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META-ANALYSIS

How Environment Affects Ontogenetic Differences in Leaf Functional Traits of Woody Plants

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ABSTRACT

Aim: The consistency of patterns in ontogenetic differences in plant traits across the globe has not been thoroughly studied. Environmental conditions affect leaf functional traits, and these effects can differ between adult trees and saplings due to varying environmental conditions in their aerial and soil environments. Our integrative analysis aims to reveal the global universality of woody plants' ontogeny and explores influencing factors.

Location: Global.

Time Period: Studies published in 1989–2023.

Major Taxa Studied: Woody plants.

Methods: We performed a global meta-analysis of woody plants with different plant functional types at 64 sites around the world, assessed the ontogenetic differences in nine key leaf traits and explored the environmental factors that affected the ontogenetic differences.

Results: We observed that (1) leaf traits differed significantly between adult trees and saplings, with environmental factors playing varying roles. Photosynthetic capacity per unit area (A_a) and nitrogen content per unit dry mass (N_m) were lower in saplings than in adults under low solar radiation, but this trend reversed with increased solar radiation. Differences in stomatal density (SD) and stable carbon isotope composition ($\delta^{13}C$) between adults and saplings were greatest under low solar radiation; (2) ontogenetic differences in leaf thickness (LT), leaf dry mass per area (LMA) and stomatal conductance (g_s) were greater at lower mean annual temperature (MAT); (3) at high mean annual precipitation (MAP), adults had higher nitrogen content per unit area

(N_a), while saplings had higher N_m than adults; (4) soil conditions were strongly correlated with ontogenetic differences in LT and SD, with soil pH as a key driver of variation in A_a, LT, SD, N_a and N_m.
Main Conclusions: Our findings indicate that ontogeny strongly modifies leaf functional traits and that multiple environmental factors influence the magnitude of ontogenetic differences in leaf traits. This underscores the importance of considering ontogeny when predicting trait values across plant developmental stages, modelling vegetation composed of individuals of different ages and forecasting vegetation responses to environmental changes.

1 | Introduction

As trees mature, they increase both in size and in structural complexity (An et al. 2024; Han 2011; Niinemets 2010; Tumber-Dávila et al. 2022; Wang et al. 2023). Many functional characteristics, including primary production and photosynthesis, change with the size or age of individual trees (Ambrose et al. 2009; Cavender-Bares and Bazzaz 2000; Liu et al. 2021; Mencuccini et al. 2007). In addition to the direct effects of age, size and structural complexity, natural selection is likely to produce developmental patterns that are genetically determined, as young and old trees experience systematic differences in their environment (Barton 2024; Thomas and Winner 2002). Thus, in general, it is the complex interplay between genetically regulated phase transitions (genetically regulated phenotype change), increases in age and size and phenotypic plasticity that leads to ontogenetic differences (Barton 2024). Barton (2024) concluded that most studies predict ontogenetic differences based on the *Light Hypothesis* and the *Relative Growth Rate (RGR) Hypothesis*. In trees, ontogenetic trait variation appears to be primarily driven by adaptation to predictable increases in light availability, while selection for RGR may occur across a variety of plant functional types (Barton 2024).

Leaf traits influence various plant functions via their effects on resource acquisition and use (Hikosaka et al. 1999; Reich et al. 2014). The leaf economic spectrum (LES) is a conceptual framework that characterises the combinations of leaf structural, chemical and physiological traits along a variation spectrum ranging from slow to rapid return on investments of nutrients and dry mass in leaves (Onoda et al. 2017; Pan et al. 2020; Wright et al. 2004; Zhang et al. 2024). Previous work has shown that there is wide variation in LES traits within species (Niinemets 2015; Siefert et al. 2015; Wang et al. 2024) and that plant functional traits differ between adults and young individuals (Ambrose et al. 2009; Cavender-Bares and Bazzaz 2000; Greenwood et al. 2008; He and Yan 2018; Mencuccini et al. 2007; Palow et al. 2012; Steppe et al. 2011; Thomas and Winner 2002). However, studies investigating these differences sometimes report conflicting findings. For example, some work has found that leaf nitrogen content and photosynthetic capacity change with tree age (Houter and Pons 2012; Niinemets 2002; Reich et al. 1999), but other studies have not identified significant differences between individuals of different ages (Magnani et al. 2008; Merilo et al. 2009).

In a meta-analysis of differences in gas exchange characteristics between saplings and mature trees of 35 species, Thomas and Winner (2002) found that leaf dry mass per area (LMA) was higher among adults than saplings in all studied cases. This suggests that differences in LMA are universal, regardless of species or growth conditions. However, although photosynthetic rate per leaf area (A_a) was higher in the canopy-top leaves of adults than of saplings when all species were pooled, differences in A_a were not significant when only evergreen or conifer species were compared. This implies that the size dependence of A_a differs among PFTs. It has also been shown that angiosperms and gymnosperms have obvious differences in hydraulic characteristics (Sanchez-Martinez et al. 2020), and they respond and acclimate differently to environmental stress, especially to drought stress (Adams et al. 2017). In terms of resource economics strategy, evergreen species with conservative growth strategy and deciduous species with rapid growth strategy often occupy opposite ends of LES (Reich et al. 2014; Wright et al. 2004). Different suites of trait combinations, differences in stress response among plant functional types (PFT) and possible consequences of these differences in the impact of ontogeny on trait variation motivated us to explore the ontogenetic differences among different PFTs.

In general, the top leaves of adult trees tend to be exposed to direct sunlight, whereas light conditions experienced by saplings can vary from very low in forest overstorey to moderately high in canopy gaps (Niinemets 1997; Niinemets et al. 2015). Barton (2024) also brought up this point in the description of the *Light Hypothesis*, that is, older trees might have a greater LMA, photosynthetic rate and nitrogen content. Other growth conditions such as solar radiation, precipitation, temperature, soil organic matter content and soil moisture can also influence leaf traits (Björkman et al. 2018; Maire et al. 2015; Niinemets 2001; Ramírez-Valiente et al. 2022; Schmitt et al. 2022; Wright et al. 2001). LMA tends to be higher in plants growing in relatively low temperatures with limited water and nutrient availability (Poorter et al. 2009). Even when adult trees and saplings grow in similar environments, their sensitivity to environmental changes might differ. Likewise, drought may influence adult trees more than saplings if adults experience greater hydraulic constraints due to the longer distances for transport of water from soil to leaves. Alternatively, saplings may have shallower roots in some lineages, which exacerbates water limitation under drought conditions to a greater degree than in relatively well-rooted adults.

Recent studies have demonstrated that the plant height is a stronger driver of leaf traits such as LMA than differences in light availability (Liu et al. 2020), suggesting that water use may be an important factor driving variation in leaf traits. Because adult trees receive more light than saplings and can thus assimilate more carbon, low nutrient availability may have a relatively large effect on the internal carbon–nutrient balances of adult trees. Soil pH both directly and indirectly affects the turnover and availability of key limiting nutrients, particularly nitrogen and phosphorus (SanClements et al. 2010; Viani et al. 2014),

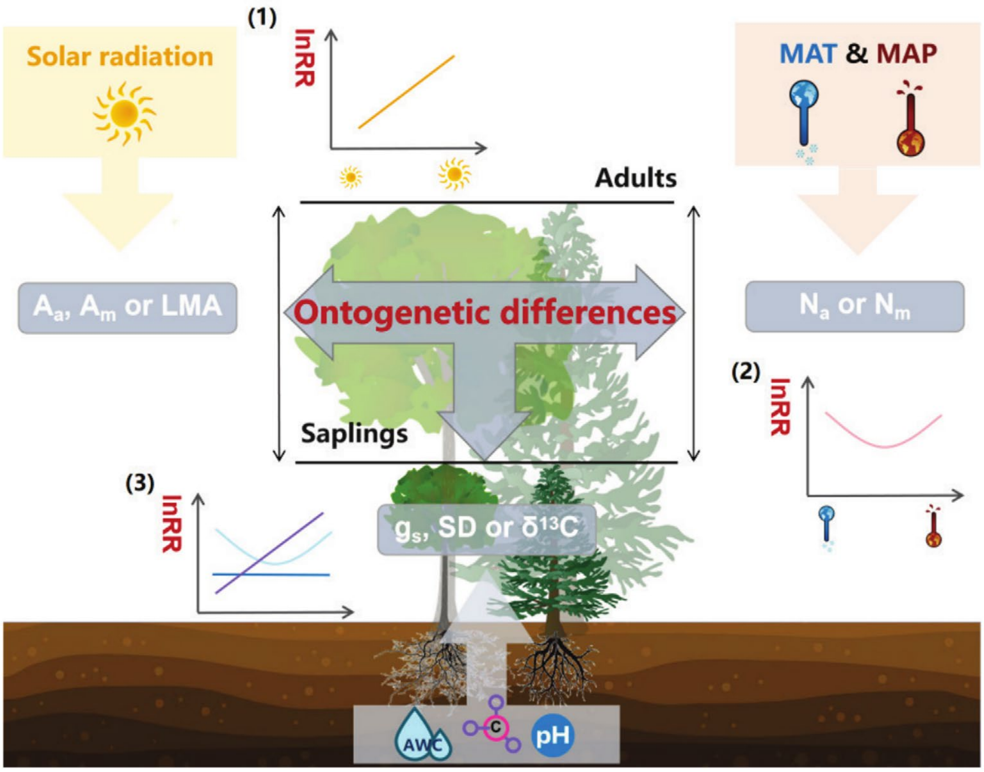

FIGURE 1 | Hypothetical relationship between environmental factors and ontogenetic differences in leaf traits. Trait responses are characterised by the response ratio (lnRR); in the equation $\text{lnRR} = \ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a given trait in saplings and m_a is the mean value of the trait in adult trees. (1), (2) and (3) correspond to five hypotheses evaluated here. δ^{13}C, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density.

and thus, soil pH is increasingly understood as one of the main drivers of plant trait variation (Rissanen et al. 2023; Westerband et al. 2023). However, to our knowledge, no work has assessed whether ontogenetic differences in leaf traits are modulated by climatic and soil factors. Determining how the relationships between trait and environmental drivers vary through plant ontogeny is crucial for predicting trait values through vegetation development (Famiglietti et al. 2024). Solar radiation has been found to drive differences between adult trees and saplings mainly via its effects on photosynthesis (Durand et al. 2021), which would be reflected in differences in photosynthetic rate and LMA in our study. In addition, the efficiency of light interception might decrease with increasing tree size (Niinemets et al. 2005).

Here, we compiled a dataset that includes nine key traits for 125 woody species: photosynthetic rate per unit leaf area (A_a) and per unit leaf dry mass (A_m), stomatal conductance (g_s), LMA, leaf thickness (LT), stomatal density (SD), stable carbon isotope composition (δ^{13}C) and nitrogen content per unit leaf area (N_a) and per unit dry mass (N_m). We asked how do ontogenetic differences in leaf traits depend on PFT and environmental factors and posed five main hypotheses of how environmental factors could affect ontogenetic differences (Figure 1):

1. Higher solar radiation is associated with greater ontogenetic differences. As differences in light availability diminish, ontogenetic differences decrease.
2. Ontogenetic differences in leaf traits related to nutrient availability (N_a and N_m; and nitrogen-dependent photosynthetic capacity) are associated with soil nitrogen availability and by climatic factors (MAT, mean annual temperature; MAP, mean annual precipitation) that alter soil microbial activity and nutrient uptake.
3. Low soil pH and high soil organic carbon content are associated with organic, often anoxic soil with shallow root systems, leading to smaller ontogenetic differences in leaf traits.
4. At low water availability/high aridity, due to the higher risk of hydraulic failure as the water transport pathway length increases (Nabeshima and Hiura 2004; Liu et al. 2019), adult plants develop a more robust leaf structure (greater LMA, lower N_m, lower A_m) than young trees, resulting in greater ontogenetic differences among these traits.
5. δ^{13}C reflects the balance between stomatal conductance and photosynthetic absorption, providing an accurate indicator of intrinsic water use efficiency, the physiological response of plants to drought and adaptation to different environmental conditions. Therefore, when soil water available capacity (AWC) is low, the ontogenetic differences in leaf traits related to water use, such as g_s, SD, especially δ^{13}C, are more pronounced. Adult trees with deeper and laterally more extensive root systems are more likely to have a better access to soil resources.

2 | Materials and Methods

2.1 | Literature Survey

Published research between 1989 and 2023 was identified using Web of Science, Google Scholar, ProQuest (http://www.proquest.com/products-services/dissertations/) and CNKI (http://www.cnki.net) in November 2023. The following search terms were used: ("seedling*" OR "sapling*" OR "young tree*" OR "small tree*" OR "short tree*" OR treelet* OR "juvenile tree*") AND ("adult tree*" OR "mature tree*" OR "big tree*" OR "tall tree*" OR "old tree*") OR ("tree size*" OR "tree height*" OR "tree age*" OR "diameter at breast height*" OR DBH) AND (photosyn* OR "leaf*" OR "needle*" OR "lamina*" OR "foliage*"). Search results were screened based on the titles and abstracts, after which the full text and reference list of each candidate paper were reviewed. To avoid missing relevant research, we supplemented the search with the top 200 results of Google Scholar and the top 100 results of ProQuest using the same search terms. Books, synthesis articles and non-peer-reviewed literature (e.g., proceedings of meetings and preprints) were excluded. A small number of relevant PhD and MSc dissertations were included. Authors of pertinent papers were also contacted for the provision of any unpublished trait data or missing meta-information. Details of our literature selection process are available in Figure S1.

Guided by the literature collection standard for meta-analyses outlined by Thomas and Winner (2002) (Figure S1), we defined three criteria to select publications. (1) Each study selected for inclusion evaluated only woody plants grown in the wild, not greenhouse or nursery specimens. (2) When seedlings, saplings and trees were studied simultaneously in a single study, we did not use data on seedlings. For studies that only provided data based on continuous variation in diameters at breast height (DBH) or tree height, we also excluded results for seedlings, defined as individuals shorter than 1 m or the DBH less than 3 cm. (3) Each study selected contained sufficient data for statistical analysis, including at least the sample size, trait means and standard deviation. When sample sizes were specified as a range, we used the minimum value. When measurements varied seasonally or diurnally, we used maximum leaf trait values. This was relevant primarily for physiological traits such as net assimilation rate. We acknowledge that it is not possible to completely eliminate the effects of sampling biases due to biogeographic coverage, due to uncertainties in leaf position (shade vs. sun), microhabitat differences, etc., despite our best efforts to harmonise the standards of all literature. The final list of included data sources is provided in Appendix S1.

2.2 | Data Extraction

In addition to sample sizes (*n*), we also extracted means and standard deviations (*s*) or standard errors (SE) for nine leaf traits (Table 1) for adults and saplings. Specific leaf area (SLA) measurements were converted to dry LMA (SLA^{-1}). When publications did not provide A_m, it was calculated as $A_a \cdot \text{LMA}^{-1}$ (A_a, photosynthetic rate per unit area). In these cases, *s* was recorded as one-tenth of the original standard deviation (Luo et al. 2006). Graphical data were extracted using Web Plot Digitizer (version 4.3; https://automeris.io/WebPlotDigitizer). Altogether, we obtained data for 125 species from 64 publications (Figure S2 and Table S2 for the geographic distribution of study sites and other basic information).

Climatic data, solar radiation (R), MAT and MAP were obtained from the WorldClim database (Fick and Hijmans 2017) (https://www.worldclim.org/). We employed the '*raster*', '*sp*' and '*rgdal*' packages in R ver. 4.0.2 (R Core Team 2020) to extract climate data using the geographic coordinates of each study site. Soil pH, AWC and SOC data for the top 30 cm of soil were downloaded from the Harmonized World Soil Database ver. 1.2. We categorised study sites according to AWC using the protocol developed by the Food and Agriculture Organization of the United Nations (Table S1). Soil pH was used to classify soil as acidic, neutral or alkaline (Table S1). The use of large-scale databases has certain limitations as the estimates obtained might not exactly match the actual soil characteristics. Nevertheless, soil traits were missing in many studies, and estimates of soil traits in individual studies might also vary due to methodological differences. Thus, we consider the data obtained from the global soil database as best achievable for the current analysis.

2.3 | Calculation of the Effect Size

The natural logarithm of the response ratio (lnRR) was used as the effect size to quantify the influence of age (Osenberg et al. 1999); the effect size was weighted according to the sample size throughout the analysis:

$$y_i = \text{lnRR} = \ln\left(\frac{m_a}{m_s}\right) \tag{1}$$

where m_s is the mean value of a given trait among samplings and m_a is the mean value of the trait in adult trees. The sampling variance (v_i) of lnRR was calculated as:

$$v_i = \frac{s_\text{a}^2}{n_\text{a} m_\text{a}^2} + \frac{s_\text{s}^2}{n_\text{s} m_\text{s}^2} \tag{2}$$

where n_s and n_a are trait sample sizes in saplings and adult trees, respectively, and s_s and s_a are the standard deviations of the traits in saplings and adult trees, respectively. The reciprocal of the variance was used as the weighting factor (*w*), and the average effect size (RR_+) of all study cases (*n*) was calculated by weighting each effect size as follows:

$$\text{RR}_+ = \frac{\sum_{i=1}^{n} w_i \times \text{RR}_i}{\sum_{i=1}^{m} w_i} \tag{3}$$

where RR_i is the logarithmic response ratio of case *i*, and w_i is the corresponding weighting factor.

2.4 | Statistical Analyses

The statistical analysis was conducted in the following sequence. First, we used the random-effect model to calculate the overall effect sizes across all studies. Effect sizes were considered significant if their corresponding 95% confidence intervals did not

TABLE 1 | Ontogenetic differences (the difference between adult trees and saplings, lnRR) in nine leaf traits for each plant functional type. A positive lnRR indicates that the trait value is higher in adult trees compared to saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings.

Trait	Plant functional type	Number of species (*n*)	Number of studies (*k*)	95% CI	Effect size (lnRR)
Photosynthetic rate per unit area (A_a)	All data pooled	35	51	(−0.0251, 0.2483)	0.1116 ns
	Evergreen conifer	8	11	(−0.3901, −0.1670)	−0.2786***
	Evergreen broad-leaved	5	6	(−0.1714, −0.0117)	−0.0915*
	Deciduous broad-leaved	22	34	(0.0997, 0.4579)	0.2788**
Photosynthetic rate per unit dry mass (A_m)	All data pooled	20	25	(−0.4851, −0.0655)	−0.2753*
	Evergreen conifer	4	5	(−1.0666, −0.3307)	−0.6987***
	Evergreen broad-leaved	3	3	(−0.0667, −0.0216)	−0.0442***
	Deciduous broad-leaved	13	17	(−0.4024, 0.0944)	−0.1540ns
Stomatal conductance (g_s)	All data pooled	35	47	(−0.3093, −0.0158)	−0.1626*
	Evergreen conifer	8	10	(−0.5933, −0.2709)	−0.4321***
	Evergreen broad-leaved	6	7	(−0.6905, 0.2157)	−0.2374ns
	Deciduous broad-leaved	21	30	(−0.2305, 0.1518)	−0.0393ns
Leaf dry mass per area (LMA)	All data pooled	104	153	(0.1753, 0.2815)	0.2284***
	Evergreen conifer	14	28	(0.1436, 0.2538)	0.1987***
	Evergreen broad-leaved	47	61	(0.0841, 0.2877)	0.1859***
	Deciduous broad-leaved	43	64	(0.1892, 0.3807)	0.2850***
Leaf thickness (LT)	All data pooled	50	54	(0.0766, 0.1601)	0.1183***
	Evergreen conifer	5	6	(0.0650, 0.1671)	0.1161***
	Evergreen broad-leaved	29	31	(0.0544, 0.1729)	0.1137***
	Deciduous broad-leaved	16	17	(0.0437, 0.2059)	0.1248***
Stomatal density (SD)	All data pooled	11	27	(0.1732, 0.4462)	0.3097***
	Evergreen conifer	2	11	(0.0701, 0.3094)	0.1897**
	Evergreen broad-leaved	2	2	(−0.2474, 0.1356)	−0.0559ns
	Deciduous broad-leaved	7	14	(0.2371, 0.6855)	0.4613***
Stable carbon isotope composition (δ^{13C})	All data pooled	27	50	(−0.1110, −0.0483)	−0.0797***
	Evergreen conifer	8	24	(−0.0643, −0.0302)	−0.0473***
	Evergreen broad-leaved	2	3	(−0.0527, −0.0254)	−0.0390***
	Deciduous broad-leaved	17	23	(−0.1839, −0.0518)	−0.1179***
Nitrogen content per unit area (N_a)	All data pooled	25	43	(0.1405, 0.2740)	0.2072***
	Evergreen conifer	8	20	(0.1674, 0.3227)	0.2450***
	Evergreen broad-leaved	2	2	(−0.1369, 0.1424)	0.0027ns
	Deciduous broad-leaved	15	21	(0.0563, 0.2960)	0.1762**
Nitrogen content per unit dry mass (N_m)	All data pooled	27	46	(−0.0228, 0.0612)	0.0192ns
	Evergreen conifer	9	22	(−0.0009, 0.1109)	0.0550ns
	Evergreen broad-leaved	4	4	(−0.2803, −0.0315)	−0.1559*
	Deciduous broad-leaved	14	20	(−0.0511, 0.0751)	0.0120ns

Note: Trait values are presented as means ±95% confidence intervals (CI). Significance levels: ns, $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

overlap with zero ($\alpha = 0.05$). The differences between adult trees and saplings with all traits were evaluated as a whole. Given that the fixed effects model is appropriate only when all included data originate from the same species or population (Nakagawa et al. 2017), we employed the random effects model to account for variations across studies. Due to sample size constraints, we did not apply multilevel meta-analytic models that could accommodate interspecific differences (Nakagawa and Santos 2012; Nakagawa et al. 2017).

For these analyses, we assessed the heterogeneity using formal Cochran's Q-test (Q_E), which tests whether the variability of the effect size or outcome is greater than the variability based on sampling alone. As expected in the biology meta-analysis (Nakagawa and Santos 2012), there was significant residual heterogeneity in the random-effects meta-analysis of each trait data set ($p < 0.0001$), which we tried to explain using different environmental factors (Table S1).

With the addition of impact factors (climatic and soil factors), the model used was changed from a random-effects model to a mixed-effects model. The '*glmulti*' package was used to analyse all possible combinations of impact factors in the mixed-effects model. We used omnibus tests (Q_m) to evaluate the heterogeneity of impact factor capture in each mixed-effects model; $p < 0.05$ indicated that the regulatory factor had a significant influence on the effect size.

Before we present the results of the single mixed-effects model, we use the multivariate mixed-effects model to show the ranking of all factors' effects on ontogenetic differences. We set a threshold of 0.8 for AIC to distinguish between important factors and non-important factors. The importance of each impact factor was expressed as the sum of Akaike weights of the model containing the explain variable. The ranking results of the important values of all factors are shown in Figure S3.

Because studies reporting significant results are more likely to be published, publication bias is likely to occur in any meta-analysis (Nakagawa et al. 2023). Here, we used Funnel plot and Egger tests to assess the likelihood of publication bias (Egger et al. 1997). To assess resilience to publication bias as well as the robustness of our results, we also calculated Rosenberg's fail-safe numbers, that is, the number of cases required to cause significant results to become non-significant in a meta-analysis (Rosenberg 2005). We found that our results were robust and likely not affected by publication bias, except for g_s and N_m (Table S4).

To explore the correlation between the leaf economic spectrum (LES) traits, A_m, LMA and N_m, we standardised the trait values in R using the scale function to adjust the mean value of the data to 0 and the variance to 1, making the data conform to the standard normal distribution (Figure S4a,b). The data that had paired A_m and N_m values represented a small and non-representative subset, so they were not included in the analysis.

Statistical analyses and plot generation were carried out using the '*metafor*' (Viechtbauer 2010) and '*ggplot2*' (Wickham 2016) packages in R ver. 4.0.2 (R Core Team 2020).

3 | Results

3.1 | General Patterns

Overall, LMA, LT, SD and N_a were significantly higher for adult trees than for saplings ($p < 0.01$; Table 1), while A_m and g_s were significantly lower ($p < 0.01$; Table 1). Because δ^{13}C had negative values in all cases, negative lnRR of δ^{13}C values indicates that δ^{13}C values were higher in adult trees. A_a and N_m did not differ between saplings and adult trees ($p > 0.05$).

Values of lnRR for A_m, g_s, LMA, LT and δ^{13}C were similar for the three PFTs (Table 1). A_a was higher in adult trees than in saplings in deciduous broad-leaved species but was lower in evergreen adults than in saplings. SD was higher in adults in coniferous ($p < 0.01$) and deciduous species ($p < 0.001$) but was not significantly different between evergreen broad-leaved adults and saplings ($p > 0.05$). N_a was lower in saplings only in deciduous broad-leaved species ($p < 0.01$), while N_m was lower in adult trees only in evergreen broad-leaved species ($p < 0.01$).

3.2 | Solar Radiation (R) Effects on Ontogenetic Differences in Leaf Traits (H1)

We evaluated six environmental factors (Table S1). R correlated with lnRR values for A_a ($p < 0.05$), SD ($p < 0.001$), N_m ($p < 0.05$) and δ^{13}C ($p < 0.0001$; Figure 2; Table S3). Values of A_a and N_m were lower in saplings than adults under low R, but the relationship was reversed with increasing R (Figure 2a,i). Differences in the values of lnRR for SD and δ^{13}C between adults and saplings were greatest under relatively low R (Figure 2f,g).

3.3 | Impacts of Climatic Drivers on Ontogenetic Differences in Leaf Traits (H2)

MAT was associated with significant differences in g_s ($p < 0.05$), LMA ($p < 0.05$) and LT ($p < 0.001$) between saplings and adult trees (Figure 3b–d). Values of lnRR for g_s, LMA and LT were the highest under low MAT (Figure 3b–d). MAP had a significant influence on leaf nitrogen content ($p < 0.05$); however, under high MAP, N_a was higher in adults than in saplings (Figure 4h), while N_m was higher in saplings than in adults (Figure 4i).

3.4 | Ontogenetic Differences in Leaf Traits in Relation to Soil Characteristics (H3–H5)

Values of lnRR for LT ($p < 0.001$) increased, whereas those for SD ($p < 0.05$) decreased with increasing SOC content, respectively (Figure 5e,f). AWC correlated with ontogenetic differences in LT ($p < 0.05$) and SD ($p < 0.05$), and both LT and SD were higher in adult trees regardless of AWC class (Figure 6). Soil pH correlated with A_a ($p < 0.05$), LT ($p < 0.05$), SD ($p < 0.05$), N_a ($p < 0.05$) and N_m ($p < 0.05$) (Figure 7).

3.5 | Relationships Between LES Traits

LMA was significantly and negatively correlated with A_m ($p = 0.0045$); however, this effect was only significant among adult trees ($p = 0.0412$) and not saplings ($p = 0.0574$) (Figure S4a). We found a significant negative correlation between LMA and N_m in both adults ($p < 0.001$) and saplings ($p = 0.0011$) (Figure S4b). The directionality of this relationship varied across PFTs (Figure S4c), with a significant positive

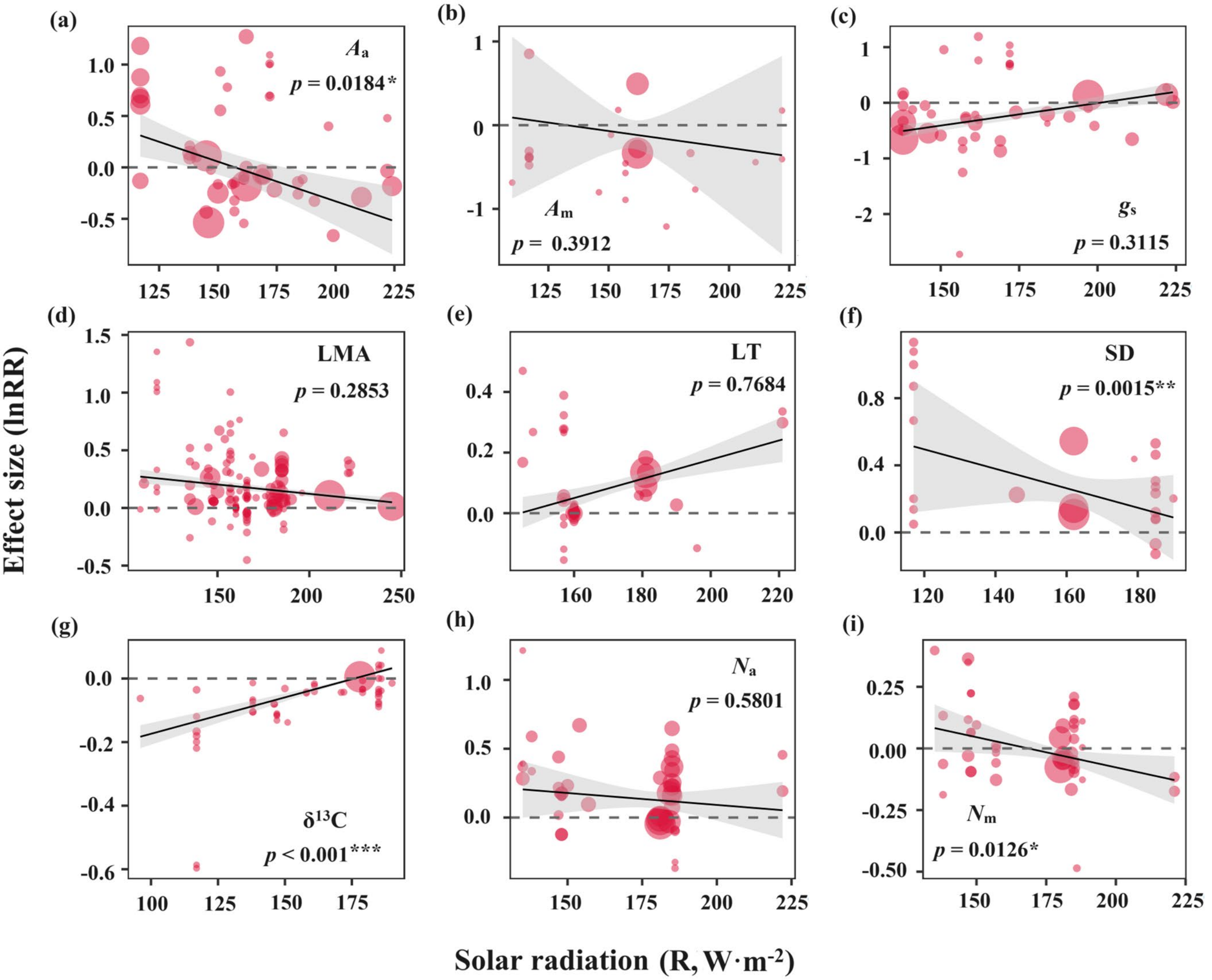

FIGURE 2 | Effects of solar radiation (*R*) on ontogenetic differences (the difference between adult trees and saplings, lnRR) in leaf traits (a-i). Point size is proportional to observation weight (1/SE). 95% confidence intervals of the fitting curve are indicated by grey shading. The dashed grey line demarcates zero effect size. $\delta^{13}C$, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density. $\mathrm{lnRR} = \ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a trait in saplings and m_a is the mean value of the trait in adult trees. A positive lnRR indicates that the trait value is higher in adult trees than in saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings. The effects of R on lnRR were evaluated by a mixed-effects model. The figure shows the linear trend of a simple linear model. Significance was assessed at the $p < 0.05$ level, from the mixed-effect model of various factors (Table S3). *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

correlation between the two variables in evergreen broad-leaved trees ($p = 0.0026$) and a significant negative correlation in evergreen conifers ($p < 0.001$).

4 | Discussion

4.1 | General Patterns

Our findings are consistent with some of the conclusions of an earlier meta-analysis by Thomas and Winner (2002): LMA was higher and A_m was lower for adult trees than for saplings (Table 1). In addition, ontogenetic differences in A_a and A_m of deciduous broad-leaved tree species were opposite to one another, similar to the findings of the original study (Thomas and Winner 2002). Our meta-analysis also revealed that LT, SD and N_a were higher and that $\delta^{13}C$ was lower for adult trees than for saplings (Table 1). However, in contrast with the findings of the previous study, g_s was significantly higher in young trees than in adults (Table 1) (Thomas and Winner 2002). This may have been due to the fact that our study included more data from arid areas. The lower A_m observed in mature trees could be attributed to a greater allocation of resources towards structural support, whereas younger trees prioritised the investment in photosynthetic tissues to achieve higher photosynthetic rates. In deciduous broad-leaved species, the higher A_a in adult trees was associated with larger and thicker leaves, enabling more efficient utilisation of environmental resources during the growing season. The increased N_a in mature trees was primarily due to thicker leaves with higher LMA.

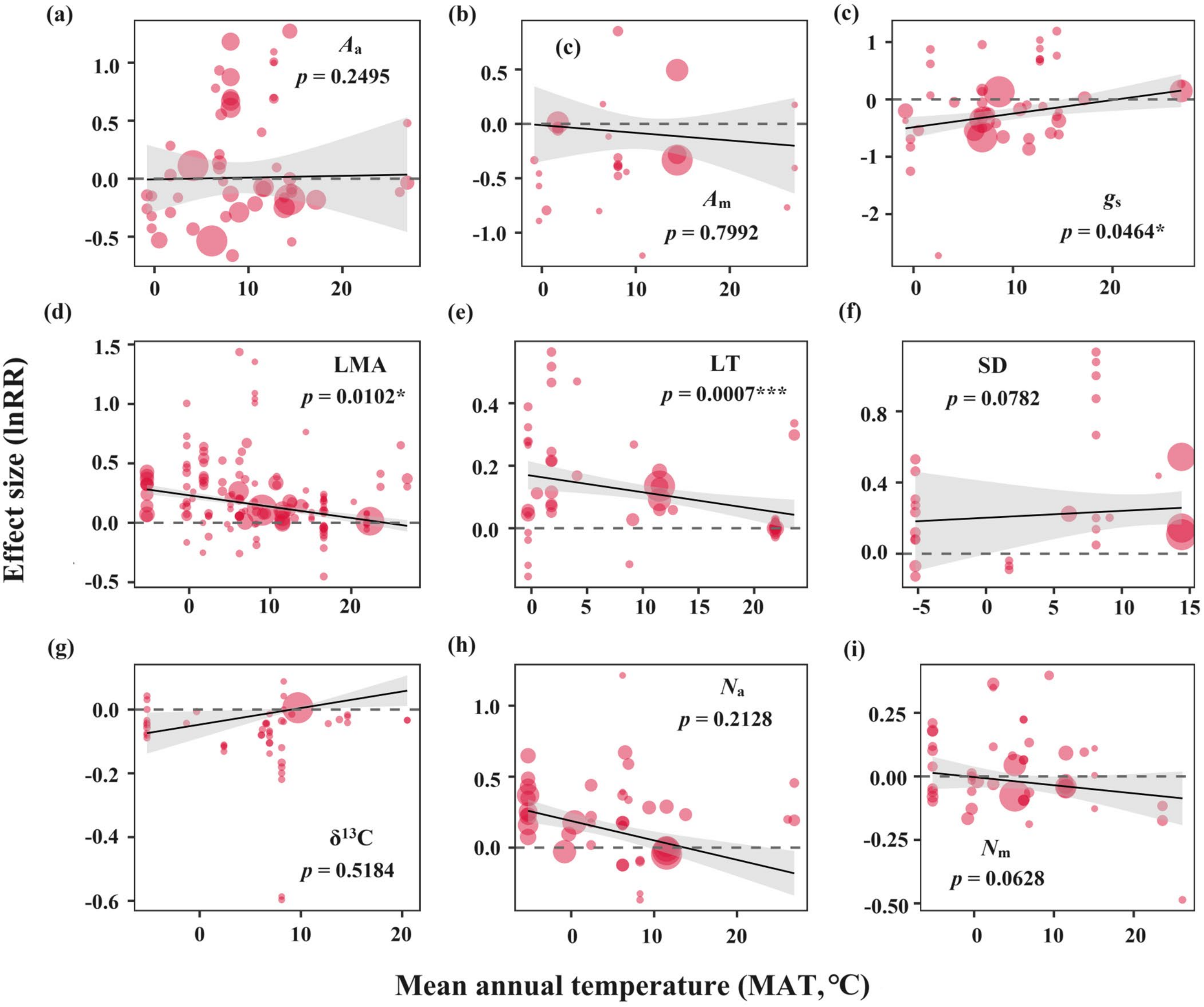

FIGURE 3 | Effects of mean annual temperature (MAT) on ontogenetic differences (the difference between adult trees and saplings, lnRR) in leaf traits (a-i). Point size is proportional to observation weight (1/SE). 95% confidence intervals of the fitting curve are indicated by grey shading. The dashed grey line demarcates zero effect size. $\delta^{13}C$, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density. $\mathrm{lnRR} = \ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a trait in saplings and m_a is the mean value of the trait in adult trees. A positive lnRR indicates that the trait value is higher in adult trees than in saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings. The effects of MAT on lnRR were evaluated by a mixed-effects model. The figure shows the linear trend of a simple linear model. Significance was assessed at the $p < 0.05$ level, from the mixed effect model of various factors (Table S3). $^*p < 0.05$; $^{***}p < 0.001$.

4.2 | Solar Radiation Effects on Ontogenetic Differences in Leaf Traits (H1)

Thomas and Winner (2002) demonstrated that A_a was higher for adult trees than for saplings when the upper canopy leaves of adult trees and leaves of understorey saplings were compared. However, there was no significant difference when the upper canopy leaves of adult trees were compared to leaves from saplings growing in the open habitats, suggesting that light availability is a critical factor for size-dependent variation in leaf traits. Leaf traits can change depending on growth irradiance. For example, LMA, A_a and nitrogen content per unit leaf area (N_a) are higher in leaves grown under relatively high light (Björkman 1981; Gulmon and Chu 1981; Niinemets et al. 2015; Rijkers et al. 2000). As reported by Thomas and Winner (2002), we found that light environment (solar radiation, R) was the most important driver of ontogenetic differences (Figure 2). R was not only related to differences in traits related to photosynthesis (A_a and N_m) but influenced $\delta^{13}C$ and SD, traits which are related to water use. With increasing size, plant resource capture might increase in proportion to size (size-dependent symmetric competition) or disproportionately more with increasing size (asymmetric competition). In particular, light competition is strongly asymmetric as taller individuals shade the lower individuals and gain disproportionately more resources than their share in community total biomass (Forrester 2019; Weiner 1990). However, photosynthetic light saturation is achieved at 30%–50% of maximum light availability, and this might reduce differences in

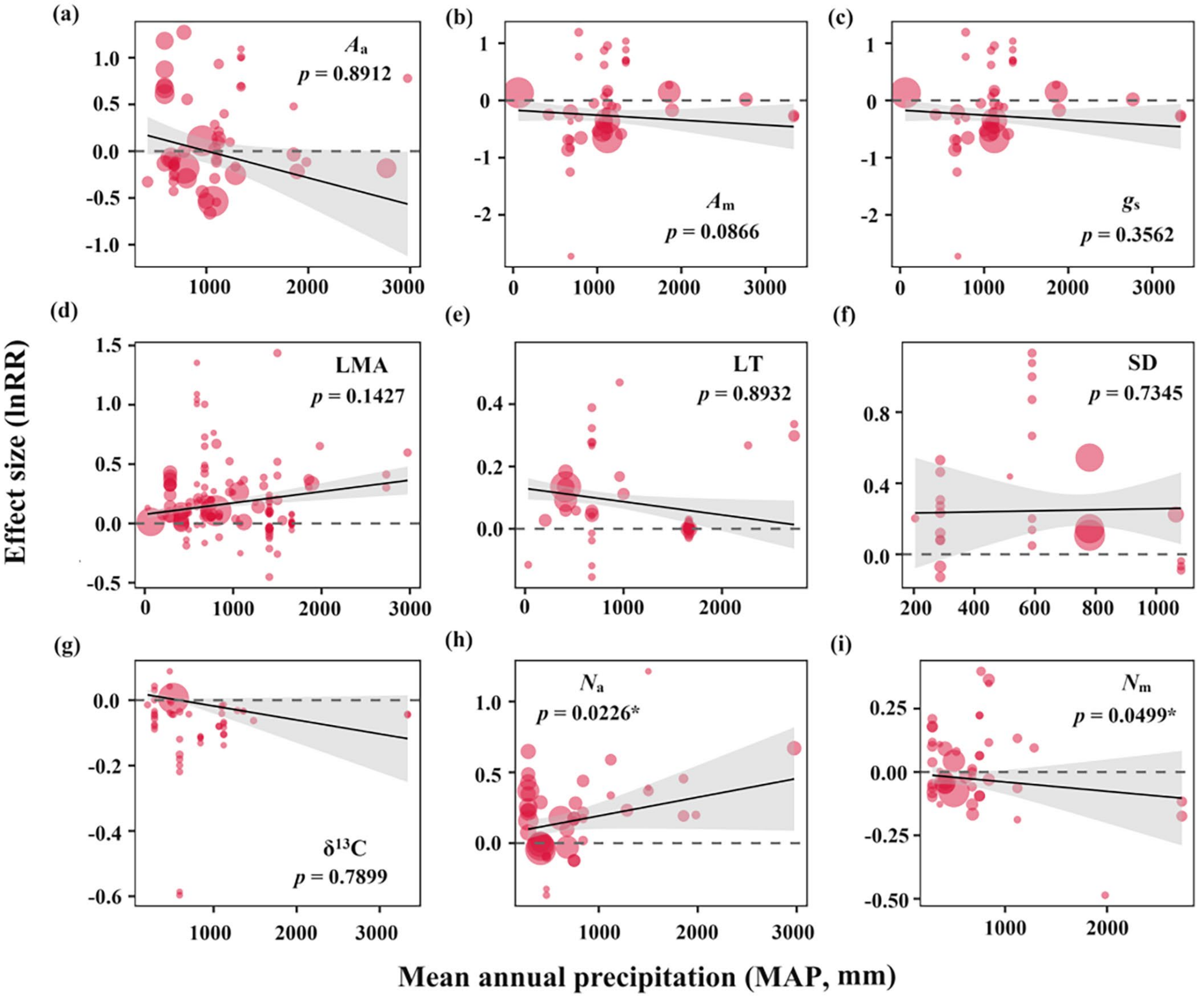

FIGURE 4 | Effects of mean annual precipitation (MAP) on ontogenetic differences (the difference between adult trees and saplings, lnRR) in leaf traits (a-i). Point size is proportional to observation weight (1/SE). 95% confidence intervals of the fitting curve are indicated by grey shading. The dashed grey line demarcates zero effect size. $\delta^{13}C$, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density. $\text{lnRR} = \ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a trait in saplings and m_a is the mean value of the trait in adult trees. A positive lnRR indicates that the trait value is higher in adult trees than in saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings. The effects of MAP on lnRR were evaluated by a mixed-effects model. The figure shows the linear trend of a simple linear model. Significance was assessed at the $p < 0.05$ level, from the mixed-effects model of various factors (Table S3). $^*p < 0.05$.

photosynthesis between younger and older trees. In addition, relatively high R and associated higher leaf temperatures might shorten the leaf payback time, allowing construction of higher photosynthetic activity leaves in mature trees (Niinemets 2001).

4.3 | Impacts of Climatic Drivers on Ontogenetic Differences in Leaf Traits (H2)

The effects of MAT on leaf structure can also be explained by the leaf payback period (Niinemets 2001; Poorter 1994; Williams et al. 1989). Here, MAT was an important driver of ontogenetic changes in LMA and LT (Figure 3), and the effects of MAP on ontogenetic differences in N_a and N_m are consistent with hypothesis (2) (Figures 1 and 4; Table S3). Nutrient contents of leaves are more sensitive to drought stress compared to other plant organs as leaves are most distant from roots, and accordingly, MAP-dependent changes in mass flow and transpiration rate impact the leaves the most (He et al. 2024). This is because drought restricts stomatal function, affecting the cycling, absorption and utilisation of nitrogen (Heckathorn et al. 1997; Streeter 2003).

LT is a component of LMA, LMA = LT * LD (leaf tissue density) and lower lnRR of LT indicates that growth and photosynthesis are more limited in adult trees than in young trees under water-limited conditions (Koch et al. 2004; Ryan and Yoder 1997). In our study, the ontogenetic differences of LMA and LT in

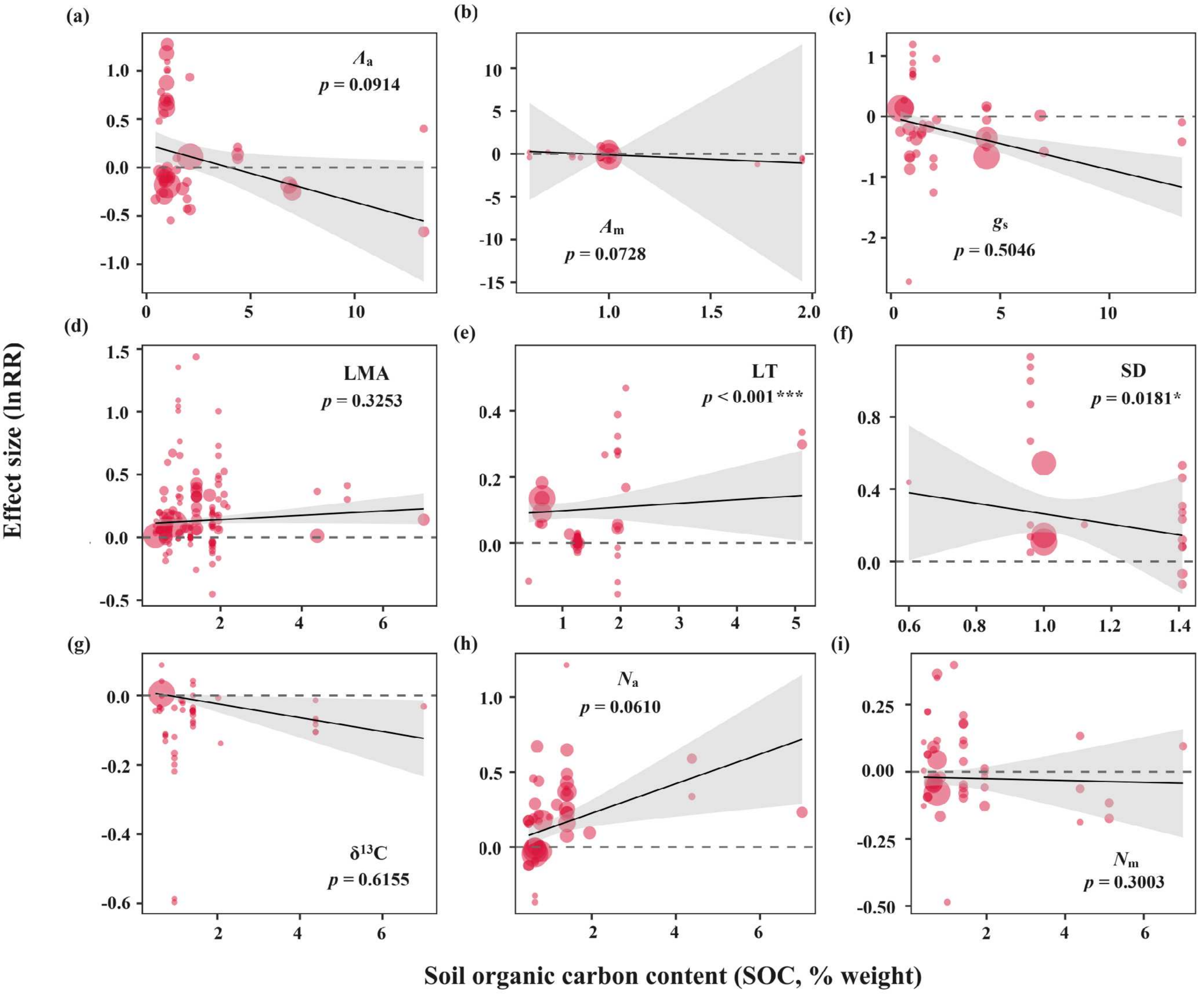

FIGURE 5 | Effects of soil organic carbon content (SOC) on ontogenetic differences (the difference between adult trees and saplings, lnRR) in leaf traits (a-i). Point size is proportional to observation weight (1/SE). 95% confidence intervals of the fitting curve are indicated by grey shading. The dashed grey line demarcates zero effect size. $\delta^{13}C$, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density. $\mathrm{lnRR} = \ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a trait in saplings and m_a is the mean value of the trait in adult trees. A positive lnRR indicates that the trait value is higher in adult trees than in saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings. The effects of SOC on lnRR were evaluated by a mixed-effects model. The figure shows the linear trend of a simple linear model. Significance was assessed at the $p < 0.05$ level, from the mixed-effect model of various factors (Table S3). *$p < 0.05$; ***$p < 0.001$.

different functional types were highly consistent (Table 1). Griffith et al. (2016) proposed that the higher LMA of adult trees is caused by leaf cell wall thickening and higher inputs of non-structural carbon, which also results in higher LT in adult trees (De La Riva et al. 2016; Griffith et al. 2016; Niinemets 1997). The thickness of palisade parenchyma increases with light (Bongers and Popma 1988).

4.4 | Ontogenetic Differences in Leaf Traits in Relation to Soil Characteristics (H3–H5)

Our findings that LT and SD were the traits most affected by soil factors are inconsistent with the hypotheses (3–5) (Figures 5–7; Table S3). We observed that a relatively high SOC was associated with higher LT and lower SD in adult trees (Figure 5). However, these correlations do not necessarily imply that SOC directly influences the ontogenetic differences in these traits. Climate seasonality and extremes are closely related to stomatal distribution (Liu et al. 2023), and correlations of SOC with other climatic drivers might have resulted in a correlation between SOC and SD. Light is a unidirectional resource and light absorption is thus advantageous for taller plants, whereas plant height itself does not influence soil nutrient capture ability, but taller plants typically also have more extensive and deeper root systems to avoid toppling. Nevertheless, competition for nutrients might be more symmetric than competition for light. In addition, since SOC is closely related to the rhizosphere, soil microorganisms (Xu et al. 2021) and nutrient cycling (Quinton et al. 2010), these may be explained by plants' internal carbon to nutrient balance.

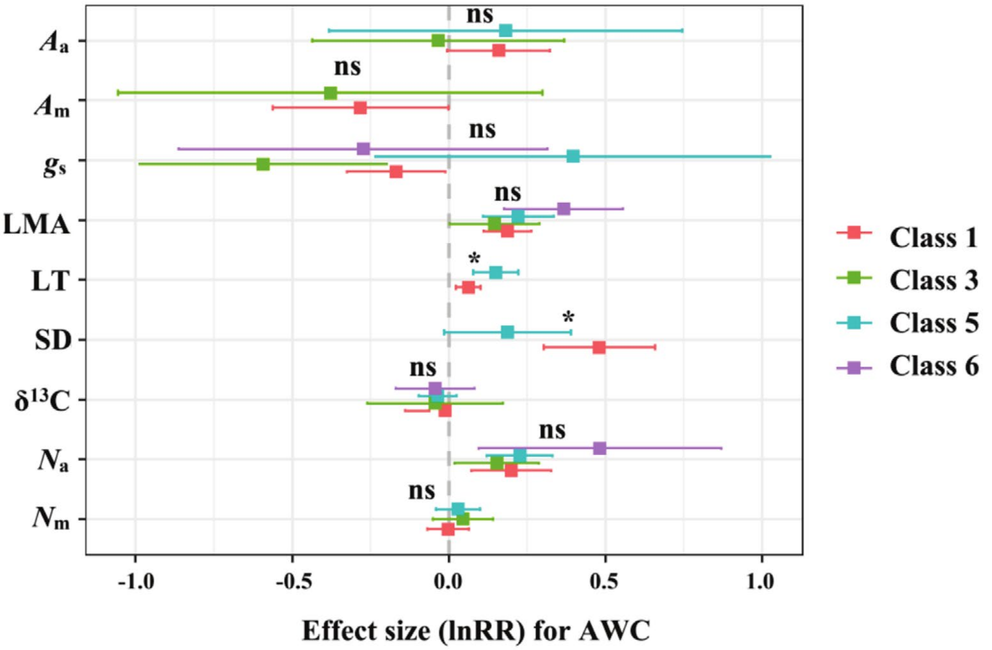

FIGURE 6 | Effects of soil available water capacity (AWC) on ontogenetic differences (the difference between adult trees and saplings, lnRR) in leaf traits. Squares indicate the estimated effect size, and horizontal lines represent the 95% confidence intervals. The protocol developed by the Food and Agriculture Organization of the United Nations was used to classify AWC into classes 1–7 (0 to 150 mm m^{-1}, Table S1), and different line colours correspond to different AWC levels. δ^{13}C, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density. lnRR = $\ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a trait in saplings and m_a is the mean value of the trait in adult trees. A positive lnRR indicates that the trait value is higher in adult trees compared to saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings. The effects of AWC on lnRR were evaluated by a mixed effects model. Asterisks indicate significant differences among AWC classes (*$p < 0.05$, ns = not significant).

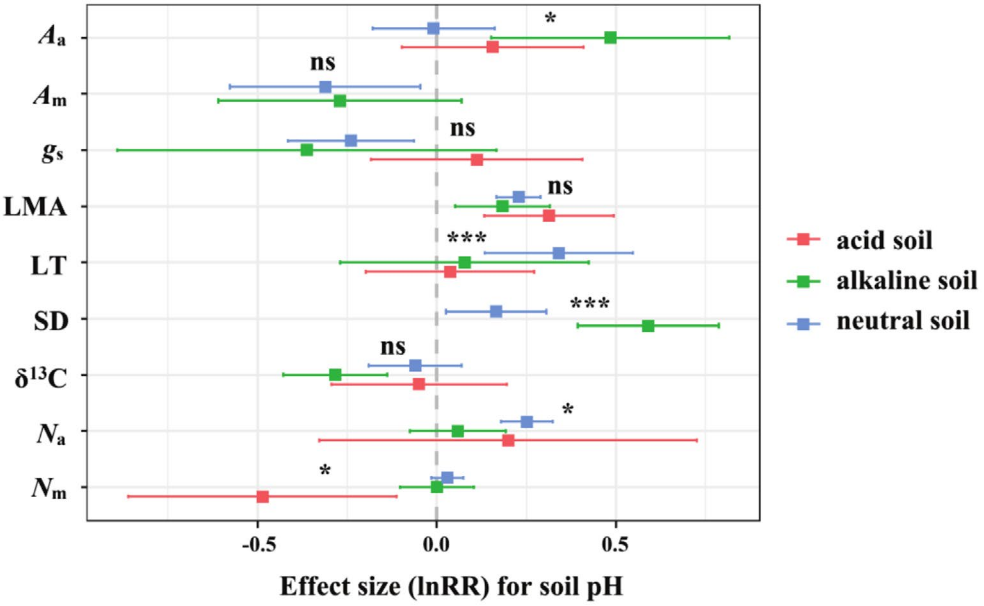

FIGURE 7 | Effects of soil pH on ontogenetic differences (the difference between adult trees and saplings, lnRR) in leaf traits. Squares indicate the estimated effect size, and horizontal lines represent the 95% confidence intervals. δ^{13}C, stable carbon isotope composition; A_a, photosynthetic rate per unit area; A_m, photosynthetic rate per unit dry mass; g_s, stomatal conductance; LMA, leaf mass per area; LT, leaf thickness; N_a, nitrogen content per unit area; N_m, nitrogen content per unit mass; SD, stomatal density. lnRR = $\ln\left(\frac{m_a}{m_s}\right)$, m_s is the mean value of a trait in saplings and m_a is the mean value of the trait in adult trees. A positive lnRR indicates that the trait value is higher in adult trees compared to saplings, whereas the negative lnRR indicates that the trait value is lower in adult trees relative to saplings. The effects of pH on lnRR were evaluated by a mixed-effects model. Asterisks indicate significant differences among soil pH classes (*$p < 0.05$, ***$p < 0.001$, ns = not significant).

As tree growth rate gradually slows down with increasing size (Bialic-Murphy et al. 2024), nutrient requirement is expected to decrease as well, and thus at a given soil nutrient availability, saplings are expected to be relatively more nutrient-limited and more sensitive to low soil nutrient availability than adult trees.

AWC did not drive differences in traits related to water use between saplings and adults, but it was related to the ontogenetic dependence of LT and SD (Figure 6; Table S3). As a complex indicator, soil pH can reflect both large-scale changes in climatic conditions, such as drought, and various processes related to nutrient availability and soil microbial communities (Joswig et al. 2022; Slessarev et al. 2016). Here, we found that pH is an important factor affecting the size dependence of plant traits, and its influence on values of lnRR for LT and SD was more prominent than that of other factors (Figure 7; Table S3). The soil pH can not only directly affect nutrient availability, for example, availability of cations but also indirectly affect via altering soil microbial activity, with potentially major effects on plant growth (Philippot et al. 2024; Zhong et al. 2023). In turn, soil microbial activity, litter decomposition and root exudation may affect soil pH (Liu et al. 2022; Philippot et al. 2024), and thus, pH might feedback on ontogenetic differences of leaf traits. How soil pH interacts with leaf functional traits and the mechanisms underlying the influence of soil properties on plant growth need to be studied further.

Stomatal density is one of the stomatal traits most affected by environmental factors (Xie et al. 2022). Larger SD in adult trees (Table 1) may be due to differences in tree height. Similarly, Zhou et al. (2012) have found that the number of stomata and stomatal rows of *Pinus koraiensis* increased with tree age, albeit a maximum SD was found at an intermediate age and SD further declines in the oldest trees. The hydraulic path length increases in adult trees, and this might result in increased stomatal limitation and reduced carbon sequestration (Hubbard et al. 1999; Nabeshima and Hiura 2004). Nevertheless, this can be compensated by increased xylem cross-sectional area (Sperry et al. 2002; Wang et al. 2019), and greater SD in such a case would allow a higher transpiration rate and carbon fixation. Furthermore, mature trees tend to have a relatively high capacity to avoid drought because of their deep rooting depth and their ability to adjust their water use efficiency—greater capacity to avoid drought by deeper rooting depth and adjusting their water use efficiency (Cavender-Bares and Bazzaz 2000; Sun et al. 2021). In contrast, younger trees may only be able to resist drought by closing their stomata, inevitably reducing their carbon uptake (Cavender-Bares and Bazzaz 2000). Adult trees tend to close their stomata to suppress transpiration. Beerling and Woodward (1996) demonstrated that the stomatal sensitivity of young trees to environmental conditions was significantly lower than that of adults. Other work identified similar ontogenetic differences in g_s in response to drought in *Quercus rubra* (Cavender-Bares and Bazzaz 2000).

4.5 | Relationships Between LES Traits

Our study provides further evidence for the broad applicability of LES with some specific patterns. We found that LMA was negatively correlated with A_m and N_m in adult trees, consistent with the LES model. The correlation between LMA and A_m in saplings was not significant (Figure S4a, Figure S4b; Wright et al. 2004). This is mainly because plants need to adjust resource allocation and nutrient utilisation strategies under nitrogen limitation (Hikosaka 2004, 2016). The significant negative correlation between LMA and N_m reflects the circumstance that more robust leaves have a greater fraction of support tissue (Onoda et al. 2017). However, we found that the relationship between LMA and N_m was completely reversed for different PFTs (Figure S4c). This might be indicative of differences in the contributions of leaf density and thickness on LMA variation; increases in thickness should not necessarily scale with enhanced investments in support tissues, while increases in density are typically associated with thicker cell walls and increased investment in mechanical cells (Niinemets 1999; Wuyun et al. 2024).

5 | Conclusions

Understanding the complex mechanisms of tree development in relation to biological and abiotic factors is needed to predict the modifications of tree performance with aging. In this study, we analysed nine leaf functional traits across 125 species of adult trees and saplings from diverse global environmental gradients to explore tree size-dependent changes in leaf functional traits. Our findings highlight solar radiation as a key factor influencing ontogenetic differences in leaf traits, especially in traits characterising photosynthesis and water use. Although significant for some trait differences, mean annual precipitation had smaller impacts on the ontogenetic differences between adult trees and saplings. Soil factors, particularly soil pH, also emerged as significant drivers of ontogenetic differences. Among the traits studied, leaf thickness (LT) and stomatal density (SD) were the most sensitive to ontogenetic development. Our research contributes to the understanding of physiological and ecological changes throughout tree development and the adaptability of tree structure and function to environmental conditions.

Author Contributions

Z.L., Z.Z. and Ü.N. conceived the ideas. Q.H., L.Z., D.H., E.Y. and G.J. provided some data. Z.Z. analysed the data. Z.Z., K.H., Ü.N. and J.C.-B. interpreted the results. Z.Z. wrote the first draft of the manuscript, and all authors, including MGH, contributed to revisions and gave final approval for publication.

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Ethics Statement

The authors confirm that they have adhered to the ethical policies of the journal.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available at https://figshare.com/s/7c3a6282a39c7ca37100.

Biosketch

The authors are researchers with diverse backgrounds, including ecology, plant science and soil environment studies, whose research has helped to better understand the different scale impacts of global change on plants. Through the results obtained, the authors hope to advance the current research on plant response to environmental change and provide a good basis for the protection of global ecosystems and forest vegetation.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70133-sup-0001-Supinfo.docx. **Data S2:** geb70133-sup-0002-Supinfo1.zip. **Appendix S1:** geb70133-sup-0003-Appendix1.docx.