrations in tree organs vary across biomes and leaf habits, but are independent of the fast-slow plant economic spectrum	10.3389/fpls.2024.1375958
30	Ni, X.	Sun, L.; Cai, Q.; Ma, S.; Feng, Y.; Sun, Y.; An, L.; Ji, C.	2022	Variation and determinants of leaf anatomical traits from boreal to tropical forests in eastern China	10.1016/j.ecolind.2022.108992
31	Streher, A. S.	Torres, R. d. S.; Morellato, L. P. C.; Silva, T. S. F.	2020	Accuracy and limitations for spectroscopic prediction of leaf traits in seasonally dry tropical environments	10.1016/j.rse.2020.111828

32	Zhao, C.	Lin, Q.; Tian, D.; Ji, C.; Shen, H.; Fan, D.; Wang, X.; Fang, J.	2023	Nitrogen addition promotes conservative resource-use strategies via aggravating phosphorus limitation of evergreen trees in subtropical forest	10.1016/j.scitotenv.2023.164047
33	Yu, Z.	Zheng, X.; Lin, W.; Yan, G.; He, W.; Luo, Y.; Lin, X.; Zhu, H.; Peng, C.	2023	Differences in leaf photoprotection strategies of tree species at different successional stages in subtropical forests under seasonal climate change and their relationship to construction cost strategies	10.1016/j.envexpbot.2023.105230
34	Lima, A.	Rodal, M.	2010	Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil	10.1016/j.jaridenv.2010.05.009
35	Muscarella, R.	Uriarte, M.; Erickson, D. L.; Swenson, N. G.; Kress, W. J.; Zimmerman, J. K.	2016	Variation of tropical forest assembly processes across regional environmental gradients	10.1016/j.ppees.2016.09.007
36	ProÃŸ, T.	Bruelheide, H.; Potvin, C.; Sporbert, M.; Trogisch, S.; Haider, S.	2021	Drivers of within-tree leaf trait variation in a tropical planted forest varying in tree species richness	10.1016/j.baae.2020.11.001
37	Han, T.	Ren, H.; Hui, D.; Wang, J.; Lu, H.; Liu, Z.	2020	Light availability, soil phosphorus and different nitrogen forms negatively affect the functional diversity of subtropical forests	10.1016/j.gecco.2020.e01334
38	Vergara-GÃ³mez, D.	Williams-Linera, G.; Casanoves, F.	2020	Leaf functional traits vary within and across tree species in tropical cloud forest on rock outcrop versus volcanic soil	10.1111/jvs.12826
39	Arcand, N.	Kagawa, A. K.; Sack, L.; Giambelluca, T. W.	2008	Scaling of Frond Form in Hawaiian Tree Fern Cibotium glaucum: Compliance with Global Trends and Application for Field Estimation	10.1111/j.1744-7429.2008.00434.x
40	Rodrigues, A. V.	PastÃ³rio, F. F.; Bones, F. L. V.; Esquivel-Muelbert, A.; Vibrans, A. C.; Gasper, A. L. d.	2022	A test of the fast-slow plant economy hypothesis in a subtropical rain forest	10.1080/17550874.2022.2039313
41	Zeballos, S. R.	Giorgis, M. A.; Cabido, M.; Gurvich, D. E.	2016	Unravelling the coordination between leaf and stem economics spectra through local and global scale approaches	10.1111/aec.12455
42	Fagundes, M. V.	Souza, A. F.; Oliveira, R. S.; Ganade, G.	2022	Functional traits above and below ground allow species with distinct ecological strategies to coexist in the largest seasonally dry tropical forest in the Americas	10.3389/ffgc.2022.930099

43	RamÃrez-Valiente, J. A.	Cavender-Bares, J.	2017	Evolutionary trade-offs between drought resistance mechanisms across a precipitation gradient in a seasonally dry tropical oak (Quercus oleoides)	10.1093/treephys/tpx040
44	Wang, R.	Wang, Q.; Liu, C.; Kou, L.; Zhao, N.; Xu, Z.; Zhang, S.; Yu, G.; He, N.	2018	Changes in trait and phylogenetic diversity of leaves and absorptive roots from tropical to boreal forests	10.1007/s11104-018-3816-1
45	Hogan, J. A.	Valverde-Barrantes, O. J.; Ding, Q.; Xu, H.; Baraloto, C.	2020	Morphological variation of fine root systems and leaves in primary and secondary tropical forests of Hainan Island, China	10.1007/s13595-020-00977-7
46	Zhang, Y.	Yang, D.; Zhang, K.; Bai, X.; Wang, Y.; Wu, H.; Ding, L.; Zhang, Y.; Zhang, J.	2022	Higher water and nutrient use efficiencies in savanna than in rainforest lianas result in no difference in photosynthesis	10.1093/treephys/tpab099
47	Fauset, S.	Gloor, M.; Fyllas, N. M.; Phillips, O. L.; Asner, G. P.; Baker, T. R.; Bentley, L. P.; al., e.	2019	Individual-Based Modeling of Amazon Forests Suggests That Climate Controls Productivity While Traits Control Demography	10.3389/feart.2019.00083
48	Harrison, D.	Q., J. A. G.; SÃ¡nchez-Azofeifa, G. A.	2021	Leaf Anatomical Traits of Lianas and Trees at the Canopy of Two Contrasting Lowland Tropical Forests in the Context of Leaf Economic Spectrum	10.3389/ffgc.2021.720813
49	Doughty, C. E.	Santos-Andrade, P. E.; Goldsmith, G. R.; Blonder, B.; Shenkin, A.; Bentley, L. P.; Chavana-Bryant, C.; al., e.	2017	Can Leaf Spectroscopy Predict Leaf and Forest Traits Along a Peruvian Tropical Forest Elevation Gradient?	10.1002/2017JG003883
50	Tang, J.	Sun, B.; Cheng, R.; Shi, Z.; Luo, D.; Liu, S.; Centritto, M.	2019	Seedling leaves allocate lower fractions of nitrogen to photosynthetic apparatus in nitrogen fixing trees than in non-nitrogen fixing trees in subtropical China	10.1371/journal.pone.0208971
51	Werden, L. K.	Waring, B. G.; Smith-Martin, C. M.; Powers, J. S.	2018	Tropical dry forest trees and lianas differ in leaf economic spectrum traits but have overlapping water-use strategies	10.1093/treephys/tpx135
52	Thomson, E. R.	Malhi, Y.; Bartholomeus, H.; Oliveras, I.; Gvozdevaite, A.; Peprah, T.; Suomalainen, J.; Quansah, J.; Seidu, J.; Adonteng, C.; Abraham, A. J.; Herold, M.; Adu-Bredu, S.; Doughty, C. E.	2018	Mapping the Leaf Economic Spectrum across West African Tropical Forests Using UAV-Acquired Hyperspectral Imagery	10.3390/rs10101532

53	Tellez, P. H.	Arnold, A. E.; Leo, A. B.; Kitajima, K.; Bael, S. A. V.	2022	Traits along the leaf economics spectrum are associated with communities of foliar endophytic symbionts	10.3389/fmicb.2022.927780
54	Yang, Y.	Xiao, C.; Wu, X.; Long, W.; Feng, G.; Liu, G.	2021	Differing Trade-Off Patterns of Tree Vegetative Organs in a Tropical Cloud Forest	10.3389/fpls.2021.680379
55	Araújo, I.	Morandi, P. S.; Miller, A. O.; Mariano, L. H.; Alvarez, F.; Silva, I. V. d.; Junior, B. H. M.; Marimon, B. S.	2022	Leaf functional traits and monodominance in Southern Amazonia tropical forests	10.1007/s11258-021-01201-w
56	Damptey, F. G.	Birkhofer, K.; Menor, I. O.; Riva, E. G. d. l.	2022	The Functional Structure of Tropical Plant Communities and Soil Properties Enhance Ecosystem Functioning and Multifunctionality in Different Ecosystems in Ghana	10.3390/f13020297
57	Axelsson, E. P.	Abin, J. V.; Lardizabal, M. L. T.; Ilstedt, U.; Grady, K. C.	2022	A trait-based plant economic framework can help increase the value of reforestation for conservation	10.1002/ece3.8855
58	Sezen, U. U.	Worthy, S. J.; UmaÃ±a, M. N.; Davies, S. J.; McMahon, S. M.; Swenson, N. G.	2022	Comparative transcriptomics of tropical woody plants supports fast and furious strategy along the leaf economics spectrum in lianas	10.1242/bio.059184
59	Chauvin, K. M.	Asner, G. P.; Martin, R. E.; Kress, W. J.; Wright, S. J.; Field, C. B.	2018	Decoupled dimensions of leaf economic and anti-herbivore defense strategies in a tropical canopy tree community	10.1007/s00442-017-4043-9
60	Asner, G. P.	Knapp, D. E.; Anderson, C. B.; Martin, R. E.; Vaughn, N.	2016	Large-scale climatic and geophysical controls on the leaf economics spectrum	10.1073/pnas.1604863113
61	Agudelo, C. M.	Benavides, A. M.; Taylor, T.; Feeley, K. J.; Duque, A.	2019	Functional composition of epiphyte communities in the Colombian Andes	10.1002/ecy.2858
62	Baltzer, J. L.	GrÃ©goire, D. M.; Bunyavejchewin, S.; Noor, N. S. M.; Davies, S. J.	2009	Coordination of foliar and wood anatomical traits contributes to tropical tree distributions and productivity along the Malay-Thai Peninsula	10.3732/ajb.0800414
63	Giraldo-Kalil, L. J.	Campo, J.; Paz, H.; NÃºÃ±ez-FarfÃ¡n, J.	2022	Patterns of leaf trait variation underlie ecological differences among sympatric tree species of Damburneya in a tropical rainforest	10.1002/ajb2.16056
64	Baraloto, C.	Paine, C. E. T.; Poorter, L.; Beauchene, J.; Bonal, D.; Domenach, A.; HÃ©rault, B.; PatiÃ±o, S.; Roggy, J.; Chave, J.	2010	Decoupled leaf and stem economics in rain forest trees	10.1111/j.1461-0248.2010.01517.x

65	Esquivel, J.	Park, B. B.; Casanoves, F.; Delgado, D.; Park, G.; Finegan, B.	2019	Altitude and species identity drive leaf litter decomposition rates of ten species on a 2950 m altitudinal gradient in Neotropical rain forests	10.1111/btp.12730
66	Yaseen, M.	Long, W.; Khalid, F.; Bahadur, S.; Noushahi, H. A.	2022	Shifts in Community Vegetative Organs and Their Dissimilar Trade-Off Patterns in a Tropical Coastal Secondary Forest, Hainan Island, Southern China	10.3390/d14100823
67	Li, Y.	Liu, C.; Sack, L.; Xu, L.; Li, M.; Zhang, J.; He, N.	2022	Leaf trait network architecture shifts with species-richness and climate across forests at continental scale	10.1111/ele.14009
68	Radford-Smith, J.	Lai, H. R.; Weeren, E. C.; Dwyer, J. M.	2024	A Functional Basis for the Assembly of Australian Subtropical Rainforest Tree Communities	10.1111/ele.70014
69	Ferreira-Santos, K.	Garbin, M. L.; Carrijo, T. T.; Torres-Leite, F.; Cavatte, P. C.; Dias, A. T. C.	2024	Post-drought community turnover and functional redundancy in a tropical forest understorey	10.1111/jvs.13256
70	Guo, C.	Tuo, B.; Seibold, S.; Sai, B.; Qin, H.; Yan, E.; Cornelissen, J. H. C.	2024	Ecology and methodology of comparing traits and decomposition rates of green leaves versus senesced litter across plant species and types	10.1111/1365-2745.14287
71	Lam, W. N.	Huang, J.; Tay, A. H. T.; Sim, H. J.; Chan, P. J.; Lim, K. E.; Lei, M.; Aritsara, A. N. A.; al., e.	2024	Leaf and twig traits predict habitat adaptation and demographic strategies in tropical freshwater swamp forest trees	10.1111/nph.19876
72	Sanaphre-Villanueva, L.	Pineda-GarcÃa, F.; DÃ¡ttilo, W.; PinzÃ³n-PÃ©rez, L. F.; RicaÃ±o-Rocha, A.; Paz, H.	2022	Above- and below-ground trait coordination in tree seedlings depend on the most limiting resource: a test comparing a wet and a dry tropical forest in Mexico	10.7717/peerj.13458
73	Acosta-Rojas, D. C.	Barczyk, M. K.; Espinosa, C. I.; Farwig, N.; Homeier, J.; Tiede, Y.; Tinoco, B. A.; Velescu, A.; Wilcke, W.; Neuschulz, E. L.; Schleuning, M.	2023	Abiotic factors similarly shape the distribution of fruit, seed and leaf traits in tropical fleshy-fruited tree communities	10.1016/j.actao.2023.103953
74	Cintra, I.	Sfair, J. C.; Takata, E. S.; Almeida, J.	2024	Functional structure of an herbaceous community on a natural regeneration gradient in a seasonally dry tropical forest	10.1016/j.actao.2024.103997

75	Qin, Y.	Wang, C.; Zhou, T.; Fei, Y.; Xu, Y.; Qiao, X.; Jiang, M.	2024	Interactions between leaf traits and environmental factors help explain the growth of evergreen and deciduous species in a subtropical forest	10.1016/j.foreco.2024.121854
76	Mensah, S.	Dimobe, K.; NoulÃ¨koun, F.; Plas, F. v. d.; Seifert, T.	2024	Phylogenetic diversity and community wide-trait means offer different insights into mechanisms regulating aboveground carbon storage	10.1016/j.scitotenv.2023.167905
77	Zhu, L.	Lu, L.; Zhao, P.	2024	Conserved responses of water use to evaporative demand in mixed forest across seasons in low subtropical China	10.1016/j.scitotenv.2024.176826
78	Martinelli, L. A.	Nardoto, G. B.; Soltangheisi, A.; Reis, C. R. G.; Abdalla-Filho, A. L.; Camargo, P. B.; Domingues, T. F.; Faria, D.; ...,	2021	Determining ecosystem functioning in Brazilian biomes through foliar carbon and nitrogen concentrations and stable isotope ratios	10.1007/s10533-020-00714-2
79	Ávila-Lovera, E.	Urich, R.; Coronel, I.; Tezara, W.	2019	Seasonal gas exchange and resource-use efficiency in evergreen versus deciduous species from a tropical dry forest	10.1093/treephys/tpz060
80	Pineda-García, F.	Paz, H.; Meinzer, F. C.; Angeles, G.	2015	Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest	10.1093/treephys/tpv124
81	González-Rebeles, G.	Terrazas, T.; Méndez-Alonzo, R.; Paz, H.; Brodribb, T. J.; Tinoco-Ojanguren, C.	2021	Leaf water relations reflect canopy phenology rather than leaf life span in Sonoran Desert trees	10.1093/treephys/tpab032
82	Tian, M.	Yu, G.; He, N.; Hou, J.	2016	Leaf morphological and anatomical traits from tropical to temperate coniferous forests: Mechanisms and influencing factors	10.1038/srep19703
83	Long, W.	Zhou, Y.; Schamp, B. S.; Zang, R.; Yang, X.; Poorter, L.; Xiao, C.; Xiong, M.	2020	Scaling relationships among functional traits are similar across individuals, species, and communities	10.1111/jvs.12893
84	Santiago, L. S.	—	2007	Extending the leaf economics spectrum to decomposition: Evidence from a tropical forest	10.1890/06-1841
85	Derroire, G.	Powers, J. S.; Hulshof, C. M.; Varela, L. E. C.; Healey, J. R.	2018	Contrasting patterns of leaf trait variation among and within species during tropical dry forest succession in Costa Rica	10.1038/s41598-017-18525-1

86	Silva, M. A. M.	Pinto, A. V. F.; Nascimento, L. M. d.; Lins-e-Silva, A. C. B.; Lima, A. L. A. d.; Sampaio, E. V. S. B.; Rodal, M. J. N.	2017	Traits and functional strategies as predictors of demographic variations over a chronosequence	10.1007/s40415-017-0389-9
87	Somavilla, N. S.	Kolb, R. M.; Rossatto, D. R.	2014	Leaf anatomical traits corroborate the leaf economic spectrum: a case study with deciduous forest tree species	10.1007/s40415-013-0038-x
88	Kusumoto, B.	Enoki, T.; Kubota, Y.	2013	Determinant factors influencing the spatial distributions of subtropical lianas are correlated with components of functional trait spectra	10.1007/s11284-012-0993-x
89	Pandi, V.	Babu, K. N.; Dar, A. A.	2023	Differential impact of liana colonization on the leaf functional traits of co-occurring deciduous and evergreen trees in a tropical dry scrub forest	10.1007/s10265-023-01474-4
90	Paula, R. R.	Guillemot, J.; Delarmelina, W. M.; Souza, P. H. d.; Moraes, C. R. d.; Campanharo, Í. F.; Mendes, L. J.; outros, e.	2022	Exploring the forestry potential of two legume species with contrasting ecological strategies in a seasonally dry tropical region	10.1007/s00468-022-02298-w
91	Guimarães, Z. T. M.	Santos, V. A. H. F. d.; Ferreira, M. J.	2022	Chlorophyll a fluorescence parameters are related to the leaf economics spectrum of tropical tree species in a mixed plantation	10.1007/s00468-021-02248-y
92	Iida, Y.	Abe, S.; Tanaka, N.; Abe, T.	2019	Associations among species traits, distribution, and demographic performance after typhoon disturbance for 22 co-occurring woody species in a mesic forest	10.1007/s00442-019-04531-9
93	Grossiord, C.	Christoffersen, B.; Alonso-Rodríguez, A. M.; Anderson-Teixeira, K.; Asbjornsen, H.; outros, e. m.	2019	Precipitation mediates sap flux sensitivity to evaporative demand in the neotropics	10.1007/s00442-019-04513-x
94	Patiño, S.	Quesada, C. A.; Aragão, L. E. O. C.; Phillips, L.; al., e.	2012	Coordination of physiological and structural traits in Amazon forest trees	10.5194/bg-9-775-2012
95	Poorter, L.	Ouden, L. P. A.; Bongers, F.	2008	Leaf traits are good predictors of plant performance across 53 rain forest species	10.1007/s00442-008-1131-x
96	Slot, M.	Sterck, F.; Bongers, F.; Poorter, L.	2010	The gap between potential and realized photosynthesis in tropical forest sun and shade leaves	10.1007/s00442-010-1579-3

97	Aguilar-Peralta, J. S.	Maldonado-López, Y.; Espírito-Santo, M. M.; Reyes-Chilpa, R.; al., e.	2022	Contrasting successional stages lead to intra- and interspecific differences in leaf traits and herbivory	10.1007/s10342-021-01434-4
98	Blanchard, G.	Munoz, F.; Ibanez, T.; Hequet, V.; al., e.	2019	Regional rainfall and local topography jointly drive tree community assembly in lowland tropical forests	10.1111/jvs.12781
99	Collins, C. G.	Wright, S. J.; Wurzburger, N.	2016	Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees	10.1007/s00442-015-3410-7
100	Braga, N. d. S.	Vitória, A. P.; Souza, G. M.; Barros, C. F.; Freitas, L.	2016	Weak relationships between leaf phenology and isohydric and anisohydric behavior in tropical forest trees	10.1111/btp.12324
101	Neyret, M.	Bentley, L. P.; Oliveras, I.; Marimon, B. S.; Marimon-Junior, B. H.; al., e.	2016	Examining variation in the leaf mass per area of dominant species across two contrasting tropical gradients	10.1002/ece3.2281
102	Lohbeck, M.	Lebrija-Trejos, E.; Martínez-Ramos, M.; Meave, J. A.; Poorter, L.; Bongers, F.	2015	Functional Trait Strategies of Trees in Dry and Wet Tropical Forests Are Similar but Differ in Their Consequences for Succession	10.1371/journal.pone.0123741
103	Baltzer, J. L.	Thomas, S. C.	2010	A Second Dimension to the Leaf Economics Spectrum Predicts Edaphic Habitat Association in a Tropical Forest	10.1371/journal.pone.0013163
104	Tng, D. Y. P.	Jordan, G. J.; Bowman, D. M. J. S.	2013	Plant Traits Demonstrate That Temperate and Tropical Giant Eucalypt Forests Are Ecologically Convergent with Rainforest Not Savanna	10.1371/journal.pone.0084378
105	Raspé, O.	Meerts, P.; Degreef, J.; Muledi, J. I.; Drouet, T.	2016	Multiscale assemblage of an ectomycorrhizal fungal community: the influence of host functional traits and soil properties in a 10-ha miombo forest	10.1093/femsec/fiw151
106	Lohbeck, M.	Bongers, F.; Ramos, M. M.; Sterck, F.	2015	How do Light and Water Acquisition Strategies Affect Species Selection during Secondary Succession in Moist Tropical Forests?	10.3390/f6062047
107	He, Y.	Zang, R.	2018	Recovery of Functional Diversity Following Shifting Cultivation in Tropical Monsoon Forests	10.3390/f9090506
108	Biswas, S. R.	Yin, C.; Qing, Y.; Biswas, P. L.	2022	Shifting Importance of Abiotic versus Biotic Filtering from Intact Mature Forests to Post-Clearcut Secondary Forests	10.3390/f13050672

109	Prachanun, N.	Sonsuthi, A.; Chanthorn, W.; Brockelman, W. Y.; Nathalang, A.; Lin, L.; Bongers, F.	2022	Whole-Plant Seedling Functional Traits Suggest Lianas Also Support “Fast-Slow” Plant Economics Spectrum	10.3390/f13070990
110	Liu, S.	Tong, F.; Chen, B.; Kuang, Y.	2018	Dominant Species in Subtropical Forests Could Decrease Photosynthetic N Allocation to Carboxylation and Bioenergetics and Enhance Leaf Construction Costs during Forest Succession	10.3389/fpls.2018.00117
111	Huang, J.	Xu, H.; Zang, R.; Ding, Y.; Li, Y.; Lin, M.; Wang, J.; Zhang, C.	2019	Plant Functional Traits Are the Mediators in Regulating Effects of Abiotic Site Conditions on Aboveground Carbon Stock-Evidence From a 30 ha Tropical Forest Plot	10.3389/fpls.2018.01958
112	Zhang, X.	Guo, D.; Song, X.; Ma, K.; Chen, H. Y.; Cao, M.; Schulze, D.	2019	Allocation strategies for nitrogen and phosphorus in forest plants	10.3389/fpls.2019.01412
113	Bakker, M. A.	Carreño-Rocabado, G.; Poorter, L.	2011	Leaf economics traits predict litter decomposition of tropical plants and differ among land use types	10.1111/j.1365-2435.2010.01802.x
114	Fortunel, C.	Fine, P. V.; Baraloto, C.	2012	Leaf, stem and root tissue strategies across 758 Neotropical tree species	10.1111/j.1365-2435.2012.02020.x
115	Slot, M.	Rey-Sánchez, C.; Winter, K.; Kitajima, K.	2014	Trait-based scaling of temperature-dependent foliar respiration in a species-rich tropical forest canopy	10.1111/1365-2435.12263
116	Peñuelas, J. R.	Sardans, J.; Canadell, J.; Albert, J. S.; Milchunas, D. G.; Cleveland, C. C.; al., e.	2015	Functionality and distribution of plant traits in relation to climate and soil in tropical and subtropical forests	10.1111/1365-2435.12313
117	Pierce, S.	Wild, J.; Brůna, J.; Duckworth, D.; Kalusová, V.; Moravcová, L.; al., J. C. e.	2016	A global method for calculating plant CSR ecological strategies applied across biomes worldwide	10.1111/1365-2435.12519
118	Gleason, S.	Westoby, M.; Jansen, S.; Choat, B.; Hacke, U.; Smith, S.; Zanne, A.	2017	Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world’s woody plant species	10.1111/1365-2435.12972
119	Guo, D.	Cong, J.; Xiao, W.; Li, L.; Yuan, Y.; Wang, Z.	2019	Global synthesis of environmental controls and seasonality of fine-root lifespan	10.1111/1365-2435.13413
120	Wallwork, A.	Banin, L.; Dent, D.; Skiba, U.; Sayer, E.	2022	Soil carbon storage is related to tree functional composition in naturally regenerating tropical forests	10.1111/1365-2435.14221

121	Wang, M.	Wan, P.; Guo, J.; Xu, J.; Chai, Y.; Yue, M.	2017	Relationships among Leaf, Stem and Root Traits of the Dominant Shrubs from Four Vegetation Zones in China	10.1163/22244662-06301005
122	Pasquini, B.	Wright, I.; Santiago, L.	2015	Leaf traits capture the effects of land use changes and climate on litter decomposability of tropical plants	—
123	Flack-Prain, S.	Meir, P.; Malhi, Y.; Smallman, T.; Williams, M.	2020	Does economic optimization explain LAI and leaf trait distributions across an Amazon soil moisture gradient?	10.1111/gcb.15368
124	Vleminckx, J.	Fortunel, C.; Valverde-Barrantes, O.; Engel, J.; outros, e.	2021	Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species	10.1111/oik.08284
125	Mumbanza, F.	Bauters, M.; Makelele, I.; Meunier, F.; Kearsley, E.; Boeckx, P.; Verheyen, K.; Ewango, C.; Mbula, I.; al., e.	2022	Lianas rapidly colonize early stages of tropical forests, presumably through leaf trait diversification	10.1111/jvs.13162
126	Ouedraogo, D.	Doucet, J. L.; Dainou, J. L.; Gillet, J. C.; Cannière, A. D.; Sop, D.; Belemvire, L.	2016	Functional traits of tropical tree species and their relationships with environmental filters in West Africa	10.1111/1365-2745.12411
127	Méndez-Alonzo, R.	Sack, L.; Valverde-Barrantes, G.; Blanchard, N.	2012	Leaf and stem functional coordination in tropical dry forest trees: do leaves shed in coordination with stem functions?	10.1111/j.1469-8137.2012.04249.x
128	Vargas, G.	Bonal, D.; Baraloto, D.; Guehl, M.	2021	Leaf economic spectrum and whole-plant strategies in tropical forest trees	10.1111/nph.17103
129	Rahman, M. A.	Posada, J. M.; Sierra, C. A.; Wolf, A.; Scherer-Lorenzen, M. O.	2023	Tropical tree carbon allocation patterns along environmental gradients explained by functional traits	10.1111/nph.18820
130	E.G., P.	Adams, ; R.I., ; Broadbelt, ; L.J., ; Busby, ; P.E., ; Peay, ; K.G., ; al., e.	2010	The physiological ecology of ant-plant mutualisms	—
131	W.R.L., A.	Klein, ; T., ; Bartlett, ; M., ; Sack, ; L., ; Pellegrini, ; A.F.A., ; al., e.	2021	Tree mortality from drought, insects, and their interactions in a changing climate	10.1093/nsr/nwaa163
132	I., M.	Bartlett, ; M.K., ; Chave, ; J., ; Engel, ; J., ; Fortunel, ; C., ; al., e.	2019	Leaf drought tolerance cannot be inferred from commonly measured leaf functional traits in tropical trees	10.1111/1365-2745.13321
133	L.S., S.	Goldstein, ; G., ; Meinzer, ; F.C., ; Fisher, ; J.B., ; Machado, ; K., ; al., e.	2013	Leaf structural diversity is related to hydraulic capacity in tropical rain forest trees	10.1073/pnas.1216057111

134	Slot, M.	Winter, K.	2017	In situ temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests	10.1111/nph.14469
135	Fortunel, C.	Stahl, C.; Heuret, P.; Nicolini, E.; Baraloto, C.	2020	Disentangling the effects of environment and ontogeny on tree functional dimensions for congeneric species in tropical forests	10.1111/nph.16393
136	Blonder, B.	Salinas, N.; Bentley, L. P.; Shenkin, A.; al., e.	2018	Structural and defensive roles of angiosperm leaf venation network reticulation across an Andes–Amazon elevation gradient	10.1111/1365-2745.12945
137	Kröber, W.	Plath, I.; Heklau, H.; Bruelheide, H.	2015	Relating Stomatal Conductance to Leaf Functional Traits	10.3791/52738
138	Eller, C. B.	Barros, F. d. V.; Bittencourt, P. R.; Rowland, L.; al., e.	2018	Xylem hydraulic safety and construction costs determine tropical tree growth	10.1111/pce.13106
139	Han, X.	Huang, J.; Zang, R.	2021	Shifts in ecological strategy spectra of typical forest vegetation types across four climatic zones	10.1038/s41598-021-93722-7
140	Powers, J. S.	G., G. V.; Brodribb, T. J.; Schwartz, N. B.; Pérez-Aviles, D.; Smith-Martin, C. M.; Becknell, J. M.; Aureli, F.; Blanco, R.; Calderón-Morales, E.; Calvo-Alvarado, J. C.; Calvo-Obando, A. J.; Chavarría, M. M.; Carvajal-Vanegas, D.; Jiménez-Rodríguez, C. D.; Chacon, E. M.; Schaffner, C. M.; Werden, L. K.; Xu, X.; Medvigy, D.	2020	A catastrophic tropical drought kills hydraulically vulnerable tree species	10.1111/gcb.15037
141	Petter, G.	Kreft, H.; Ong, Y.; Zotz, G.; Cabral, J. S.	2021	Modelling the long-term dynamics of tropical forests: From leaf traits to whole-tree growth patterns	10.1016/j.ecolmodel.2021.109735
142	Álvarez, F. S.	Finegan, B.; Delgado, D.; Ramos, Z.; Utrera, L. P.; Granda, V.	2021	Dispersal limitation, soil, and fire affect functional properties of tropical secondary forests on abandoned cattle ranching landscapes	10.1016/j.ppees.2021.125632

143	O'Sullivan, K. S. W.	Vilà-Cabrera, A.; Chen, J.; Greenwood, S.; Chang, C.; Jump, A. S.	2022	High intraspecific trait variation results in a resource allocation spectrum of a subtropical pine across an elevational gradient	10.1111/jbi.14336
144	Peguero, G.	Coello, F.; Sardans, J.; Asensio, D.; Grau, O.; Llusià, J.; Ogaya, R.; Urbina, I.; Langenhove, L. V.; Verryckt, L. T.; Stahl, C.; Bréchet, L.; Courtois, E. A.; Chave, J.; Hérault, B.; Janssens, I. A.; Peñuelas, J.	2023	Nutrient-based species selection is a prevalent driver of community assembly and functional trait space in tropical forests	10.1111/1365-2745.14089
145	Falcão, H. M.	Medeiros, C. D.; Almeida-Cortez, J.; Santos, M. G.	2017	Leaf construction cost is related to water availability in three species of different growth forms in a Brazilian tropical dry forest	10.1007/s40626-017-0087-9
146	Falster, D. S.	Duursma, R. A.; FitzJohn, R. G.	2018	How functional traits influence plant growth and shade tolerance across the life cycle	10.1073/pnas.1714044115
147	Gotsch, S. G.	Nadkarni, N.; Darby, A.; Glunk, A.; Dix, M.; Davidson, K.; Dawson, T. E.	2015	Life in the Treetops: Ecophysiological Strategies of Canopy Epiphytes in a Tropical Montane Cloud Forest	10.1890/14-1076.1
148	Araújo, I.	Scalon, M. C.; Amorim, I.; Menor, I. O.; Cruz, W. J.; Reis, S. M.; Simioni, P. F.; Marimon, B. S.	2023	Morpho-anatomical traits and leaf nutrient concentrations vary between plant communities in the Cerrado–Amazonia transition?	10.1016/j.flora.2023.152366
149	Oliveira, V. S. d.	Alencar, M. I.; Belo, A. Y.; Gomes, E. F.; Teixeira, J. d. O.; Silva, J. L. A.; Asato, A. E. B.; Pereira, V. M. L.; Monte, O. d. S.; Silva, G.; Caliman, A.	2023	Physical traits are better drivers than secondary compounds for leaf litter decomposition in a tropical heath vegetation	10.1016/j.flora.2023.152402
150	Ye, X.	Bu, W.; Hu, X.; Wang, F.; Sun, R.; He, P.; Liang, X.; Chen, F.	2023	Are small trees more responsive to nutrient addition than large trees in an evergreen broadleaved forest?	10.1016/j.foreco.2023.121129
151	Shen, Y.	Umaña, M. N.; Li, W.; Fang, M.; Chen, Y.; Lu, H.; Yu, S.	2019	Coordination of leaf, stem and root traits in determining seedling mortality in a subtropical forest	10.1016/j.foreco.2019.05.032
152	Fyllas, N. M.	Quesada, C. A.; Lloyd, J.	2012	Deriving Plant Functional Types for Amazonian forests for use in vegetation dynamics models	10.1016/j.ppees.2011.11.001

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153	Barros, V.	Melo, A.; Santos, M.; Nogueira, L.; Frosi, G.; Santos, M. G.	2020	Different resource-use strategies of invasive and native woody species from a seasonally dry tropical forest under drought stress and recovery	10.1016/j.plaphy.2019.12.018
154	Paine, C. E. T.	Baraloto, C.; Chave, J.; Hérault, B.	2011	Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests	10.1111/j.1600-0706.2010.19110.x
155	Li, L.	McCormack, M. L.; Ma, C.; Kong, D.; Zhang, Q.; Chen, X.; Zeng, H.; Niinemets, Ü.; Guo, D.	2015	Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests	10.1111/ele.12466
156	Gillison, A. N.	nan,	2019	Plant functional indicators of vegetation response to climate change, past present and future	10.1016/j.flora.2019.04.001
157	Mariano, E.	Gomes, T. F.; Lins, S. R. M.; Abdalla-Filho, A. L.; Soltangheisi, A.; Araújo, M. G. S.; ...,	2021	LT-Brazil: A database of leaf traits across biomes and vegetation types in Brazil	10.1111/geb.13381
158	Li, Q.	Su, T.; Liu, Y. (.; Quan, C.	2019	Oligocene plant ecological strategies in low-latitude Asia unraveled by leaf economics	10.1016/j.jseaes.2019.103933
159	Medina-Vega, J. A.	Bongers, F.; Poorter, L.; Schnitzer, S. A.; Sterck, F. J.	2021	Lianas have more acquisitive traits than trees in a dry but not in a wet forest	10.1111/1365-2745.13644
160	Wright, I. J.		2004	The worldwide leaf economics spectrum	10.1038/nature02403

Table 2

Leaf functional traits evaluated in studies on the Leaf Economic Spectrum in tropical vegetation

ID	A_{mass}	CCL	LL	LNC	LPC	N:P ratio	R_{mass}	SLA	LMA	$\delta^{15}N$
1	✓			✓				✓		✓
2								✓		
3				✓				✓		
4				✓	✓			✓		
5				✓	✓	✓		✓		
6				✓				✓		
7	✓		✓	✓					✓	
8				✓				✓		✓

9				✓				✓		
10				✓				✓		
11				✓	✓			✓		
12				✓				✓		
13				✓				✓		
14				✓				✓		
15								✓		
17										✓
18								✓		
19				✓	✓			✓		✓
20				✓				✓		
21									✓	
22				✓	✓				✓	
23	✓			✓	✓			✓		
24				✓	✓	✓		✓		
25	✓			✓	✓			✓		
26								✓		
27									✓	
28								✓		
29	✓			✓	✓			✓		
31									✓	
32				✓	✓	✓			✓	
33		✓								
34			✓							
35									✓	
36				✓				✓		
37				✓	✓					
38				✓	✓	✓		✓		
39								✓		
40								✓		
41								✓		
42								✓		
43	✓							✓	✓	

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44								✓	
45								✓	
46	✓			✓	✓	✓			✓
47			✓	✓	✓				✓
48	✓		✓	✓			✓		✓
49	✓			✓	✓				✓
50	✓			✓					✓
51				✓	✓			✓	
52				✓	✓				✓
53				✓					✓
54				✓	✓			✓	✓
55	✓							✓	
56								✓	
57				✓	✓			✓	
58								✓	
59				✓	✓				✓
60				✓	✓	✓			✓
61								✓	
62	✓						✓		✓
63				✓	✓	✓		✓	
64				✓	✓			✓	
65				✓	✓			✓	
66				✓	✓			✓	
67				✓	✓	✓		✓	
68								✓	
69				✓				✓	
70				✓	✓			✓	
71								✓	
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73								✓	
74				✓				✓	
75				✓	✓			✓	
76								✓	

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77				✓	✓			✓		✓
78				✓						✓
79	✓			✓				✓		✓
80	✓							✓		
81			✓						✓	
82								✓		
83									✓	
84	✓			✓	✓			✓	✓	
85				✓	✓			✓		
86				✓	✓			✓		
87								✓		
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91				✓	✓				✓	
92								✓		
93									✓	
94				✓	✓				✓	
95								✓	✓	
96	✓	✓	✓	✓	✓			✓		
97								✓		
98								✓		
99				✓	✓			✓		
100									✓	
101									✓	
102								✓		
103	✓		✓	✓	✓		✓		✓	
104									✓	
105				✓	✓			✓		
106	✓							✓		
107				✓	✓			✓		
108				✓	✓	✓		✓		
109								✓		

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110	✓	✓		✓				✓	
111								✓	
112				✓	✓			✓	
113				✓	✓			✓	
114				✓	✓			✓	
115	✓				✓		✓		✓
117				✓	✓			✓	
118				✓					✓
119				✓	✓			✓	
120				✓				✓	
121				✓	✓			✓	
122				✓	✓			✓	
123	✓		✓	✓	✓		✓		✓
124				✓	✓			✓	
125				✓	✓	✓		✓	
126			✓						
127			✓						✓
128				✓	✓			✓	
129				✓				✓	
130								✓	
131				✓	✓	✓		✓	
132				✓	✓				✓
133				✓	✓				✓
134				✓	✓			✓	
139								✓	
140				✓	✓			✓	
141				✓				✓	
142				✓	✓			✓	
143				✓	✓			✓	
144				✓					
145								✓	
146				✓					✓
147	✓							✓	

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148				√	√			√		
149				√	√			√		
150	√			√	√				√	
151				√	√			√		
152			√	√	√			√		
153		√		√	√			√		
154				√	√			√		
155				√	√			√		
156				√					√	
157			√							
158				√	√	√			√	
159	√		√	√	√		√		√	
160			√	√	√				√	
Total Geral	**24**	**4**	**14**	**98**	**71**	**12**	**6**	**106**	**42**	**7**

Amass - Photosynthetic assimilation rates, CCL - Construction cost leaf, LL - Leaf lifespan, LNC - leaf nitrogen concentrations, LPC- leaf phosphorus concentrations, N:P ratio - molar or mass-based ratio between nitrogen (N) and phosphorus (P) concentrations, Rmass - Dark respiration rate, SLA - Specific Leaf Area, LMA - Leaf mass per area, δ15N - stable nitrogen isotopes ($^{15}N/^{14}N$).