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This thesis is based on the following publications mentioned in the text by Roman numerals:

I. **S. Rodríguez-Alarcón**, R. Tamme, C. Carmona. (2024). Intraspecific variation in fine-root traits is larger than in aboveground traits in European herbaceous species regardless of drought. *Frontiers in Plant Science.* 15, 1375371. DOI: 10.3389/fpls.2024.1375371

II. **S. Rodríguez-Alarcón**, R. Tamme, C. Carmona. (2022). Intraspecific trait changes in response to drought lead to trait convergence between – but not within – species. *Functional Ecology*. 36, 1900–1911. DOI: 10.1111/1365-2435.14099

III. **S. Rodríguez-Alarcón**, R. González-M, C. Carmona, E. Tordoni. (2024). Trait-growth relationships in Colombian tropical dry forest: Incorporating intraspecific variation and trait interactions. *Journal of Vegetation Science.* 35, e13233. DOI: 10.1111/jvs.13233

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Author's contribution to the publications:
Was responsible for ***, contributed substantially **, contributed *

	Developing the idea	**Collecting the data**	**Analysing the data**	**Preparing the manuscript**
I	**	***	***	***
II	**	***	***	***
III	***	–	**	***

LIST OF USED ABBREVIATIONS

AvgD:	Average root diameter
DApit:	Pit diameter aperture
FWT:	Fiber wall thickness
GAM:	Generalized additive model
H:	Height
ITV:	Intraspecific trait variability
LA:	Leaf area
LDMC:	Leaf dry matter content
SLA:	Specific leaf area
SRL:	Specific root length
RDMC:	Root dry matter content
RF:	Random forest
TDF:	Tropical dry forest
TPD:	Trait probability density
VA:	Vessel area
WD:	Wood density

1 INTRODUCTION

1.1 Background

Environmental changes significantly impact ecosystem functions and plant diversity, emphasizing the importance of studying plant functional traits due to their fundamental roles in shaping individual performance and ecosystem functioning. Functional traits provide an essential tool for understanding and predicting species' responses to environmental changes and their effects on ecosystem functions (de Bello et al., 2021). Traditionally, trait-based ecology has primarily focused on trait differences among species, considering only a single mean trait value for each species, assuming that intraspecific trait variability (within-species) is negligible compared to among-species trait variability. However, recent results showing substantial variability in plant trait values within species, between populations, and even within populations sharing the same local conditions are challenging this assumption (Buchmann et al., 2018; Henn et al., 2018; Vargas G. et al., 2021; Weemstra et al., 2022).

Increasing recognition is being given to the substantial contribution of intraspecific trait variation (ITV) to the overall variability of traits (Siefert et al., 2015; Westerband et al., 2021; Wong and Carmona, 2021). For example, a global meta-analysis on 36 plant traits revealed that ITV represents 25% of the total within-community trait variance (Siefert et al., 2015), and a higher proportion (44%) has been estimated in a tropical forest (Poorter et al., 2018). Recent studies have also underscored the importance of accounting for ITV in clarifying pivotal questions and enhancing predictions about species ecological strategies, individual and population performance across environments, species interactions, community assembly, species coexistence, and ecosystem functioning (Carmona et al., 2015; Pérez-Ramos et al., 2019; Stump et al., 2022; Westerband et al., 2021; Yang et al., 2024). For instance, ITV can decrease fitness differences and lead to functionally more similar species, which reduces trait hierarchies and the intensity of competition between coexisting plants (Carmona, de Bello, Azcárate, et al., 2019). Changes in trait variation within-species can modify competitive interactions between species, thereby influencing the assembly and functioning of ecological communities (de Bello et al., 2021; Yang et al., 2024). Shifts in species and trait composition can result in the dominance of traits that alter plant functional strategies and biomass production (Craven et al., 2018), increased prevalence of deep-rooted plants that change soil resource utilization and could increase susceptibility to soil erosion (Klimešová et al., 2023), or enhanced abundance of species with thick leaves and low nitrogen content that results in a deceleration of litter decomposition (Walter et al., 2020), among other consequences for ecosystem functions influenced by different traits (de Bello et al., 2021). These changes affect multiple plant organs simultaneously, making it essential to employ multi-trait approaches and consider above- and belowground trait adjustments in response to environmental changes (Carmona, 2023; Freschet et al., 2018; Kraft et al., 2015).

Future droughts are anticipated to occur with greater frequency, severity, and duration compared to those experienced in recent decades (Ault, 2020; Ukkola et al., 2020). Accelerating drought represents a challenge for plants as it filters out species with less adapted traits and limits the range of viable trait values in a community by selecting traits best suited to endure and thrive in arid environments (de Bello et al., 2021; Rota et al., 2017; Vogel et al., 2019). Individuals may produce alternative phenotypes with trait values that align with the filter range to cope with drought (de Bello et al., 2021; Le Bagousse-Pinguet et al., 2017). Consequently, the effect of drought on community functional structure arises not only because of species turnover but also due to shifts in trait values within species, which underscores the crucial role of ITV in community assembly (Carmona et al., 2015; Gross et al., 2013; Puy, Carmona, Hiiesalu, et al., 2021). Accounting for intraspecific variation is therefore expected to provide valuable insights into plant species' response to environmental change (Martínez-Vilalta et al., 2023). Although trait variation increases species' ecological niche, the reduction in the range of trait viability imposed by drought has significant implications on ecosystem functioning. This can influence allocation strategies that impact the individual's performance and ecosystem processes, potentially affecting higher trophic levels as well (Luo et al., 2021; Smith et al., 2024; Watson et al., 2023). However, due to the complexity of plant responses to cope with water availability, it is still a challenge to reach a generalized framework to assess and predict drought effects on ecosystem functioning through the link between traits and individual's performance (de Bello et al., 2021; Rowland et al., 2021; Shipley et al., 2016).

Plants generally adopt two primary strategies to cope with drought. The first one is drought tolerance, a strategy where plants often adopt slower growth rates, enabling them to invest more carbon into storing carbohydrates within their structural tissues ("costly" tissues, hydraulically safe) (Kooyers, 2015). Drought tolerance is characterized by resource-conservative traits such as high root dry matter content (RDMC), root diameter (AvgD), and leaf dry matter content (LDMC) but low specific root length (SRL) (Blumenthal et al., 2020; Comas et al., 2013; Griffin-Nolan et al., 2019; Zwicke et al., 2015). Under the other strategy, drought avoidance, plants minimize water loss (transpiration) and carbon investment in tissues but maintain water uptake through an efficient root system ("cheap" tissues, hydraulically efficient) (Comas et al., 2013; Kapoor et al., 2020; Kooyers, 2015). This strategy often develops resource-acquisitive traits such as high SRL and thinner roots, enhancing the plant's ability to explore soil for water (Comas et al., 2013; Zwicke et al., 2015). However, plants can exhibit different resource allocations in each of these strategies, suggesting mixed strategies that indicate complexity in multiple traits involved in responses to drought (Blumenthal et al., 2020; Kramp et al., 2022; Wellstein et al., 2017).

Intraspecific trait variability is pivotal in plant responses to drought stress, determining their capacity to adapt to changing environmental conditions and influencing their performance under drought events. In dry conditions, plants often display large intraspecific differences in aboveground morphological traits such as plant height, leaf area (LA), specific leaf area (SLA), and LDMC (Guo et al., 2022; Niu et al., 2020; Weemstra et al., 2022). Conversely, other studies have shown that variation in plant height, SLA, and LDMC is primarily explained by species identity (de Bello et al., 2011; Luo et al., 2023; Weemstra et al., 2022). As for the belowground intraspecific variation in morphological fine-root traits, some investigations have found that specific root length (SRL) and average root diameter (AvgD) exhibit different responses under dry conditions depending on the considered species (Weemstra et al., 2021, 2022). However, fine-root trait variation within species is often sidelined despite its crucial role in ecosystem processes, plant performance, and belowground plant responses to environmental shifts and competition (McCormack et al., 2017; Weemstra et al., 2021, 2023). Carmona et al. (2021) contributed to this discussion on a global scale by underscoring that among-species variability in fine-root traits is smaller compared to aboveground traits across diverse botanical families, which suggests a potentially greater significance of intraspecific trait variation for belowground traits. Despite the important implications of these differences, there is still restricted knowledge regarding the magnitude of ITV in fine-root traits and how it contrasts with intraspecific variation in the traits of aboveground plant structure. Experimental studies covering a wide range of species are essential to explore this question.

The adjustments in trait variation within a species in response to environmental shifts can be reflected in changes in the positioning of species along the patterns of trait–trait coordination and trade-offs represented in the functional space (Carmona et al., 2021; Díaz et al., 2016). Knowing not only the changes in the position of the species but also the direction of this change in the functional space provides relevant information about the species' strategies to face new environmental conditions (Fenollosa et al., 2023; Vogel et al., 2019). Nevertheless, the shifts in multi-trait functional space occupation due to drought remain uncertain and have been scarcely investigated. Vogel et al., (2019) observed that communities under warming and drought treatment experienced a shift toward a “slow and tall” strategy characterized by high LDMC and height (H), along with reduced nitrogen content in the leaves. González-M et al. (2021) noted a differential impact of drought on the performance of species in the tropical dry forest depending on their position in functional space. Both drought-avoidance and drought-tolerant strategies exhibit resistance to extreme drought, with species dominance primarily determined by investment in dense tissues, resulting in increased biomass accumulation (González-M. et al., 2021). Recently, Fenollosa et al. (2023) found that species with decreased relative abundance during drought compared to control communities changed their position in the functional space, exhibiting higher H and LDMC. Conversely, drought-tolerant species, characterized by increased relative abundance in drought plots, moved toward high leaf thickness (Fenollosa et al., 2023). Despite considering multiple traits, most of these studies have overlooked intraspecies variation by relying only on a single mean trait value for each species, with a predominant focus on traits of aboveground plant structure. Consequently, evaluating intraspecific changes in functional space across different plant compartments (above and belowground) to assess whole-phenotype alterations under environmental changes has been neglected.

Ignoring the trait variability within species has been recognized as one of the potential factors contributing to the limited predictability of traits to explain individual performance in trait-based ecology (Chacón-Labella et al., 2022; Shipley et al., 2016). Trait-based ecology is founded on the premise that functional traits affect individual fitness by influencing diverse components of individual performance, such as growth rate, reproductive output, and survival (de Bello et al., 2021; Violle et al., 2007). However, various studies examining trait-performance relationships have yielded inconsistent results, with some indicating strong relationships (Gibert et al., 2016; Kamimura et al., 2023; Poorter et al., 2010; Russo et al., 2010) and others showing weaker associations (Adler et al., 2014; Paine et al., 2015; Poorter et al., 2018; Rosas et al., 2021; Smith-Martin et al., 2022). Different factors might underlie these inconsistencies, including:

- Lack of consideration of intraspecific trait variability. Few investigations have explored trait-performance relationships at the individual level (i.e., considering growth and trait values measured in the same individuals) (Liu et al., 2016; Poorter et al., 2018; Rosas et al., 2021; van der Sande et al., 2015), with most focusing on species-level analyses, ignoring the importance of intraspecific variation in modeling trait-growth relationships effectively (Liu et al., 2016; Shipley et al., 2016; Yang et al., 2018). Therefore, traits and plant performance are often uncoupled as they are measured in different individuals and locations from where the performance components are estimated, thereby challenging the reliability of trait-performance relationships (Poorter et al., 2018; Yang et al., 2018).

- The selection of traits that are not relevant in the considered environment. The absence of clear guidance on selecting relevant traits can significantly impact the results (Bueno et al., 2023; Chacón-Labella et al., 2022; van der Plas et al., 2020) since easy-to-measure traits may not strongly relate to plant performance (Rowland et al., 2021; Yang et al., 2018). For instance, while some wood anatomical traits are effective predictors of growth rates in tropical forests, measuring them is time-consuming, especially considering the diverse array of species (Poorter et al., 2010; Russo et al., 2010). Consequently, our understanding of trait-growth relationships, especially in woody plants of tropical forests, remains limited (Rosas et al., 2021; Yang et al., 2018).

- Overlooking trait interactions. Acknowledging trait interactions is essential because trait-performance relationships are not solely determined by traits acting independently. Instead, the combined effect and interplay of traits collectively shape the individual's whole phenotype and, consequently, its performance (Carmona et al., 2021; Chacón-Labella et al., 2022; Laughlin & Messier, 2015). However, trait interactions are rarely considered when examining trait-performance relationships, potentially impacting the model's outcome (Kamimura et al., 2023; Pistón et al., 2019; Worthy et al., 2020).

- Neglecting the dependence of trait values and individual performance on local environmental conditions. Some studies disregard the fact that the relationship between traits and plant performance is context-dependent (Kamimura et al., 2023) and model this relationship by averaging the trait values and performance estimations of each species, considering individuals from different environmental conditions. This approach may not accurately represent the relationship between traits and plant performance, which could weaken the validity of the model results (Yang et al., 2018).
- Using simple models that do not capture possible non-linear relationships between traits and plant performance. Most studies have modeled traits-performance relationships assuming linear relationships between plant traits and performance (Adler et al., 2014; Poorter et al., 2018; Rowland et al., 2021; Visser et al., 2016), but this approach may overlook non-linear relationships (Laughlin & Messier, 2015; Pistón et al., 2019). This oversight could lead to an inaccurate understanding of how traits influence plant performance, highlighting the need for more sophisticated modeling techniques accounting for nonlinearities (Kamimura et al., 2023; Pistón et al., 2019).

Understanding trait-performance relationships remains an open challenge in trait-based ecology, emphasizing the crucial need for alternative models that incorporate intraspecific trait variability and trait interactions to accurately predict species trait range shifts in response to environmental changes. Studying this in different species and populations in dry ecosystems and drought-prone areas is essential to enhance our ability to understand ecosystem resilience and anticipate and mitigate the impacts of climate change on biodiversity and ecosystem functioning. The tropical dry forest (TDF) is a unique biome with a marked precipitation seasonality and plant species that are well adapted to dry conditions but have low resilience to extreme drought (Murphy and Lugo, 1986; Pennington et al., 2009; Verbesselt et al., 2016), making it an important setting that can provide valuable insights into the mechanisms underlying plant adaptation to dry conditions. In this ecosystem, leaf habits define the main two strategies in woody species: evergreen species that tolerate seasonal drought and deciduous species that avoid drought by shedding their leaves in the dry season (Vargas G. et al., 2021). In general, these species have hydraulic traits related to a safety-efficiency trade-off with a strong effect on drought response (González-M. et al., 2021; Méndez-Alonzo et al., 2012). Species with hydraulically safe tissues tend to be drought-tolerant, while hydraulically efficient species are expected to be drought-avoidant (Markesteijn et al., 2011; Méndez-Alonzo et al., 2012). Therefore, examining the influence of functional traits on individuals' growth in the tropical dry forest enables us to anticipate plant responses to environmental shifts and devise more effective conservation and restoration strategies in this ecosystem.

Climate change is predicted to increase summer drought in different ecosystems, including European grasslands and tropical dry forests (Gibson & Newman, 2019; Miles et al., 2006). At large scale, woody and herbaceous species show greater intraspecific trait variation in climates with low water availability, which might foster plant populations' persistence in stressful environments (Kuppler et al., 2020). At the local scale, some studies suggest that environmental harshness acts as a selective force that drives convergence in species traits, thereby reducing among-species variation and increasing the relative importance of intraspecific trait variation (Niu et al., 2020; Shipley et al., 2016). This thesis comprehensively explores intraspecific trait diversity, examining how plants respond to environmental challenges, specifically focusing on drought conditions. I used two methodological approaches: a greenhouse experiment and a field sampling database. The greenhouse experimental design included 52 European herbaceous species under drought and control conditions, with the investigation focusing on seven morphological aboveground and fine-root traits: leaf area, specific leaf area, leaf dry matter content, plant height (aboveground traits), and specific root length, root dry matter content, and average root diameter (fine-root traits). **Paper 1** (**I**) opens the exploration by quantifying intraspecific trait variation across different plant compartments (above- and belowground) and to what extent this variation changes in response to drought. This knowledge offers critical insights into population and community resilience in the face of climate change. In addition, unraveling the implications of intraspecific trait variation (ITV) in both aboveground and belowground domains is crucial for (a) accurate functional species characterization because when ITV is high, considering a single mean trait value for each species might be unreliable, and (b) enabling meaningful interspecies comparisons, particularly when substantial ITV makes comparison between different species under similar environmental conditions more complicated (e.g., bigger plants in wet areas than in dry areas). **Paper 2** (**II**) extends the exploration to map drought resistance and intraspecific trait variability in the functional space to uncover the pivotal role of individual variation in shaping plant strategies. Mapping traits measured on multiple plant organs (e.g., roots, leaves, whole plant) allows us to explore changes in the patterns of species' occupation of functional space in response to drought, the impact of drought on trait variability across the species pool, and the role of functional traits in determining drought resistance and intraspecific variability. The findings contribute valuable knowledge on how species adapt to environmental stressors, offering implications for community assembly dynamics and ecosystem functioning. Finally, **paper 3** (**III**) broadens the scope by shifting the focus to the natural environment of Colombia's tropical dry forests, where trait-growth relationships under natural drought conditions are examined using a detailed field sampling database. The database has meticulous measurements of functional traits and relative growth rates in 967 adult trees and shrubs (263 species). This study incorporates intraspecific trait variation, trait interactions, non-linear relationships, and the impact of leaf phenology on individual growth. By examining the trait-performance relationship, this paper sheds light on how individual performance influences the different plant strategies adapted to precipitation seasonality, which in turn shape community assembly within this ecosystem and contribute to its overall functioning.

1.2 Objectives of the thesis

The main objective of this thesis was to explore the implications of intraspecific trait variation (ITV) in plants under drought, aiming to clarify its influence on plant strategies to cope with shifting environmental conditions.

The specific aims of this thesis were:

1. To examine the proportion of total variability in aboveground and fine-root traits among and within species using a greenhouse experiment with species typical to European grasslands and evaluating how these proportions are altered under drought conditions (**I, II**). Since among-species variability in fine-root traits is smaller than in aboveground traits across diverse botanical families, (H1) intraspecific trait variability would contribute more to the total variation in fine-root traits than in aboveground traits (**I**). Additionally, (H2) under drought conditions, ITV would have a greater relative contribution to total trait variation in both aboveground and fine-root traits due to the filtering effect of drought, leading to convergence in trait variation among species (**I, II**).
2. To investigate how drought influences the patterns of species' occupation in the functional space and the role of functional traits in determining both drought resistance and intraspecific variability in herbaceous species (**II**). (H3) Drought would act as a filter, reducing trait variability in the species pool. (H4) Species would move towards conservative strategies within the functional space under drought conditions, increasing their investment in protective tissues and water conservation. (H5) Species with trait values related to drought-tolerance strategy would have higher resistance (i.e., experience smaller declines in biomass compared to non-drought conditions), and the most resistant species would have greater intraspecific variability than species showing great declines in biomass.
3. To assess the relationship between growth and traits in woody plants using different trait resolutions (individual, plot, area) and considering different trait interaction levels (high, medium, low) in Colombian tropical dry forests (**III**). (H6) Traits considered at the individual level would better predict individual growth than traits averaged at the plot and study area level. (H7) Models that consider a high level of interactions between traits will better predict growth than models that include a low level of interactions. (H8) Traits would explain more variation in individual growth in deciduous species than in evergreen species.

2 METHODS

2.1 Greenhouse experiment design

For **papers I** and **II**, seeds of 52 species of herbaceous plants typical from European grassland ecosystems (18 families; 34 forbs, 16 graminoids, and two legumes) were obtained from a commercial supplier (Planta Naturalis). After species germinated in Petri dishes, the seedlings were transplanted to plastic pots (11 × 11 × 12 cm height, 1L volume). Pots were filled with a mixture of a potting substrate (Biolan Murumuld) and sand. At the end of May 2020, I established monocultures with seven individuals of a single species per pot, which were grown under well-watered conditions (10 pots per species, for a total of 520 pots). One individual was placed in the center of the pot, surrounded by six individuals of the same species, forming a hexagon, following the design of Carmona, de Bello, et al. (2019). Pots were randomly placed in the greenhouse of the University of Tartu, Estonia (**Figure 1**). Within the first week after transplanting, the seedlings that had not established successfully were replaced. One month after transplanting the seedlings to the pots, a drought treatment was applied to half of the pots (five pots per species). Control pots were well-watered every day (25–28% soil volumetric water content – VWC), and pots in the drought treatment were watered up to 20% maximal soil water capacity (5% VWC) (Marchin et al., 2020; Wehner et al., 2015). Regular hand-weeding was conducted to remove unsown species from each pot. After month-long drought treatment, the experiment was harvested in late July 2020, when the first individuals started flowering. At the end of the experiment, 465 pots (233 in control and 232 in drought treatment) had all seven living individuals, which were used for trait measurements.

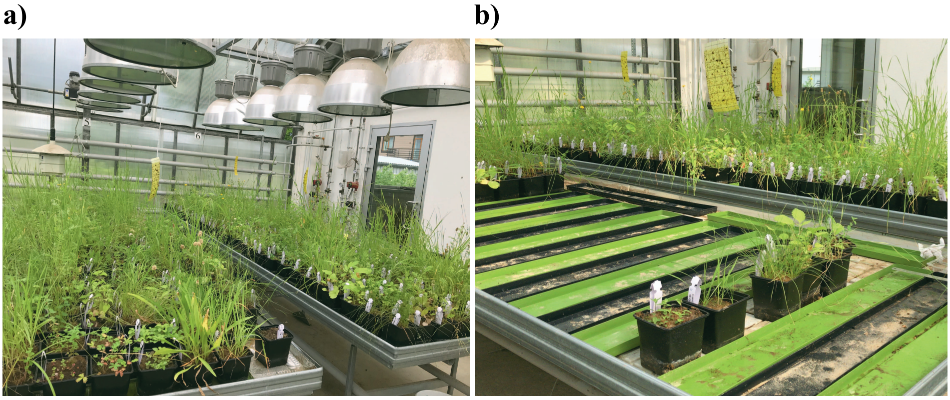


Figure 1. Photos illustrating the greenhouse experiment used in Papers I and II. **A)**. 520 pots of 52 herbaceous species in monocultures under drought and control treatments. **B)**. Harvesting. (Photos: Slendy Rodríguez).

2.2 Study area and growth rate measurements in tropical dry forest

In **paper III**, we used a database from the Alexander von Humboldt Research Institute (Bogotá, Colombia) with information on ten permanent plots (1 ha) established between August 2013 and October 2014 in mature forests of the three main formations of the Colombian TDF: Caribbean, Tropical Savannas, and the Inter-Andean valleys. Altitude ranges from 15 to 1025 m.a.s.l. across sites, the mean annual temperature is between 23.4 and 28.3°C, the aridity index is between 0.77 and 2.03, and total annual precipitation is between 899 and 2697 mm. All sites have one or two dry seasons ranging from 4 to 9 months (mean precipitation <100 mm month^{-1}). In 2015, a severe El Niño Southern Oscillation (ENSO) event impacted various Neotropical dry forest regions, including Colombian TDFs. During ENSO$_{2015}$, the Standardized Precipitation-Evapotranspiration Index (SPEI) for the study plots showed higher negative values, indicating the strongest drought in the previous 36 years (González-M. et al., 2021).

In each plot, all trees and shrubs with a diameter at breast height (DBH) ≥ 2.5 cm were tagged, identified, and measured for DBH and height. During the second census (2016–2017), the same individuals were revisited, and stem wood density (WD, g cm^{-3}) was calculated and used in the allometric equation for the dry forest to estimate individual-biomass (Alvarez et al., 2012). Each individual's biomass growth (Tn yr^{-1}) was estimated as the difference in log biomass between the last and the first census, divided by the time interval between censuses (Prado-Junior et al., 2016). I calculated the relative growth rate as biomass growth divided by the initial biomass measured in the first census. Leaf phenology information for each species was obtained from González-M. et al., (2021).

2.3 Trait measurements

Following established protocols, in **papers I** and **II**, we measured seven aboveground and fine-root morphological traits related to drought responses and resource use strategies (Pérez-Harguindeguy et al., 2013). For aboveground traits, vegetative plant height (H, cm) was measured before harvesting, and one young and fully expanded leaf was collected from three individuals in each pot. For fine-root traits, I collected a sample (10–50 mg) of the finest roots (<2 mm) from each pot. Leaves and roots were scanned (Epson Perfection 3200 and Epson V700 photo scanner, respectively) and then dried for 72 h at 60 °C to measure dry leaf and root biomass. Leaf scans were processed with ImageJ software to determine leaf area (LA, mm2). Root scans were processed with WinRHIZO Pro 2015 (Regent Instruments Inc., Canada) to calculate average root diameter (AvgD, mm) and root length (cm). With these measurements, I estimated specific leaf area (SLA, the ratio of fresh leaf area to leaf dry mass, mm^2 mg^{-1}) and leaf dry matter content (LDMC, the ratio of leaf dry mass to leaf fresh mass, mg g^{-1}) for each leaf, and averaged the values for each species at the pot level. I also calculated specific root length (SRL, the ratio of root length to root dry mass, cm g^{-1}) and root dry matter content (RDMC, the ratio of root dry mass to root fresh mass, mg g^{-1}) for each species at the pot level, due to the complexity associated with disentangling individual roots within a pot. Each pot's total aboveground and belowground biomass was oven-dried at 60 °C for 72 h and weighed. The total biomass of each pot was calculated as the sum of aboveground and belowground biomass.

For **paper III**, during the last census (2016–2017), wood and leaf traits were measured for 1167 individuals (adults). Traits were collected for all tree and shrub species within each plot following an abundance-weighted trait sampling scheme: traits were measured in five to eight individuals for the most abundant species, one to three individuals for species with less than five individuals per plot, and in one individual for species with only one individual per plot (Carmona et al., 2015; González-M. et al., 2021). The selected wood anatomical traits are related to biomass production and hydraulic safety and efficiency (González-M. et al., 2021; Méndez-Alonzo et al., 2012) and include fiber wall thickness (FWT, μm), vessel area (VA, μm^2), pit diameter aperture (DApit, μm), and wood density (WD, g cm^{-3}). Leaf traits are related to light interception, tissue investments, and carbon-gain strategies (González-M. et al., 2021) and include leaf area (LA, mm^2), leaf dry matter content (LDMC, mg g^{-1}), and specific leaf area (SLA, mm^2 mg^{-1}). Height (m) is also related to light interception, competition, plant size, and growth, continuously increasing both diameter (DBH) and height. All these traits were included in subsequent analyses because they exhibited Spearman's correlation coefficient $<|0.7|$ (Dormann et al., 2013).

2.4 Statistical analyses

In **paper I**, I performed variance partitioning to assess the variation in traits within-species (intraspecific trait variation) and among-species. I used two approaches: linear mixed-effect models (Carmona et al., 2015; Messier et al., 2010) and permutational multivariate analysis of variance (PERMANOVA) (Carmona et al., 2021; de Bello et al., 2021).

For the linear mixed effect models (LME), I fitted separate models for every trait and treatment (control and drought), including species as a random factor. Models considering species and treatment simultaneously as random factors were also explored.

For PERMANOVA, dissimilarity matrices were created based on scaled traits, considering single traits, combinations of aboveground and fine-root traits, and analogous traits between leaves (SLA and LDMC) and fine-roots (SRL and RDMC) (i.e., traits that serve similar functions in resource acquisition strategies) (Reich, 2014; Weemstra et al., 2022). These dissimilarity matrices were created for each treatment separately (control and drought) and for treatments together. For single treatments, PERMANOVA was made using species as the explanatory variable. In the case of the dissimilarity matrices based on both treatments together, species, treatment, and the species*treatment interaction were used as explanatory variables.

To evaluate if there is any differentiated response of ITV between grasses and forbs, I ran the same set of analyses (LME and PERMANOVA), independently considering each of these growth forms.

In **paper II**, I first defined the functional space occupied by the plants in the experiment using a Principal Component Analysis (PCA) based on the traits (log-transformed). The PCA was performed using the mean trait values of both treatments (control and drought) for each species. Then, following Martello et al., (2018), each species' position was projected onto the PCA based on the average traits. Horn's parallel analysis identified the PCA's first two principal components (PCs) as sufficient to explain 56.1% of total trait variance. These PCs were used to analyze how species' functional space occupation changed under drought. I carried out a linear regression model for each axis using the change (i.e., the score of the species in the axis in drought conditions minus the score in the control) as the response variable and the respective axis in the control treatment as the explanatory variable. Using a trait probability density (TPD) approach (Carmona, de Bello, Mason, et al., 2019), I estimated functional richness (FRic; the amount of functional space occupied) for all the species (i.e., species pool) for each treatment and FRic for each species in each treatment (i.e., within-species). I used a paired t-test to compare space occupation for each species (FRic) between treatments.

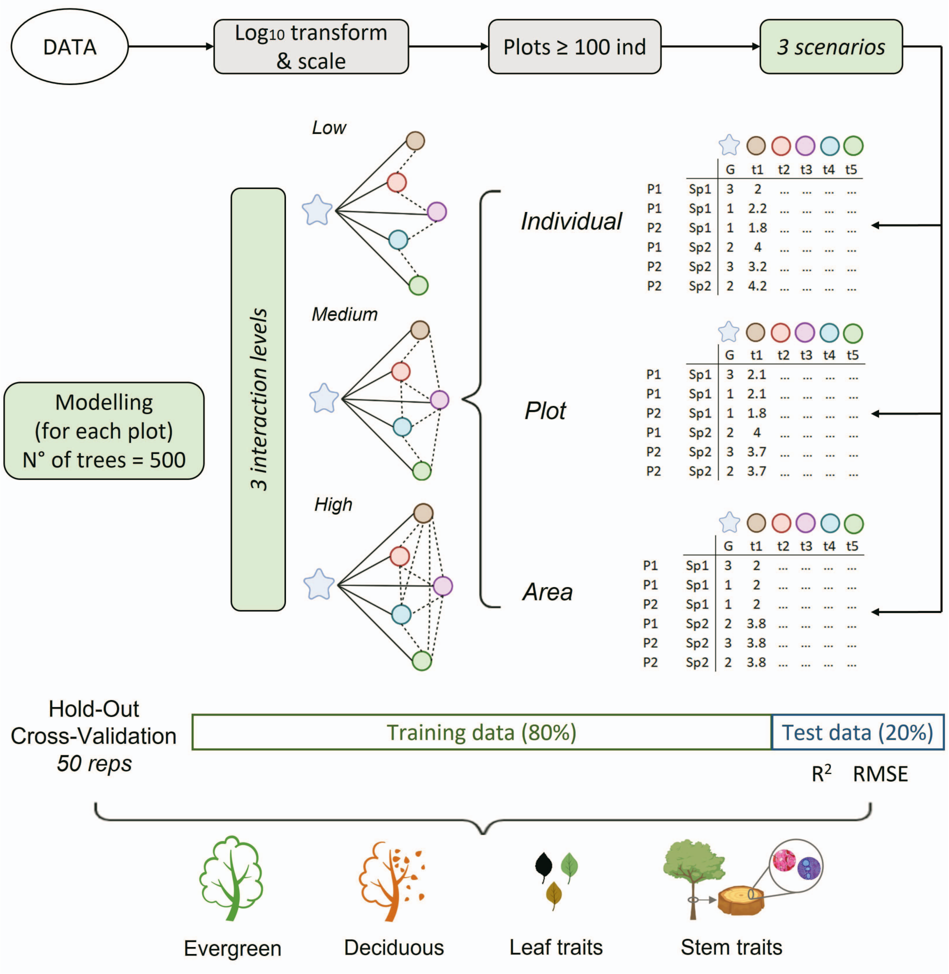
I also assessed how traits determine drought resistance (DR) and intraspecific variability in response to drought. DR was calculated as a log-ratio of biomass using each species' mean total biomass under drought compared to control. The lower (more negative) the value of this index is for a given species, the smaller the species' resistance to drought in terms of biomass (i.e., the species have less biomass in drought than in control). Intraspecific variability in response to drought was measured as the dissimilarity between TPD functions of control and drought treatments of each species. Dissimilarity ranges from 0 (identical occupation of functional space) to 1 (complete trait displacement between treatments) (Carmona, de Bello, Mason, et al., 2019).

Finally, following Carmona et al. (2021), generalized additive models (GAMs) were employed to map DR and intraspecific variability in response to drought in the functional space. Two separated models were fitted for DR and intraspecific variability as response variables. The species' average coordinates of the species in the two PCA axes were used as explanatory variables.

In **paper III**, prior to analyses, trait and growth values were $\log_{10}$-transformed and scaled to have zero mean and unit variance. Outliers were removed based on ±3 standard deviations from the mean of species values. For the subsequent models, three plots with fewer than 100 individuals were excluded to ensure numerical stability. The final database included 967 individuals in seven plots (943 trees and 24 shrubs belonging to 263 species). A decision tree-based machine learning approach (random forest – RF) was employed to explore trait-growth relationships. Mixed-effect RF models were generated with species as a random intercept and individual relative growth as the response variable. Various modeling decisions were simulated to test their impact on trait-performance relationships. This included three simulated scenarios considering trait measurements at different resolution levels (individual, plot, area) and three levels of trait interactions by adjusting tree complexity (low, medium, and high) (**Figure 2**). RF modeling of individual relative growth as a function of trait values was run independently in each scenario and for each sampling plot due to potential differences in environmental conditions across plots (Kamimura et al., 2023; Laughlin & Messier, 2015).

Model performance was evaluated through a holdout internal cross-validation, generating 50 models' evaluations. For each combination of scenario, plot, and interaction level, we randomly split the tree considering three different values of mtry (1, 3, 6). We split the data each time into two subsets: 80% for calibration (training) and 20% for evaluation (testing). On the evaluation subset, we calculated two metrics: R-squared (R^2) and root mean squared error (RMSE). These metrics were averaged across the 50 replications. Then, a one-way Analysis of Variance (ANOVA) statistical test was conducted to determine if there are significant differences in model performance metrics (R^2 and RMSE) between different scenarios and interaction levels. In total, 1350 models were run per plot (3 scenarios × 3 interaction levels × 3 mtry values × 50 replicates). We ran the same set of analyses independently for leaf phenology (evergreen and deciduous) and the type of traits (leaf and stem) (**Figure 2**). Finally, variable importance for each model was calculated using permutation by randomly shuffling the values of the predictor (each trait) and measuring how much the model's predictive ability decreases (*i.e.*, how much the error increases).

All data analyses were performed with R version 4.2.0 (R Foundation for Statistical Computing, Vienna, AT). More detailed information on specific versions and used packages can be obtained from the original papers (**I**, **II**, **III**).



Individual

		G	t1	t2	t3	t4	t5
P1	Sp1	3	2	...	...	...	...
P1	Sp1	1	2.2	...	...	...	...
P2	Sp1	1	1.8	...	...	...	...
P1	Sp2	2	4	...	...	...	...
P2	Sp2	3	3.2	...	...	...	...
P2	Sp2	2	4.2	...	...	...	...

Plot

		G	t1	t2	t3	t4	t5
P1	Sp1	3	2.1	...	...	...	...
P1	Sp1	1	2.1	...	...	...	...
P2	Sp1	1	1.8	...	...	...	...
P1	Sp2	2	4	...	...	...	...
P2	Sp2	3	3.7	...	...	...	...
P2	Sp2	2	3.7	...	...	...	...

Area

		G	t1	t2	t3	t4	t5
P1	Sp1	3	2	...	...	...	...
P1	Sp1	1	2	...	...	...	...
P2	Sp1	1	2	...	...	...	...
P1	Sp2	2	3.8	...	...	...	...
P2	Sp2	3	3.8	...	...	...	...
P2	Sp2	2	3.8	...	...	...	...

Figure 2. Schematic overview of the methodology to explore the relationship between traits and individual growth in the Colombian tropical dry forest woody species. We used mixed-effect random forest models specifying the species as a random intercept, modeling the individual growth (star) as a function of trait values (colored circles). (Designed by Slendy Rodríguez). Figure 1 in **paper III**.

3 RESULTS

3.1 ITV of above- and belowground traits under drought experiment

Given that PERMANOVA analysis allows for the integration of multiple traits, the results of these models are presented in the main text. Differences among species primarily explained the variation in aboveground and fine-root traits, except for root dry matter content (RDMC), where intraspecific trait variation was predominant (**I**). Species identity accounted for most of the height and leaf area variance, explaining 87–90% of the total variation (**Figure 3**). When considering all fine-root traits together, within-species variation (ITV) was higher for belowground traits than for aboveground traits and for analogous root traits compared to analogous leaf traits (**I**). These proportions remained relatively consistent under drought conditions, as supported by the model's incorporating treatment and the species × treatment interaction (Table 1 in **I**) and the finding of no significant differences in the amount of functional space occupied within species between the two treatments (paired t-test, $t = 0.75$, $df = 51$, $p = 0.42$ in **II**). The drought treatment had minimal effects on trait variation, with most traits displaying low R-squared values (max $R^2 = 0.04$). Similarly, the interaction between species and treatment lacked significance (max $R^2 = 0.08$). The results from both linear mixed effects models and PERMANOVA were highly consistent (Supplementary Table 3 in **I**).

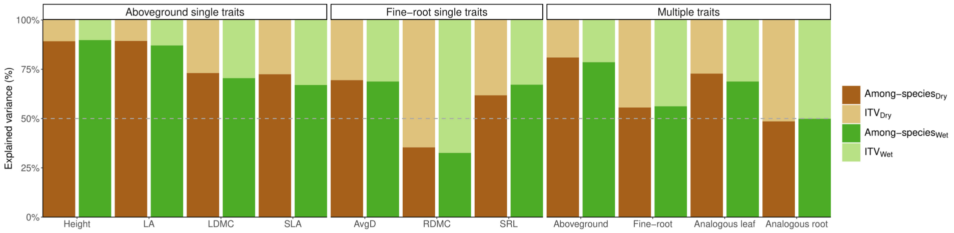


Figure 3. Variance partitioning of PERMANOVAs for all species. Models are for each individual trait (single traits) and multi-traits: for the combination of aboveground traits (LA, SLA, LDMC, and Height), the combination of fine-root traits (AvgD, SRL, and RDMC), analogous leaf traits (SLA, LDMC), and analogous root traits (SRL, RDMC), considering each treatment separately: control (green bars) and drought (brown bars). Log-traits were considered. Figure 1 in the **paper I**.

3.2 Changes in species' functional space occupation under drought

The functional space of the 52 considered species consisted of the first two dimensions of the PCA, which together explained 56,1% of the total variance (**II**). The first principal component (37.4%) was positively related to LDMC and SRL and negatively to AvgD. The second principal component (18.7%) was positively linked to H and LA and negatively to RDMC. Species with traits associated with acquisitive strategies (high SRL, low RDMC, and AvgD) are in the upper-right quadrant, and species with conservative strategies (thicker roots) are in the lower-left quadrant (**Figure 4 A**).

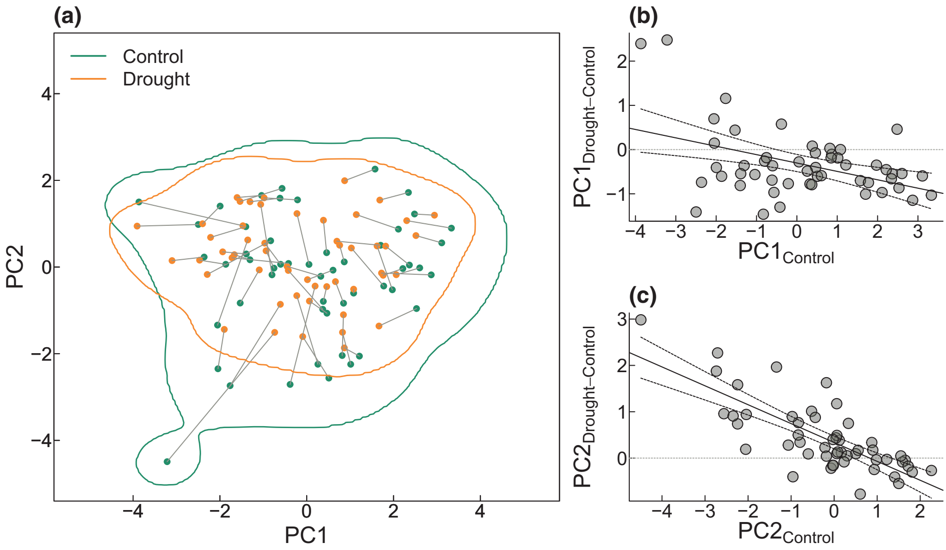


Figure 4. Changes in the species' position within the functional space in response to drought. **A**. Different patterns of occupation of the functional space by species under the drought (orange) and well-watered (green) treatments. **B**, **C**. Species shifts in the individual principal components of the functional space between control and drought conditions (i.e., the score of the species in each PC in the drought treatment minus the score in the control) depended on the position of the species in the control treatment. **B**. PC1 (Adj-$R^2 = 0.17$, $P = 0.001$, linear regression). **C**. PC2 (Adj-$R^2 = 0.57$, $P < 0.001$, linear regression). Figure 3 in **paper II**.

The drought treatment produced pronounced changes in traits associated with PC2 (RDMC, H, and LA), where species with low scores under control conditions experienced the most significant increases under drought (**Figure 4 C**). Similarly, species with high scores on PC1 under control conditions shifted slightly toward lower scores under drought, while a few species moved from low scores to high ones in response to drought (**Figure 4 B**). These trait changes led to a lower occupancy of the trait space in drought conditions compared to control when considering all species, reducing the total space occupied among species by 34.8% compared to control (FRic-control: 47.4; FRic-drought: 30.9; **Figure 4 A**). However, within-species trait variation remained the same under drought, which maintained the amount of functional space occupied (**I, II**).

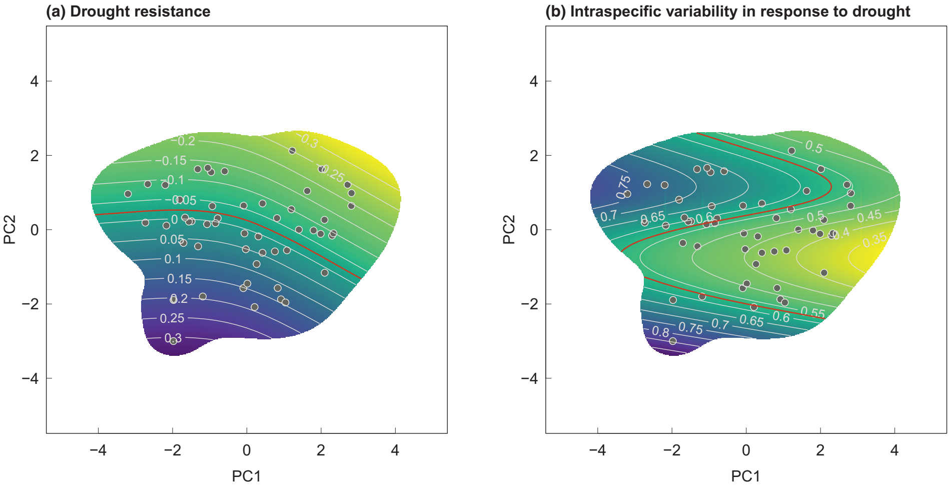


Figure 5. Drought resistance (**A**) and intraspecific variability in response to drought (**B**) in the functional space of 52 plant species. Drought resistance and intraspecific variability in response to drought were used as response variables and the position of species in the functional space as predictors in GAM. The dots represent species. Figure 4 in **paper II**.

When mapping resistance and intraspecific variability to drought in the functional space (**II**), conservative species that invest more in safe root tissues (high AvgD and RDMC) but conserve small size (low H) were more resistant and variable at the intraspecific level (**Figure 5**). The species with high intraspecific variability also tended to have leaves with a large area (high LA), while species with dense leaves (high LDMC) and fine roots (high SRL) were less variable (**Figure 5 B**). Likewise, tall species with high SRL and low AvgD lost more total biomass under drought (upper-right quadrant, **Figure 5 A**).

3.3 Trait-growth relationships in tropical dry forests

The random forest models used for growth predictions based on individual, plot, and area-level traits showed a consistently low out-of-sample predictive power (< 10% in all cases) with no significant differences in R^2 and RMSE across the trait resolutions and interaction levels (**III**). However, when incorporating leaf phenology in the modeling of trait-growth relationships, deciduous species models performed better than evergreen species models (overall median $R^2 \approx 0.25$ and $R^2 \approx 0.10$, respectively) (**Figure 6**).

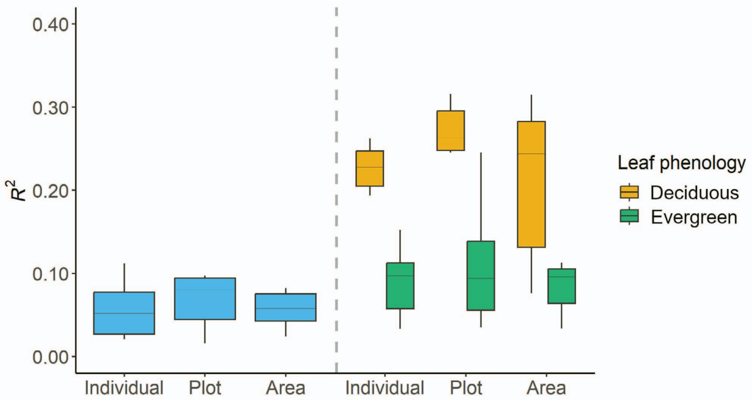


Figure 6. Random forest models of relative growth to a medium level of trait interactions at individual, plot, and area resolutions. Boxplots show the distribution of R^2 for each plot (n = 1350, corresponding to 50 repetitions per plot). For each model, R^2 values were based on the evaluation subset of data (20% observations). Different boxplots correspond to models using the trait data at the individual-level, plot-level (mean trait values of all individuals for each species per plot), and area-level (mean trait values for each species across all plots). Figure 2 in **paper III**.

Among the examined traits in **paper III**, VA, LA, and DApit emerged as the primary contributors to the variation in growth models considering all species (**Figure 6**). For deciduous species, significant proportions of variance were accounted for by DApit, SLA, and LA. In the case of evergreen species, VA, LA, and WD were the main traits explaining growth differences. **Figure 7** illustrates the relative importance of each trait predictor in models at the individual resolution, results that exhibited consistency across the three trait resolution scenarios.

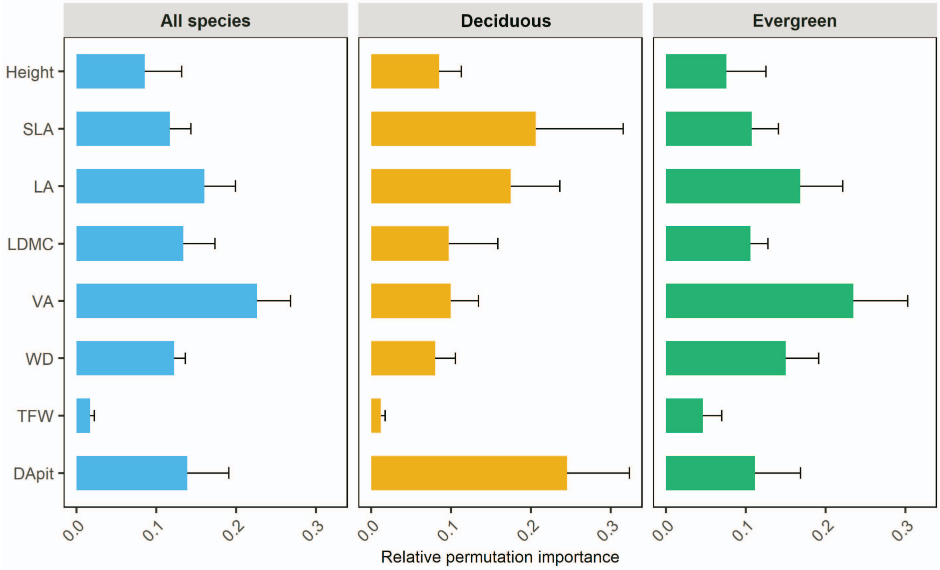


Figure 7. The relative importance of traits for explaining growth in woody species from the Colombian TDFs at the individual trait resolution. The value of importance for each trait in each plot was relativized by the sum of the total importance in the plot (scaled to sum up to one). The barplots represent the average importance of that trait across plots and the error bar represents its standard error. Figure 3 in **paper III**.

4 DISCUSSION

Intraspecific trait variation (ITV) is increasingly recognized as a significant contributor to overall trait variability, influencing ecological strategies, individual performance, species interactions, and community assembly. However, considerable gaps exist in understanding ITV across plant compartments, particularly in fine-root traits, whole-phenotype changes within species in response to drought, and the relationship between traits and individual plant performance considering trait interactions. In this thesis, I addressed these critical gaps and advanced knowledge on how ITV varies between aboveground and belowground plant compartments (**I**) elucidating the whole-phenotypic changes and trait variability in response to drought in the functional space (**II**) and integrating trait variation within species and trait-trait interactions to study trait-growth relationships in forests under prolonged natural drought conditions (**III**).

4.1 Trait variability and drought-driven dynamics in functional space among herbaceous species

As expected (H1), in the set of 52 species typical for European grasslands, intraspecific trait variation belowground was significantly higher than aboveground (**I**), which could be attributed to soil heterogeneity and microbial interactions, promoting a greater variation within species – as individuals uniquely adapt to their immediate soil environment – and stronger belowground competition among conspecifics (Paganeli & Batalha, 2021; Read et al., 2017; Spitzer et al., 2023; Weemstra et al., 2022). Moreover, variation in mycorrhizal colonization rates is linked to individual root architecture, which could result in increased flexibility in belowground resource allocation (i.e., a wider species' niche), boosting adaptability to diverse environments and promoting intraspecific variability (Bergmann et al., 2020; Gerz et al., 2018). Consequently, fine-root traits may exhibit a nuanced response that produces a reduced trait differentiation among species, as observed in prior family-level studies (Bueno et al., 2023; Carmona et al., 2021). Therefore, considering multiple traits within species for functional characterization could be more reliable than considering only mean trait values, especially belowground (**I, II**) (Weemstra et al., 2021; Westerband et al., 2021; Wong & Carmona, 2021).

A larger proportion of variance was explained by among-species trait variation compared to intraspecific trait variation, except in the case of root dry matter content (RDMC), where ITV accounted for twice as much variation as among-species differences (**I**, **Figure 3**). As RDMC is a surrogate of fine root tissue density and roots with high tissue density are long-lived (Birouste et al., 2014), it is likely that some individuals prioritize longer-lived roots through higher dry matter allocation, while others emphasize nitrogen uptake for faster resource investment but with shorter lifespan (Bergmann et al., 2020; Carmona et al., 2021).

Therefore, high levels of ITV in RDMC suggest no uniform strategy within species, providing plant populations with adaptability to thrive in diverse soil conditions by adjusting their resource allocation strategies, either in scenarios of optimal water availability or drought. Indeed, when analysing shifts in the species position in the functional space (**II**), there was a stronger displacement towards smaller RDMC values under drought, which indicates an adaptive advantage in response to changing environments attributed to the high ITV in this trait (Spitzer et al., 2023). However, contrary to expectations (H2), the drought did not significantly change the proportion of variation within species for any trait in the analysed species pool (**I**), which was also further supported when analysing multiple traits simultaneously, revealing similar amounts of functional space occupied by single species in each treatment (**II**). The finding that ITV remained constant across treatments suggests that it helps maintain functional volume within species to allow for diverse strategies under drought conditions, which in turn fosters species resilience. The intraspecific variation stability could influence competitive interactions and niche differentiation among species, thereby influencing coexistence dynamics and the assembly of ecological communities (Carmona, de Bello, Azcárate, et al., 2019; de Bello et al., 2021; Yang et al., 2024). The consistent trait expression, regardless of drought, also highlights the importance of within-species variation to buffer the effects of environmental filtering during community assembly to maintain ecological functions and ultimately stabilize plant communities, which can contribute to both climate change mitigation and adaptation (Hetzer et al., 2021; Luo et al., 2023; Niu et al., 2020).

The variance partitioning analysis highlighted significant contributions from among-species differences in aboveground traits (**I**), particularly in height and leaf area (Bueno et al., 2023). These findings underscored the plant height as a highly conserved trait with a prominent source of variation residing between families (Bueno et al., 2023; Tumber-Dávila et al., 2022). Low proportions of ITV in size-related traits could suggest limited plasticity but does not necessarily imply a lack of adaptation to environmental gradients (Palacio-López et al., 2015; Siefert et al., 2015). Indeed, analyses under the multi-trait approach showed a displacement towards parts of the functional space associated with a larger size (height and leaf area), lower values of SRL, and larger root diameter (**II**). Contrary to expectations (H4), traits of conservative species (positioned lower in the functional space, **Figure 4**) shifted under drought conditions towards parts of the functional space associated with less conservative trait strategies (large size and low RDMC). While reductions in specific root length (SRL) have been observed in response to drought (Comas et al., 2013; Lozano et al., 2020), the effects remain uncertain, as plants can exhibit varied responses by altering SRL and root diameter (Bristiel et al., 2019; Kramer-Walter et al., 2016; Olmo et al., 2014). Species adopting acquisitive strategies (drought-avoidance) invest less in tissues and have shorter root lifespans (Reich, 2014), reducing both aboveground and belowground biomass in response to drought (**Figure 5 A**) (de Vries et al., 2016; Eziz et al., 2017; Zhou et al., 2018).

By contrast, conservative species that reduced their leaf size and height and invested in root tissues (RDMC and AvgD) were more drought-resistant and had high intraspecific variability (**Figure 5 A, B**) (Lozano et al., 2020; Zhou et al., 2018; Zwicke et al., 2015), confirming (H5). Surprisingly, species with high intraspecific variability also tended to be taller and have larger leaves, which may exhibit a tendency to reduce leaf area to mitigate water loss and decrease their average height, resulting in smaller individuals (Pérez-Ramos et al., 2019). These changes may range from a drought-avoidance strategy that allows the plant to take advantage of short water availability periods to sustain plant growth to a drought-tolerance strategy in which the plant conserves water to ensure survival under intense drought (Berdugo et al., 2020; Bristiel et al., 2019). In addition, the relationship between size and "costly" root tissues suggests a combination of traits that converge in an optimal part of the trait space where drought strategies may be mixed. This could be related to the fact that some root traits do not align with the leaf economics spectrum or with whole-plant economics, especially when plants face limited resources (Carmona et al., 2021; Kramer-Walter et al., 2016). Indeed, the significant within-species variation in specific root length (SRL) and average root diameter (AvgD) in graminoids (**I**) underscores the adaptability of grasses to diverse soil conditions and resource uptake strategies (Bergmann et al., 2020; Carmona et al., 2021; Weemstra et al., 2021, 2023). These findings implicate a broad spectrum of strategies within the root economic spectrum, encompassing efficient soil exploration with cost-effective roots to collaborative resource acquisition through mycorrhizal fungi (Bergmann et al., 2020).

As a result of the trait displacements, the species pool converged towards more similar parts of the trait space under drought conditions, suggesting a reduced set of trait strategies that allow species to cope with drought (**II**). This aligns with the expectation (H3) that, within the considered species pool, greater diversity of strategies is allowed for species when water availability is higher, as drought acts as a strong filter of the traits of species, especially on conservative ones (Rota et al., 2017; Vogel et al., 2019). This reduction of the functional space indirectly sheds light on potential mechanisms driving community assembly since it leads to the convergence of trait combinations that thrive under drought, determining well-suited functional strategies and what species are most likely to occur in the new environmental conditions (Lin et al., 2011; Vogel et al., 2019). Drought-induced limitations on the range of functional traits between species can influence species interactions within communities experiencing similar conditions, potentially affecting species coexistence and community stability and resilience. However, despite the reduction in the size of the functional space occupied by the species pool, the fact that the highest percentage of trait variation is species-specific emphasizes the retention of different strategies, resource use-acquisition, and competitive abilities (Bueno et al., 2023; Meilhac et al., 2020; Vogel et al., 2019). The wide range of trait values explained by species (**I**), the observation that within-species trait variability remained unchanged under drought (**I**, **II**), and the detected trait displacements in the functional space (**II**) collectively suggest a variety of responses under changing conditions. Despite experiencing a decrease in biomass under drought conditions for most species, the stability in trait variation could be a strategy to maintain core physiological functions while plants adjust biomass to cope with water limitation (**I**, **II**). Furthermore, aboveground trait variation among species and stronger belowground competition within-species (**I**) may promote coexistence through resource use differentiation and niche partitioning (Meilhac et al., 2020; Streit et al., 2022). However, further exploration of ITV at the community level is essential to understand plant community dynamics and stability (Streit et al., 2022; Westerband et al., 2021; Wong & Carmona, 2021). Likewise, further studies focused on distinguishing genetic and phenotypic plasticity components of ITV would enhance our ability to estimate the role of trait variability under environmental changes accurately. The utilization of individuals with reduced phenotypic plasticity, such as those subjected to demethylation treatment (e.g., demethylation treatment) (Puy, Carmona, Dvořáková, et al., 2021), as well as investigations into transgenerational inheritance and epigenetic variation could complement these experiments in the future (Sobral, 2023).

A diverse array of morphological traits among species (**I**) can help maintain different species' roles and strategies that, in turn, underlie ecosystem-level processes such as nutrient cycling, decomposition, and productivity (Reich, 2014; Szefer et al., 2017). The changes in traits of individuals can scale up to impact ecosystem functioning. For instance, the transition towards taller phenotypes with larger leaves (**II**), observed at the community level in other studies (Fenollosa et al., 2023; Vogel et al., 2019), implies increased light competition, potentially leading to higher primary productivity and carbon gains (Li et al., 2020; Vogel et al., 2019), and enhancing ecosystem functions such as edaphic fauna, root biomass, and soil nutrients (van der Plas et al., 2020). Similarly, the shift towards larger diameter roots may influence soil water retention, the ecosystem carbon cycle, and the net plant nitrogen uptake rate (Freschet et al., 2021). These changes of direction in traits can influence community composition and stability in biomass production and ecosystem functions over time (Lin et al., 2011; Vogel et al., 2019). Therefore, increased biomass of drought-resistance species would help not only the ecosystem stability and resistance but also ecosystem functioning in processes such as productivity, ecosystem carbon cycling, litter decomposition, resource use efficiency, and resilience (Berdugo et al., 2020; Vogel et al., 2019). However, these shifts occurred at the within-species level, and species turnover could determine different trajectories within the functional space at the whole-community level (**II**). The absence of changes in the proportion of ITV in single and combined traits in response to drought treatment might suggest that trait differences at the community level are more likely attributed to shifts in community composition (species' turnover) rather than intraspecific adaptations (**I**, **II**), but this potential outcome requires verification (Streit et al., 2022; Weemstra et al., 2021).

4.2 Trait variability and individual growth relationships in woody species of the tropical dry forests

Considering intraspecific trait variation involves complex and time-consuming measurements of traits for each individual, which is why few studies include multiple species not only in herbaceous communities (**I**, **II**) but also in forests (**III**). The results of **paper III** showed that considering traits for each individual does not improve the prediction of individual growth of woody species. Examining trait-growth relationships in 263 woody species across seven Colombian dry forests (**III**) revealed that functional traits poorly predict individual growth in these ecosystems ($R^2 < 0.10$) (**Figure 6**), even when traits were considered at the individual level resolution (contrasting H6). Even though the R^2 values reported here reflect the models' ability to predict data that has not been used in the model training, weak trait-growth relationships have also been reported in other studies (Poorter et al., 2018; Rosas et al., 2021). The lack of effect on trait resolution could be attributed to the high trait variability between tree species compared to within species (Rosas et al., 2021). Ongoing research conducted by the Alexander von Humboldt Research Institute, Colombia, would corroborate if the trait variation is mainly due to the species identity in these forests, as previously confirmed in herbaceous plants (**I**, **II**). Moreover, the substantial variation in soil nutrients and water content within individual plots in the Colombian tropical dry forest (Caleño-Ruiz et al., 2023) could influence the relationship between traits and growth among individuals. This heterogeneity in the abiotic conditions occurring within each plot might be reflected in a large variation in the relationship between traits and growth among individuals, which, in turn, might hamper our ability to effectively detect the trait-growth relationship (Poorter et al., 2018; Smith-Martin et al., 2022). Additionally, the short duration of the growth monitoring period, limited to a single census, might have influenced the results since it could amplify the signal-to-noise ratio in the dataset, posing challenges in capturing the underlying effect of traits on growth. Given that plant growth involves a series of complex processes such as biotic interactions, environmental factors, and complex trait combinations, conducting studies at individual environmental scales that include neighborhood composition and over a longer growth monitoring period may help disentangle the growth-trait relationship (Bhadouria et al., 2016; Liu et al., 2016; Pulla et al., 2021; Sobral, 2021).

Despite previous research highlighting the importance of trait interactions (Laughlin & Messier, 2015; Pistón et al., 2019), the complexity of trait interactions did not significantly contribute to explaining growth variation in the studied TDFs (contrasting H7). One possible explanation is that the tropical dry forest spans a range of aridity levels, rainfall seasonality, and soil water availability, collectively serving as an environmental filter. This filtering process selects species that are coordinated and inherently equipped with traits that confer resilience to the environmental and climatic conditions of this unique ecosystem (González-M. et al., 2021; Markesteijn et al., 2011; Méndez-Alonzo et al., 2012). Consequently, the dominant influence of environmental selection on species composition and coordinated trait expression likely outweighs the effects of trait interactions in shaping growth patterns within these ecosystems. Additionally, the existence of different viable trait combinations that lead to similar growth rates in the ecosystem could also explain the lack of significant importance of trait interactions on growth in the TDFs (Marks & Lechowicz, 2006; Worthy et al., 2020). Further comparisons with regional flora traits are needed to determine the extent to which traits have been subject to environmental filtering processes, as there are notable differences in precipitation levels among study plots. Concurrently, delving deeper into trait coordination mechanisms through additional studies may improve predictions of trait-growth relationships. This knowledge would be essential to develop conservation strategies to sustain optimal ecosystem growth outcomes.

As expected (H8), trait interactions were more important in modeling growth variation in deciduous than in evergreen species (**Figure 6**). This difference could be attributed to higher trait variation in deciduous species, which adjust their hydraulic machinery during dry periods by reducing water demand and shedding leaves while increasing hydraulic efficiency and photosynthetic rates during optimal conditions (Markesteijn, Poorter, Tomlinson et al., 2014; Vargas G. et al., 2021). In addition, deciduous species differ in their timing and extent of leaf shedding according to their distinct water potential capacity (*i.e.*, different degrees of leaf retention of trees) (Wolfe et al., 2016), which gives more trait variation to deciduous species to grow in dry ecosystems (Vargas G. et al., 2021, 2022). In contrast, evergreen species maintain conservative xylem dynamics to withstand seasonal water scarcity; hence, traits facilitating conservative water transport and maintaining growth, such as narrow vessels and small leaves, were important predictors of growth variation (**Figure 7**) (Fu et al., 2012; Markesteijn et al., 2011; Tomlinson et al., 2013, 2014; Vico et al., 2015). Small vessels and pits help maintain water balance and prevent embolism, while small, thick leaves aid in conserving water and maintaining growth (Markesteijn et al., 2011; Tomlinson et al., 2013; Venturas et al., 2017). Investing in tissues also enhances hydraulic safety, so evergreen species often have a higher wood density than deciduous plants (Fu et al., 2012; Markesteijn et al., 2011). In deciduous species, traits enhancing photosynthetic capacity and hydraulic conductivity, such as large pit diameters and high specific leaf area, were important predictors of growth variation (**Figure 7**) (Fu et al., 2012; Vargas G. et al., 2021; Venturas et al., 2017). Large pits enhance water transport efficiency, and large and thin leaves favor photosynthetic capacity, which is beneficial for growth (Markesteijn et al., 2011; Tomlinson et al., 2013; Venturas et al., 2017). Therefore, the findings suggest that the importance of the traits depends on leaf phenology, which indicates that growth is probably limited by different factors depending on the species' physiology.

Drought stress is the dominant assembly mechanism at a regional scale shaping tree composition in the tropical dry forest (Méndez-Toribio et al., 2020; Muscarella et al., 2016), where the trait physiology of deciduous and evergreen species influence adaptation strategies, competition dynamics, community composition, and assembly patterns (Álvarez-Yépiz et al., 2017; Salazar Villegas et al., 2023; Subedi et al., 2019). Specifically, traits related to the safety-efficiency trade-off influence plant responses to drought, which is a strong selective driving community assembly (González-M. et al., 2021; Méndez-Alonzo et al., 2012). Likewise, trait coordination of the phenological strategies involves differences in leaf morphology and xylem architecture to withstand drought, affecting resource allocation and consequently impacting ecosystem functioning. With longer rainy seasons, evergreen plants enhance vigor due to the prolonged, longer-lasting leaves, which results in higher carbon gain and more evolutionary stable communities, while with longer dry seasons, deciduous species are more productive (i.e., with higher net carbon gain) (Vico et al., 2017). Leaf phenology not only influences carbon cycling but also water regulation, energy fluxes, biotic interactions, and community dynamics (Alberton et al., 2019; Silva et al., 2015). Additionally, rainfall seasonality determines decomposition rates, nitrogen cycling (e.g., legume nodulation), and carbon cycling processes (e.g., net primary production and soil respiration) in TDFs (Powers et al., 2015, 2018). This marked seasonality influences the investment in plants' tissues, which is crucial for both efficient (deciduous) and safe (evergreen) species since hydraulic efficiency and high tissue investment contribute to carbon gain and provide protection against prolonged droughts (González-M. et al., 2021; Somavilla et al., 2014). However, with prolonged drought periods, only evergreen species with deep roots and long-lasting leaves can be more productive than deciduous ones (Vico et al., 2017). In general, deciduous trees allocate more biomass to stems and coarse roots and less biomass to leaves, while evergreen trees allocate less biomass to stems and more to coarse and deeper roots (Smith-Martin et al., 2020). While plants typically invest more deep root systems in dry ecosystems, significant variation in rooting depth within and among species may represent differences in growth and considerable potential for belowground niche differentiation (Paz et al., 2015; Tumber-Dávila et al., 2022). This highlights the importance of the belowground compartment under drought conditions (**I**, **II**), yet few studies have been conducted to determine root variation among species for mature individuals in the tropical dry forest (**III**) due to the challenges of excavating complete root systems and the threatened state of this ecosystem (Smith-Martin et al., 2020). Therefore, considering not only environmental factors at a fine scale and neighborhood composition but also root traits could improve the predictions of individual growth in woody species of the TDFs. Moreover, empirical studies testing the effects of within-species trait variation on ecosystem functioning, including nutrient cycling and carbon and water dynamics, would fill an important gap in the field of functional ecology (Sobral, 2023).

Extreme drought can alter the structure and function of tropical dry forests (**III**) and European grasslands (**I**, **II**) in the future (Fenollosa et al., 2023; González-M. et al., 2021; Vogel et al., 2019). Trait variation among and within species contributes to ecosystem stability and resilience to environmental changes since it allows species to be flexible in strategies to withstand drought and maintain ecosystem functioning. Species with different trait combinations exhibit differential responses to environmental shifts, such as water availability. By understanding trait variation in dry conditions, we can predict how ecosystems could respond to future drought events and identify species that may have greater resilience or vulnerability to drought (**I**, **II**, **III**). Resilient individuals within species may be capable of adjusting their traits to fit under new conditions, helping to mitigate loss of functions and maintain ecosystem stability (**I**, **II**). Understanding trait variation and their relationship with biomass growth under drought environments can help anticipate changes in ecosystem functioning and inform adaptation strategies in the face of climate change (**I**, **II**, **III**). Gaining insight into trait-growth relationships can improve our ability to understand ecosystem resilience and predict the impacts of climate change on ecosystem dynamics (**III**). It can also help identify and prioritize conservation actions for threatened species and advance our ecological knowledge of plant responses to environmental stressors (**I**, **II**, **III**). Yet, these findings also serve as a warning, as the reduction of biomass and functional space among species under future drier scenarios could affect the ecosystem's multifunctionality and stability (Berdugo et al., 2020; González-M. et al., 2021; Rota et al., 2017; Valencia et al., 2015). Even if evolutionary or plastic responses to climate change occur, this does not necessarily mean that the responses would be sufficient to keep pace with the current rate of climate change (Franks et al., 2014).

5 CONCLUSIONS

In this thesis, I demonstrate the significance of intraspecific trait variation (ITV) and its implications for ecological strategies and individual performance under changing environmental conditions, particularly drought.

1: ITV was significantly higher for fine-root than for aboveground traits. For aboveground traits, species-level differences were the primary drivers of trait variation, particularly in height (H) and leaf area (LA). Belowground, flexibility in biomass and nutrient allocation within-species could be driven by the complex interplay between soil heterogeneity and microbial associations. Aboveground, diverse plant strategies and competitive abilities among species might facilitate niche differentiation and ecosystem multifunctionality (**I**). These findings underscore the importance of considering multiple traits within species for reliable functional characterization, especially belowground (**I**, **II**).

2: Drought did not significantly alter the proportion of variation within species for single or multiple traits considered simultaneously (**I**, **II**). However, there was a noticeable displacement towards smaller root dry matter content (RDMC) values under drought (**II**), indicating an adaptive advantage attributed to the high ITV in this trait (**I**). Although there was adjustment of traits in response to the drought, ITV remained stable under control and drought (**I**, **II**). High within-species variation in RDMC could allow species to adopt diverse strategies for nutrient and water acquisition (resource allocation), enhancing resilience to environmental changes. Moreover, the stability in ITV across treatments suggests that it helps maintain functional volume within species, which in turn enhances adaptability to allow diverse strategies under drought conditions. Such adaptability could not only influence the maintenance of ecological functions but could also promote the coexistence and resilience of species in response to fluctuating water availability (**I**, **II**).

3: Drought induced significant trait displacement towards less conservative strategies (tall plants and low RDMC), leading to a reduction in the functional space occupied by the species pool (trait convergence among species). Meanwhile, the most drought-resistant species displayed both higher ITV and conservative traits (small size and thick roots), suggesting a convergence of traits in an optimal part of the functional space where drought strategies can be mixed to enhance plants' ability to adjust biomass to withstand drought (**II**). Therefore, declines in biomass and functional space among species under future drier scenarios could compromise ecosystem multifunctionality and stability, emphasizing the need for proactive conservation strategies.

4: Trait-growth relationships in tropical dry forests (TDFs) were generally weak, with no significant differences among trait resolutions or levels of interactions between traits (**III**). This may be attributed to the idiosyncratic responses of individuals to the wide microenvironmental variation within TDF plots, highlighting the importance of accounting for non-uniform abiotic and biotic conditions at the local scale due to the complexity of plant growth dynamics in these ecosystems. The dominance of environmental selection on species composition and coordinated trait expression likely outweighs the effects of trait interactions in shaping growth patterns within TDFs. However, trait-growth relationships vary between deciduous and evergreen species, with deciduous species explaining higher proportions of growth variation. This difference reflects the distinct hydraulic strategies employed by different leaf phenologies in response to rainfall seasonality, underscoring the importance of considering the environment and species-specific physiological traits in predicting individual growth dynamics (**III**).

5: Overall, this thesis advances our understanding of ITV, trait-growth relationships, and drought-driven dynamics in plant functional space. By elucidating these intricate interactions, we gain insights into plant adaptation strategies, community assembly processes, and ecosystem functioning, providing valuable knowledge for biodiversity conservation and ecosystem management in the face of ongoing environmental changes (**I**, **II**, **III**).

SUMMARY

In the face of climate change, the study of functional traits deepens our ecological understanding of how plants respond and shape ecosystems under changing environmental conditions, shedding light on ecosystem functioning and resilience. While traditional ecology has primarily focused on among species trait differences, recent recognition of the substantial contribution of intraspecific trait variation (ITV) to overall trait variability highlights its importance in shaping ecological strategies, individual performance, community assembly, and ecosystem functioning. ITV can also promote species coexistence by facilitating resource partitioning and shifting competitive abilities between species. Considering the variation within species can offer valuable insights into plant species' response to environmental change.

One of the main consequences of climate change is the increase in frequency, severity, and duration of future drought. As a major environmental filter, drought constrains the range of viable trait values and filters out species with less adapted traits. This filtering effect not only leads to changes in species composition but also alters trait values within species, highlighting the crucial role of ITV in community assembly. Understanding how ITV shapes species responses to drought and influences whole-phenotype alterations is essential for predicting ecosystem resilience and implementing effective conservation strategies.

Despite its importance, ITV has been overlooked in traditional trait-based ecology, leading to limited predictability of trait-performance relationships. Challenges include the lack of consideration of ITV, neglect of trait interactions, and the context-dependent nature of the trait-performance relationship. Additionally, reliance on simple models that do not capture non-linear relationships and interactions among multiple traits. Addressing these challenges is crucial for accurately understanding species response to environmental changes and, ultimately, community assembly because individual-level traits vary in relation to the abiotic and biotic environment.

In this thesis, I demonstrate the significance of intraspecific trait variation across plant compartments and its implications for ecological strategies, individual performance, and community assembly under drought. By investigating ITV in aboveground and belowground plant compartments, exploring drought-induced dynamics in functional space among herbaceous species, and examining trait-growth relationships in tropical dry forests considering trait variation within-species and individual growth, this study advances our understanding of how ITV influences plant responses to environmental stressors and ecosystem functioning.

When evaluating trait variation among and within-species in a greenhouse experiment with herbaceous species, the findings showed that belowground ITV exceeds aboveground variation, emphasizing the significance of soil heterogeneity and microbial interactions in driving intraspecific variability. Moreover, the high ITV of root dry matter content (RDMC) allows for diverse resource allocation strategies, enhancing adaptability to varying soil conditions and promoting

species resilience. The findings also support previous research indicating that most of the total trait variance in European herbaceous species is explained by among-species differences. This suggests complementarity in resource use, ecosystem stability, and diverse responses to environmental changes, facilitating species persistence and coexistence. However, the proportion of trait variation attributed to species differences varies depending on the growth form, the pool of species considered, and the trait of interest. For instance, intraspecific trait variation plays a significant role in explaining variation in RDMC, which highlights the importance of studying trait sets from different individuals within a species for accurate functional species characterization, especially belowground.

Surprisingly, drought does not significantly alter ITV, indicating its stability in maintaining functional volume within species and fostering species coexistence dynamics. However, significant shifts in plant traits were detected in response to drought in the greenhouse experiment, particularly among the species with the most conservative water use strategies. These shifts lead to functionally more similar species, as evidenced by a reduction in the occupation of the species pool's functional space under drought conditions. The direction and magnitude of trait shifts depend strongly on species’ trait values in optimal conditions, with different traits showing adjustments that suggest mixed strategies to withstand drought. Trait displacement towards taller size and low RDMC were most common, but species that invest more in safe root tissues and maintain small size exhibit greater resistance and variability at the intraspecific level in response to drought, sometimes even increasing biomass compared to well-watered conditions. These results emphasize the importance of examining within-species trait distribution in the functional space in response to environmental fluctuations and how such changes affect overall occupation, which is crucial to understanding community assembly. However, further investigation is needed to understand the variability of ITV in natural environments and its origins, which may arise from genotypic variation within populations or variation of trait values within genotypes. Future studies should aim to disentangle the role of genetic diversity in intraspecific phenotypic variation and consider additional nutrient leaf and root traits, as well as different growth forms.

By extending the exploration to natural environments with drought conditions, trait-growth relationships of woody species in Colombian tropical dry forests showed limited predictability of individual growth based on functional traits, with no significant difference in the models using different trait resolutions or levels of trait interactions. This weak relationship may stem from individual idiosyncratic responses to microenvironmental variation within tropical dry forest plots, hindering our ability to detect trait-growth relationships. The complex interplay of environmental factors and trait variability between and within species contributes to the challenges in modeling trait-growth relationships. Despite topographical and soil resource variation, the strong precipitation seasonality and high temperatures in tropical dry forests select species adapted to these conditions from a regional species pool. This likely explains the lack of importance of trait complexity interactions in explaining growth variation. However, trait interactions become significant to explaining individual growth when considering leaf phenology, indicating that growth limitation varies depending on the species' physiology. Deciduous species exhibit better model performance, likely due to changes in hydraulic machinery in response to rainfall seasonality, while evergreen species adapt to climatic variability with a more conservative hydraulic response. These distinct trait strategies of deciduous and evergreen species could influence competition dynamics, community composition, and ecosystem functioning. However, more studies on individual growth are needed that encompass fine-scale microenvironmental variation, physiological hydraulic traits, and root traits in dry ecosystems. A whole-plant trait coordination approach is also necessary to better understand plant performance and demographic rates in tropical dry forests.

Overall, the results of this thesis contribute to our understanding of the complex dynamics shaping plant strategies and highlight the nuanced above- and belowground responses of plants to environmental shifts. Moreover, analysing the influence of trait interactions on individual performance could inform forest dynamics and ecosystem resilience. This knowledge is essential for informing conservation efforts and predicting the impacts of climate change on ecosystem functioning.

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SUMMARY IN ESTONIAN

Taimetunnuste liigisisene varieeruvus ning selle mõju kooslustele ja ökosüsteemide toimimisele

Muutuva kliima tingimustes on oluline uurida taimede funktsionaalseid tunnuseid, sest need annavad täpsemaid teadmisi selle kohta, kuidas taimed muutuvale keskkonnale reageerivad ning ökosüsteeme kujundavad. Varasemalt on ökoloogias keskendutud peamiselt tunnuste erinevustele liikide vahel, kuid hiljutised uuringud on rõhutanud tunnuste liigisisese varieeruvuse olulist panust üldisele tunnuste mitmekesisusele. Liigisisene varieeruvus mängib rolli nii taimeliikide ökoloogiliste strateegiate kujunemisel, üksikisendite edukusel, koosluste moodustumisel kui ka ökosüsteemide toimimisel. Samuti võib liigisisene varieeruvus edendada liikide kooseksisteerimist, kui taimeliikide eri isenditel on võime saada hakkama erinevates tingimustes ning vältida konkurentsi. Seega tuleb keskkonnamuutuste mõjude uurimisel taimeliikidele arvestada ka sama liigi üksikisendite mitmekesisusega.

Kliimamuutuste üks tagajärgi on sagedasemad, rängemad ja kauakestvamad põuad. Ajutine sademete vähesus käitub kui keskkonnafilter, mis piirab sobivate taimetunnuste väärtuste vahemikku ja filtreerib välja põuatingimustele vähem kohastunud liigid. See filter ei mõju ainult liikidele, vaid eraldab ka selliste tunnustega üksikisendid, kes muutunud veetingimustes ellu ei jää. Tunnuste liigisisene varieeruvus määrab seega koosluste liigilise koosseisu ning mõjutab seda, kuidas taimed reageerivad põuatingimustele. See teadmine aitab ennustada ka ökosüsteemide vastupidavust keskkonnamuutustele ning rakendada tõhusamaid looduskaitsemeetmeid.

Vaatamata oma olulisusele on tunnuste liigisisene varieeruvus pälvinud traditsioonilises tunnustepõhises ökoloogias vähe tähelepanu. Seetõttu on seni olnud keeruline seostada taimetunnuseid ka taime kasvu ja kohasusega. Probleemideks on olnud nii liigisisese varieeruvuse, tunnuste vastastikmõjude kui ka konkreetsete keskkonnatingimuste eiramine, mis kõik võivad tunnuste ja taimekasvu seost mõjutada. Samuti on seni kasutatud lihtsaid statistilisi mudeleid, mis ei kajasta mittelineaarseid seoseid ja mitmete tunnuste vastastikmõjusid. Et paremini aru saada, kuidas liigid ja kooslused reageerivad keskkonnamuutustele, on vaja lahendusi nendele probleemidele.

Käesolevas doktoritöös näitan tunnuste liigisisese varieeruvuse olulisust nii maapealsetele kui ka maa-alustele taimeorganitele ning selle varieeruvuse mõju ökoloogilistele strateegiatele, üksikisenditele ja kooslustele põua tingimustes. Ma uurisin tunnuste liigisisest varieeruvust maapealsetes ja maa-alustes taimeosades ning põuatingimuste poolt põhjustatud muutusi rohttaimede funktsionaalses tunnusruumis. Samuti vaatlesin tunnuste ja taimekasvu suhteid troopilistes kuivades metsades, võttes arvesse tunnuste liigisisese varieeruvuse. See doktoritöö panustab tunnuste ökoloogiasse uute teadmistega selle kohta, kuidas liigisisene varieeruvus mõjutab taimede vastust keskkonnastressoritele ning ökosüsteemi toimimist.

Uurides rohttaimede tunnuste varieerumist liikide vahel ja liigisiseselt kasvuhoonekatses, leidsime, et liigisisene varieeruvus maa-alustes tunnustes on suurem kui maapealsetes tunnustes. See viitab, et sama liigi üksikisendite mitmekesisust võib põhjustada mulla heterogeensus ja koosmõjud mulla mikroorganismidega. Lisaks võimaldab mõne juure tunnuse (nt juure kuivaine sisaldus) suur liigisisene varieeruvus mitmekesistada toitainete ja vee kättesaamise strateegiaid, suurendades nii liikide kohanemisvõimet ja vastupidavust erinevates mullatingimustes. Samas me leidsime, et rohttaimede tunnuste üldist varieerumist seletavad siiski paremini liikidevahelised erinevused. Sarnaseid tulemusi on leitud ka varasemates uuringutes Euroopa rohttaimedega ning seda võib seletada sellega, et erinevatel taimeliikidel on kujunenud erinevad strateegiad toitainete ja vee kättesaamiseks, mis tagab koosluste liigilise mitmekesisuse ja ökosüsteemide säilenõtkuse. Siiski sõltub liikidevaheliste erinevuste osakaal tunnuse üldisest varieerumisest nii taime kasvuvormist, liigirikkusest, kui ka uuritavast tunnusest. Näiteks on liigisisesel varieeruvusel oluline roll juurte kuivaine sisalduse tunnuse üldise mitmekesisuse seletamisel. Seega on oluline mõõta taimeliigi tunnuste väärtuseid sama liigi erinevatel isenditel ja seda eriti maa all.

Üllatav tulemus oli, et eelpool kirjeldatud kasvuhoonekatses ei mõjutanud põuatingimused märkimisväärselt tunnuste liigisisest varieeruvust, mis näitab funktsionaalse mitmekesisuse püsivust muutuvates keskkonnatingimustes ja soodustab liikide kooseksisteerimist. Siiski muutusid põuatingimustes mitmed taimetunnused, eriti veekadu vältiva strateegiaga liikide seas. Uurides kõiki katses olnud liike ja tunnuseid ühises funktsionaalses tunnusruumis, leidsime, et põuatingimustes vähenes tunnusruumi hõivatus ehk taimed muutusid üksteisega sarnasemaks. Mis suunas ja kui palju iga taimeliik põuatingimustes muutus, sõltus tunnusest ja tunnuse väärtusest soodsates tingimustes. See viitab, et põua talumiseks võivad erinevatel taimeliikidel olla ka erinevad strateegiad, milles mängivad rolli mitmed tunnused. Kõige sagedasemad muutused olid taimekõrguse suurenemine ja juurte kuivaine sisalduse vähenemine põuatingimustes, kuid vastupidiste muutustega liigid (kõrguse vähenemine ja juurekudedesse investeerimine) olid põuatingimustes edukamad, säilitades liigisisese varieeruvuse ja tootes sageli ka rohkem biomassi. Need tulemused rõhutavad vajadust uurida nii erinevate tunnuste liigisisest varieeruvust ühises funktsionaalses tunnusruumis kui ka seda, kuidas keskkonnatingimuste muutused mõjutavad tunnusruumi üldist hõivatust, et mõista koosluste dünaamikat muutuvas kliimas. Vaja on ka uurida tunnuste liigisisest varieeruvust looduslikes kooslustes ja teha kindaks, kas see varieeruvus tuleneb populatsioonisisesest genotüüpide mitmekesisusest või tunnuste plastilisusest genotüüpide sees. Edaspidised uuringud peaksid hindama geneetilise mitmekesisuse rolli taimetunnuste liigisiseses varieeruvuses, mõõtma täiendavaid lehtede ja juurte tunnuseid ning kaasama erinevaid kasvuvorme.

Laiendades uurimistööd põuale aldis looduslikele kooslustele Colombia troopilistes kuivades metsades, ei leidnud me tugevat ennustuslikku seost puittaimede tunnuste ja kasvu vahel. Olulist mõju ei avaldanud ka see, kas tunnuste varieeruvust oli mõõdetud liigisiselt või muul tasemel, ning mil määral arvestati tunnuste vastastikmõjusid. See nõrk seos võib tuleneda uurimisala keskkonnatingimuste väikeseskaalalisest heterogeensusest, mistõttu on keeruline hinnata taimekasvu pelgalt tunnuste järgi. Vaatamata topograafilisele ja mullatoitainete väikeseskaalalisele varieerumisele filtreerivad tugev sademete hooajalisus ja kõrged temperatuurid troopilistes kuivades metsades välja kindlad liigid, mis on nende tingimustega kohastunud. Tõenäoliselt seetõttu ei olnud puittaimede kasvu seletamisel ka tunnuste omavahelised seosed nii olulised. Need seosed muutusid oluliseks aga siis, kui heitlehiseid ja igihaljaid puid uuriti eraldi. Leidsime, et meie ennustuslikud mudelid taimetunnuste ja -kasvu seosest töötasid paremini heitlehiste liikide puhul. Seda tõenäoliselt seetõttu, et heitlehiste puude lehed ja veejuhtimisega seotud tunnused reageerivad tugevalt sademete hooajalisusele, samas igihaljastel puudel on püsivalt konservatiivne veekasutusstrateegia. Nende erinevate strateegiate koosesinemine troopilistes kuivades metsades võib mõjutada konkurentsi, koosluste ülesehitust ja ökosüsteemi toimimist. Põhjalikumaks ülevaateks troopiliste kuivade ökosüsteemide kohta on aga vaja rohkem üksikisendite kasvu uuringuid, mis hõlmaksid nii keskkonna väikeseskaalalist heterogeensust, füsioloogilisi veejuhtimisega seotud taimetunnuseid kui ka juurte tunnuseid. Vajalik on kaasata kõikide taimeosade tunnuseid, et paremini mõista, milline on taimede kasv ja populatsioonide dünaamika troopilistes kuivades metsades.

Kokkuvõttes, selle doktoritöö tulemused aitavad paremini mõista, milliste strateegiatega taimed muutunud keskkonnatingimustele reageerivad ning näitavad, et maapealsed ja -alused taimetunnused võivad nendele muutustele reageerida erinevalt. Lisaks leidsime, et oluline on arvestada ka tunnuste omavahelise vastastikmõjuga, et parandada meie arusaama puittaimede kasvu, metsakoosluste dünaamika ja ökosüsteemi säilenõtkuse kohta. Doktoritöös saadud tulemused on vajalikud arendamaks sobivaid looduskaitsemeetmeid ning ennustamaks kliimamuutuste mõju ökosüsteemide toimimisele.

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“*It is not the strongest of the species that survives… it is the one that is most adaptable to change*” Charles Darwin.

Thesis dedicated to all the women of my lineage and those committed to sorority, equity, and social justice.

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S. Rodríguez-Alarcón, R. González-M, C. Carmona. (2022) Intraspecific hydraulic trait variation influences plant growth and productivity in the Colombian Tropical Dry Forest. International Association for Ecology (INTECOL), Geneva, Switzerland. (oral presentation)

S. Rodríguez-Alarcón, R. Tamme, C. Carmona. (2021) Changes in the space-trait occupation of species in response to drought. Ecological Society of America (ESA), online. (oral presentation)

S. Rodríguez-Alarcón, N. Rodríguez-Eraso, R. López. (2018) Biomasa aérea en un paisaje fragmentado de bosque alto andino: el efecto del tamaño del parche. II National Symposium of Landscape Ecology, Bogotá, Colombia. (oral presentation)

L. Rodríguez-Posso, **S. Rodríguez-Alarcón**, N. Rodríguez-Eraso. (2018) Evaluando la biomasa aérea en ecosistemas fragmentados altoandinos: una comparación de datos de campo e índices espectrales. *II National Symposium of Landscape Ecology*, Bogotá, Colombia. (poster)

S. Rodríguez-Alarcón, R. López, N. Rodríguez-Eraso, I. Pineda. (2017) Proposal of a reference ecosystem based on functional traits of the above-ground biomass for the restoration of the high Andean forest. VII World Conference on Ecological Restoration (SER), Foz do Iguassu, Brazil. (poster)

Teaching:

Data analysis in Community Ecology (3 ECTS). Supervising the practical part of the course and lecturing (2023–2024).

Other scientific activities:

Reviewed scientific articles for the following journals: Ecology and Evolution, Functional Ecology, Journal of Ecology, Journal of Arid Environments, Oecologia, Oikos.

In the media: Interview in *Forbes* Innovation Science. (2022). This scientist´s passion took her from Colombian forest to Estonian grasslands. Interviewer: Andrew Wight. February 16, 2022.

In the media: Interview in *El Tiempo* newspaper. (2019). Lo bueno de que llueva tanto en Bogotá y en la región. Interviewer: Ana Puentes. April 24, 2019.

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Haridustee:

2019–	Tartu Ülikool, doktoriõpe (botaanika ja ökoloogia)
2014–2018	Francisco José de Caldas'i Ülikool (Colombia), magistriõpe (metsa majandamine, kasutamine ja kaitse)
2007–2012	Francisco José de Caldas'i Ülikool (Colombia), bakalaureuseõpe (bioloogia)

Töökogemus:

2023–2024	Tartu Ülikool, Loodus- ja Tehnoloogiateaduskond, Ökoloogia- ja Maateaduste Instituut, nooremteadur
2018–2019	Bogotá Botaanikaaed (Colombia), funktsionaalse ökoloogia teadussuuna juht
2018	*Colombia National Nature Parks*, Chingaza rahvuspark, bioloog
2017	*Wildlife Conservation Society* (WCS, Colombia), Chingaza rahvuspark, bioloog
2016	Natura Sihtasutus (Colombia), funktsionaalse ökoloogia teadussuuna juht
2014–2016	Bogotá linnavalitsuse keskkonnaosakond (Colombia), keskkonnahariduse spetsialist
2012–2014	Antek SA labor (Colombia), bioloog

Uurimistoetused ja stipendiumid:

2024	Erasmus õpirände stipendium (Göttingeni Ülikool, Saksamaa)
2023	Tartu Ülikooli eesti keele suvekursuse stipendium, Euroopa Regionaalarengu Fond
2022	UAV suvekooli stipendium school, Euroopa Regionaalarengu Fond ja Haridus- ja Noorteameti IT Akadeemia programm
2022	Dora Pluss lühiajalise õpirände stipendium (*International Association for Ecology* (INTECOL) konverents, Geneva, Šveits), Euroopa Regionaalarengu Fond
2021	Dora Pluss õpirände stipendium (*Alexander von Humboldt Biological Resources Research Institute*, Colombia), Euroopa Regionaalarengu Fond

Teaduspreemiad ja tunnustused:

2024	*International Union of Forest Research Organizations* (IUFRO) konverents, parima posterettekande auhind
2016	Bogotá Botaanikaaed (Colombia), Thomas Van der Hammen'i nimeline teaduspreemia
2013	Francisco José de Caldas'i Ülikool (Colombia), magistriõppe preemia
2012	Francisco José de Caldas'i Ülikool (Colombia), bakalaureuseõppe preemia

Teadusartiklid:

S. Rodríguez-Alarcón, R. Tamme, C. Carmona. Intraspecific variation in fine-root traits is larger than in aboveground traits in European herbaceous species regardless of drought. (2024). *Frontiers in Plant Science* 15, 1375371. DOI: 10.3389/fpls.2024.1375371

S. Rodríguez-Alarcón, R. González-M, C. Carmona, E. Tordoni. Trait-growth relationships in Colombian tropical dry forest: Incorporating intraspecific variation and trait interactions. (2024). *Journal of Vegetation Science* 35, e13233. DOI: 10.1111/jvs.13233

S. Rodríguez-Alarcón, R. Tamme, C. Carmona. Intraspecific trait changes in response to drought lead to trait convergence between – but not within – species. (2022). *Functional Ecology* 36, 1900–1911. DOI: 10.1111/1365-2435.14099

S. Rodríguez-Alarcón, L. Pinzón-Pérez, J. López, D. Cabrera-Amaya. Rasgos funcionales de plantas leñosas en áreas verdes de Bogotá, Colombia. (2020). *Revista Biota Colombiana* 21, 108–133. DOI: 10.21068/c2020.v21n02a08

S. Rodríguez-Alarcón, N. Rodríguez-Eraso, I. Pineda-Rincón, R. López-Camacho. (2018) Effects of fragmentation on functional diversity associated with aboveground biomass in a high Andean forest in Colombia. *Landscape Ecology* 33, 1851–1864. DOI: 10.1007/s10980-018-0719-8

Konverentsiettekanded:

S. Rodríguez-Alarcón, R. González-M, C. Carmona, E. Tordoni. (2024) Are leaf and stem trait interactions good predictors of individual tree growth in a Tropical Dry Forests? *International Union of Forest Research Organizations* (IUFRO), Stockholm, Rootsi. (posterettekanne)

S. Rodríguez-Alarcón, R. González-M, C. Carmona. (2022) Intraspecific hydraulic trait variation influences plant growth and productivity in the Colombian Tropical Dry Forest. *International Association for Ecology* (INTECOL), Geneva, Šveits. (suuline ettekanne)

S. Rodríguez-Alarcón, R. Tamme, C. Carmona. (2021) Changes in the space-trait occupation of species in response to drought. *Ecological Society of America* (ESA), veebis. (suuline ettekanne)

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L. Rodríguez-Posso, **S. Rodríguez-Alarcón**, N. Rodríguez-Eraso. (2018) Evaluando la biomasa aérea en ecosistemas fragmentados altoandinos: una comparación de datos de campo e índices espectrales. *II National Symposium of Landscape Ecology*, Bogotá, Colombia. (posterettekanne)

S. Rodríguez-Alarcón, R. López, N. Rodríguez-Eraso, I. Pineda. (2017) Proposal of a reference ecosystem based on functional traits of the above-ground biomass for the restoration of the high Andean forest. *VII World Conference on Ecological Restoration* (SER), Foz do Iguassu, Brazil. (posterettekanne)

Õppetöö:

Õppeaine "Ökoloogiliste koosluste andmeanalüüs" (3 ECTS) kaaslektor ja juhendaja (2023–2024).

Muu teaduslik tegevus:

Retsenseerinud artikleid teadusajakirjades: Ecology and Evolution, Functional Ecology, Journal of Ecology, Journal of Arid Environments, Oecologia, Oikos.

Intervjuu veebiväljaandes *Forbes Innovation Science*. (2022). This scientist´s passion took her from Colombian forest to Estonian grasslands. Andrew Wight. 16. veebruar 2022.

Intervjuu ajalehes *El Tiempo*. (2019). Lo bueno de que llueva tanto en Bogotá y en la región. Ana Puentes. 24. aprill 2019.

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