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Variable thermal plasticity of leaf functional traits in Andean tropical montane forests

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Abstract

Tropical montane forests (TMFs) are biodiversity hotspots and provide vital ecosystem services, but they are disproportionately vulnerable to climate warming. In the Andes, cold-affiliated species from high elevations are being displaced at the hot end of their thermal distributions by warm-affiliated species migrating upwards from lower elevations, leading to compositional shifts. Leaf functional traits are strong indicators of plant performance and at the community level have been shown to vary along elevation gradients, reflecting plant adaptations to different environmental niches. However, the plastic response of such traits to relatively rapid temperature change in Andean TMF species remains unknown. We used three common garden plantations within a thermosequence in the Colombian Andes to investigate the warming and cooling responses of key leaf functional traits in eight cold- and warm-affiliated species with variable thermal niches. Cold-affiliated species shifted their foliar nutrient concentrations when exposed to warming, while all other traits did not significantly change; contrastingly, warm-affiliated species were able to adjust structural, nutrient and water-use efficiency traits from acquisitive to conservative strategies in response to cooling. Our findings suggest that cold-affiliated species will struggle to acclimate functional traits to warming, conferring warm-affiliated species a competitive advantage under climate change.

KEYWORDS
leaf functional traits, plasticity, thermal acclimation, tropical montane forests

1 | INTRODUCTION

Global temperatures are rising, projected to reach 1.5°C above preindustrial levels between 2030 and 2052 if warming continues at the current rate of 0.2°C per decade (Allen et al., 2019). In tropical South America, air temperatures over the last 35 years have increased by up to 0.5°C per decade (Harris et al., 2014) and by 2040, the likelihood of heatwave conditions—defined as mean monthly temperatures beyond the three standard deviation threshold (3-sigma events)—in the tropics during the boreal summer months (June, July and August) rises to 50% even under a low emission scenario of RCP2.6 (Coumou & Robinson, 2013). Consequently, and counter to some expectations, the tropics will be the first part of the globe to experience mean temperatures beyond the bounds of recent climate variability. At high

elevations below the snowline, factors such as decreasing cloud cover and increasing atmospheric water vapour concentration accentuate heating (Pepin et al., 2015), resulting in high rates of warming in tropical mountainous areas, similar to those at the poles (Aguilar-Lome et al., 2019). For example, western Andean slopes above 4000 m a.s.l could warm by almost 5°C by the end of the century under a medium-high emissions scenario (Urrutia & Vuille, 2009). Following the stable climatic conditions experienced in the tropics during the Holocene (Janzen, 1967; Perez et al., 2016), species in tropical montane forests (TMFs) have become adapted to little seasonality in air temperature with large diurnal variations. However, naturally-occurring changes in temperature of 3.5–4.9°C per km of elevation lost or gained (Navarro-Serrano et al., 2020) results in variable thermal ranges of TMF species, with those exposed to higher variability having broader distributions (Montaño-Centallas et al., 2023). It is thus unclear whether species in these ecosystems will be able to acclimate to rapid warming, or if they will be highly sensitive to such changes (Allen et al., 2019; Chan et al., 2016; Harris et al., 2014; Vasseur et al., 2014).

Andean TMFs are ecosystems of global importance. They are home to exceptional biodiversity (Bruijnzeel et al., 2010; Myers et al., 2000), provide drinking water and hydroelectricity for millions of people in South America (Anderson et al., 2011; Josse et al., 2009) and are an enormous carbon store due to the large area they occupy (Spracklen & Righelato, 2014). It has even been suggested that the Andean TMF carbon sink may now be stronger per unit of area than that of mature lowland forests in the Amazon, possibly due to a weakening of the Amazonian carbon sink (Brienen et al., 2015; Duque et al., 2021; Hubau et al., 2020). The large capacity to acquire and store carbon in these ecosystems is, however, likely to be strongly impacted by future climate change (Nottingham et al., 2015). Maximum temperatures in the northern tropical Andes have increased 1.2–6.6°C between 1950 and 2007 (Ruiz-Carrascal et al., 2012); rapid warming of Andean forests has been linked to changes in species composition through a process known as 'thermophilisation', where warm-affiliated species, with thermal niches conforming to hotter conditions in the lowlands, are hypothesised to be advancing upslope as temperatures rise, displacing cold-affiliated species that are more abundant at higher elevations (Duque et al., 2015; Fadrique et al., 2018; Feeley et al., 2011, 2012; Rehm & Feeley, 2015). Indeed, experimental evidence from grassland sites in southwestern Norway suggests that plant species are more able to colonise habitats where air temperatures are lower than the thermal mean of their natural distributions (Lynn et al., 2021), while the risk of mortality increases as air temperatures become increasingly higher than their geographical distribution-based estimate of thermal optima (T_{opt}). This shift towards heat-tolerant taxa in plant communities has also been observed across North, Central and South America (Feeley et al., 2020; Rosenblad et al., 2023), suggesting that the community composition of Andean TMFs will keep changing under continued warming. There is, however, uncertainty surrounding the extent to which the form and functioning of these ecosystems will be altered by rising temperatures.

Leaves are one of the most important interfaces between plants and their surrounding environment due to their essential roles in sunlight absorption, carbon assimilation, energy exchange with the atmosphere and thermoregulation (Fritz et al., 2018). Foliar structure, nutrient content and water-use efficiency (WUE) during photo-synthesis (i.e., the ratio of carbon assimilation to water loss through transpiration) affect whole plant performance and are important indicators of how plants will respond to changes in environmental conditions. Structural traits such as leaf mass per unit area (LMA) and leaf (area) are strongly linked to growth (Bartholomew, 2021), leaf thickness (LT) and leaf width (LW) are important for leaf thermo-regulation (Fauset et al., 2018), while leaf dry matter content (LDMC) is related to leaf carbon investment (Wilson et al., 1999). Foliar nutrients, particularly nitrogen (N) and phosphorus (P) are essential in leaf-level photosynthesis (Domingues et al., 2015; Evans, 1989), and are thus also connected to water-use efficiency traits, such as the internal concentration of the isotope ^{13}C fixed by C_3 plants ($\delta^{13}C$) and the marginal carbon cost of water-use (g_1; Medlyn et al., 2017). All foliar traits vary according to environmental conditions: plants growing under cold, cloudy and windy environments such as those of TMFs (Eller et al., 2020) tend to be more conservative in their resource-use to successfully grow under those conditions; on the other hand, the warmer, sunnier and more sheltered conditions in tropical forest lowlands allow plants to be more acquisitive in their growth strategies (Feng et al., 2023; Onoda et al., 2017; Poorter & Bongers, 2006; Poorter et al., 2009; Reich, 2014; Wright et al., 2004). Variation in leaf structural, nutrient and water-use efficiency traits with climate provides an excellent indicator of a plant resource-use. Observed variation in leaf traits across species indicate that plants suited to warmer conditions have larger, thinner leaves that are less efficient in their water usage, reflecting more acquisitive strategies, while the opposite is true of those growing in colder environments (Feng et al., 2023; Poorter et al., 2009; Reich, 2014).

In the tropical Andes, community-level measurements of structural traits such as LA and LW, have been shown to increase or remain similar with warming/decreasing elevation, while LT decreases to give lower LMA values at warmer, lower elevations (Homeier et al., 2021; Llerena-Zambrano et al., 2021; Martin et al., 2020; Ochoa-Beltrán et al., 2021; van de Weg et al., 2009). Foliar N and P contents expressed in dry weight basis (N_m and P_m) have often been found to be higher in lowland forests than those in the cooler highlands, while values expressed in leaf area basis (N_a and P_a) have shown less clear patterns of variation with elevation (Homeier et al., 2021; Martin et al., 2020; van de Weg et al., 2009). Photosynthetic WUE, expressed as $\delta^{13}C$ (Farquhar et al., 1989; Vitousek et al., 1990), has been shown to be lower at warmer, low-elevation locations along an Andean elevation gradient (Martin et al., 2020), indicating a lower photosynthesis to transpiration ratio. This is because plants tend to become more wasteful in their water usage with warming and so potentially less water-use efficient, as higher photosynthetic rates require more open stomata for leaf gas exchange (Cowan & Farquhar, 1977; Medlyn et al., 2017). These community-level changes suggest that plants generally shift their functional traits towards more acquisitive resource usage with decreasing elevation (e.g., Bahar et al., 2017; van de Weg et al., 2012), but it remains uncertain whether leaf traits from the same species will

shift from conservative to acquisitive, therefore displaying thermal acclimation, when individuals are displaced from their T_{opt} due to rapid climatic change.

Understanding the impacts of warming on individual species along elevation gradients is confounded by the fact that plant communities also change with altitude. Specifically, tropical elevation studies that collect measurements from the most abundant species growing at sites at different elevations and temperatures primarily reflect the adaptation of leaf traits to specific climate niches and are unable to test directly for thermal acclimation (Báez et al., 2022; Crous et al., 2022; Homeier et al., 2021; Martin et al., 2020; van de Weg et al., 2012). To circumvent this limitation, individuals from the same species can be exposed to temperatures above and below their T_{opt}. The response to warming of certain functional traits—namely LMA and leaf N and P content—has been tested in some thermal acclimation studies of tropical species in conjunction with photosynthesis and respiration in growth chambers (Cheesman & Winter, 2013; Crous et al., 2018; Scafaro et al., 2017) and under field conditions (Dusenge et al., 2021), while a recent study from the Albertine Rift in Rwanda was the first to explicitly investigate the effect of warming under field conditions on leaf functional traits of the same species transplanted to different experimental sites/temperatures (Manishimwe et al., 2022). Although variation of leaf functional traits across elevation in Andean trees has been reported (e.g., Bahar et al., 2017; van de Weg et al., 2012), the in situ thermal plasticity of such traits within the same species remains unknown.

To acclimate successfully to warmer temperatures, individual tree species in Andean TMFs will need to acclimate their gas exchange physiology—rates of photosynthesis and respiration—and demonstrate sufficient plasticity in a variety of leaf structural, chemical and water-use efficiency traits to maintain or improve their fitness (Crous, 2019). However, it remains highly uncertain whether any or all taxa are capable of this. In addition, plasticity may differ among traits, with those associated with lower investment costs, such as leaf nutrient contents and WUE, likely be more plastic than structural traits which can only be altered substantially following new leaf growth (Shiodera et al., 2008; Valladares et al., 2000). More 'favourable' environments (von Humboldt & Bonpland, 1805; Nottingham et al., 2018; Whittaker, 1960) allow for a wider range of traits and species to persist, with this higher phenotypic variability potentially increasing the chances of adjustment to changing conditions. Conversely, less favourable environments with colder temperatures, less insolation and higher wind speeds (in this case, at higher elevation) result in smaller subsets of traits and species, decreasing the available phenotypic plasticity and ability to shift in response to change (Anderson et al., 2021; Pigliucci et al., 2006; Spasojevic et al., 2014). For example, tropical lowland environments might arguably be conducive to greater plant performance because the higher temperatures, water availability and solar radiation stimulate plant growth (Currie et al., 2004; Spasojevic et al., 2014). Under this hypothesis, we expect that, at the species level, warm-affiliated species, originating from environments which allow for a

wider range of phenotypes, would have higher leaf functional trait plasticity and greater capacity for thermal acclimation; on the other hand, cold-affiliated species coming from harsher environments would exhibit lower thermal plasticity and acclimation potential, caused by lower phenotypic variability (Currie et al., 2004; Spasojevic et al., 2014). If warm-affiliated species are able to acclimate their leaf traits to changing temperature, this could confer upon them a competitive advantage over cold-affiliated species (Lynn et al., 2021; Wittemann et al., 2022) under future, warmer conditions. This scenario suggests one underlying explanation for the direction of the community compositional shifts being observed in Andean TMFs, where cold-affiliated species are being displaced by their warm-affiliated counterparts (Duque et al., 2015; Fadrique et al., 2018; Feeley et al., 2011), but this hypothesis is yet to be tested.

Transplant experiments, where individuals of the same species are moved to new climatic habitats and their responses to the new conditions are studied (Nooten & Hughes, 2017; Zimmermann et al., 2009), could offer an effective means of assessing the acclimation potential of individual TMF species to climate warming. Using this method, species found in high altitude forests can be grown at multiple locations downslope that are within and outside their known thermal niches, while those typical of lowland forests can be transplanted upslope to cooler conditions simulating their upwards migration following the thermophilisation hypothesis; this allows the plasticity of traits to various temperatures to be assessed. Although some environmental factors remain difficult to control, growing whole plants under field conditions using common soils and irrigation have numerous advantages over the artificial environments of growth chambers (Cheesman & Winter, 2013; Crous et al., 2018; Slot & Winter, 2017; Wittemann et al., 2022), where the scale of studies in terms of species numbers, plant sizes and the substrate they are planted in, as well as their timeframe, are far more limited (Nooten & Hughes, 2017).

We use a transplant approach along a 2000m tropical elevation gradient in which in three common garden plantations were established to assess the thermal plasticity of various leaf functional traits in eight mid-successional tree species that are dominant in the Colombian Andes. We exposed species of varying thermal niches to temperatures that are both within and outside the observed temperature ranges for each species, simulating the thermophilisation hypothesis (Duque et al., 2015).

The following leaf functional traits were measured: structural (LMA, LT, LA, LW and LDMC) nutrients (N_m, N_a, P_m and P_a) and water-use efficiency ($\delta^{13}C$ and g_1). We tested the following hypotheses:

1. The acclimatory responses of leaf functional traits to the short-term warming (~6 months) of our transplant experiment will be different from the adaptation responses observed along natural Andean elevation gradient studies.
2. Cold-affiliated species will be less able to acclimate leaf functional traits to warming due to their low phenotypic plasticity. On the other hand, the greater phenotypic plasticity of warm-affiliated species will render them more able to acclimate traits to cooling.

3. Trait responses to temperature change will be related to species' thermal niches, with species exhibiting more conservative traits (e.g., higher LMA and lower leaf N and P) when transplanted away from the mean of their thermal distributions.

2 | MATERIALS AND METHODS

2.1 | Common garden sites

Data collection was carried out at three experimental sites, named after their mean annual temperatures (MAT)—'14°C site', '22°C site' and '26°C' site—along a 2000 m elevation and 12°C temperature gradient in the north-western Colombian Andes (Table 1). The sites are geographically close to one another, with a maximum of approximately 20 km distance between the 14°C and 22°C sites, and between the 22°C and 26°C sites. Precipitation levels are above 2000 mm yr^{-1} at all sites (Table 1), but to prevent any confounding effects of drought, since planting, all trees have been irrigated during dry periods (January–March and June–August) with 8–24 L of water, three times per week. Soil for all trees was sourced from a high-elevation site (MAT of 14°C) with similar soil characteristics to the montane forest from which the seeds for the study were collected from. After being propagated in poly-pots in a nursery at 22°C for 2 years, the juvenile trees were planted at the experimental sites between November and December 2018 using c. 400 kg of soil for each tree in 0.32 m^3 pits.

At each site, 15 of the 27 most dominant non-palm species, characteristic of intermediate forest succession in the Colombian TMFs and adapted to sun germination, were planted in open areas in four 600 m^2 plots, each consisting of six 94 m^2 blocks. For this study,

eight of these 15 species were selected; time constraints prevented any more species from being sampled. Each block contained one tree from each species, planted 2.5 m apart from one another in the open areas to give high light conditions, with the position of trees in each block being randomised. The sixth block in each plot was fertilised on a monthly basis with 100 g in total of N, P, K and secondary minor elements to give artificially high soil nutrient content (so, 1 tree × 5 blocks × 4 plots = 20 nonfertilised trees, per species, per site; 1 tree × 1 block × 4 plots = 4 fertilised trees, per species, per site; Supporting Information: Figure S1). Changing environmental conditions along elevation gradients can affect nutrient mineralisation rates in soils (Rustad et al., 2001), which, in turn, can influence foliar nutrient content and physiological capacity. Controlling soil nutrient content therefore allows us to study both the direct and indirect effects of temperature on leaf nutrients and related functional traits.

2.2 | Sampling

Fieldwork for this study was carried out between June and August 2019, approximately 5–6 months after planting. We collected leaf material from two warm-affiliated species—defined here as those with thermal means, calculated from their observed thermal distributions, higher than 18°C—from the *Inga* genus, which are known to associate with N-fixing bacteria (Franche et al., 2009) and are abundant at low elevations. We also collected material from six cold-affiliated species—defined as those with thermal means below 18°C—which are more abundant at high elevations (Table 2). By transplanting individuals from these species to sites with three different MATs, we exposed them to temperatures that were both within and outside their thermal ranges. Specifically, cold-affiliated species were planted close to their T_{opt} at the 14°C site, at the hot ends of their thermal range at the 22°C site and beyond their thermal range at the 26°C site. Similarly, the warm-affiliated species (*Inga spectabilis* and *I. marginata*) were planted close to their T_{opt} at the 22°C site and at the 26°C site, and at the cold end of their ranges at the 14°C site. At each site, we collected 12 fully expanded, healthy, sunlit leaves from randomly-chosen trees in three nonfertilised blocks from each of the four plots (3 × 4 = 12 non-fertilised leaves per species per site), as well as from the fertilised block from each plot (1 × 4 = 4 fertilised leaves per species). Warm-affiliated species were sampled from all three sites, while cold-affiliated species were only sampled from the 14°C and 22°C sites, due to very low survival rates at the 26°C site.

2.3 | Leaf structural traits

After collection, leaves were sealed in individually labelled plastic bags containing damp cotton wool and placed out of direct sunlight to prevent premature drying. High-precision electronic callipers (AK9622EV; Sealey Group) were then used to measure thickness from three areas of each leaf, avoiding the central vein, with the

TABLE 1 Environmental conditions at the study sites.

	14°C site	22°C site	26°C site
Elevation (m.a.s.l)	2516	1357	736
MAT (°C)	14.1	21.8	25.9
T min (1% ile, °C)	9.7	16.8	20.4
T max (99% ile, °C)	33.1	39.2	44.2
MAP (mm yr^{-1})	2774	2045	2298
Mean VPD (kPa)	0.82	1.14	1.83
Location (latitude, longitude)	5.54° N, −75.68° W	5.60° N, −75.62° W	6.01° N, −75.85° W

Note: Mean annual temperature (MAT) includes both day and night-time air temperatures; mean daytime vapour pressure deficit (VPD) was calculated using daytime (0600–1800) VPD values.

TABLE 2 Tree species included in our study are given in ascending order of their geographical thermal means.

Species	Thermal mean (°C)	Thermal maximum (°C)	Thermal minimum (°C)	Minimum altitude (m.a.s.l)	Maximum altitude (m.a.s.l)
Cold-affiliated					
Andesanthus lepidota	13.2	19.1	7.2	1000	3500
Clethra fagifolia	13.4	19.1	7.1	500	3500
Weinmannia pubescens	15	19.9	9.3	1500	3000
Clusia multiflora	15.3	20.3	9.9	1000	3500
Quercus humboldtii	16.4	21.2	11.8	1500	3500
Miconia theaezans	17.2	24	9	500	3000
Warm-affiliated					
Inga marginata	22.7	30.4	15.2	0	2000
Inga spectabilis	25.4	30.9	19.8	0	1500

Note: Thermal maxima and minima from observed geographical distributions are also given, as well as the lowest and highest altitudes at which they are found in the Colombian Andes (Fick & Hijmans, 2017), and whether they are cold- or warm-affiliated.

average of these three measurements taken to be LT (mm). Images were taken of each leaf using a CanoScan LiDE 300 flatbed scanner and then processed using the R environment (v4.2.1; R Core Team, 2022) to calculate LA (cm^2) and LW (mm): LA was obtained using the 'LeafArea' package in R (Katabuchi, 2015), which automates the ImageJ programme (ImageJ, v.1.52a; National Institutes of Health [NIH]), while LW values were calculated using the 'LeafJ' plugin (Maloof et al., 2013) for ImageJ. Following scanning, leaves were weighed to give their wet weight before being dried in an oven to constant mass for approximately 48 h at 70°C, then re-weighed to give their dry weight. LDMC (mg g^{-1}) was calculated as the quotient of leaf dry weight to leaf wet weight (Wilson et al., 1999), while LMA (g m^{-2}) was calculated by dividing dry weight by LA (Pérez-Harguindeguy et al., 2013).

2.4 | Leaf nutrient analyses

To obtain leaf N and P content, dried leaf samples were transported to the UK for elemental analysis. Leaves were ground into a powder using a shaker mill (model MM400; Retsch) and approximately 1 mg of sample for each was then packed into tin capsules and run through an infrared mass spectrometer (Callisto CF IRMS; SerCon Limited) to return %N values, or nitrogen content on a dry-weight basis (N_m). For leaf P content, 0.1–0.2 g of sample was subjected to ICP-OES analysis with a unique Dichroic Spectral Combiner (model 5110, Agilent Technologies); this returned phosphorus content on a dry-weight basis (P_m). Both leaf N and P can be expressed on an area-basis (N_a and P_a) by dividing by LMA. All analyses were tested against laboratory standards.

2.5 | Leaf water-use efficiency traits

Infrared mass spectrometer analysis also returned $\delta^{13}C$ values for each leaf sample. In addition, the water-use parameter 'g_1', a measure of intrinsic plant water-use efficiency (Medlyn et al., 2012), was derived from spot measurements of diurnal cycle net photosynthesis (A_n) and stomatal conductance (g_s) of individual leaves ($n = 4$, one leaf per plot, per species per site) under ambient environmental conditions over the course of a day. Measurements were collected in the field using a LI-6400XT portable photosynthesis system (Li-Cor Inc.) from a subsample of trees (all of those in Table 1, except *C. fagifolia*). For these measurements, the ambient conditions (photosynthetically active radiation, relative humidity, air temperature and 410 ppm CO_2) for each leaf were replicated within the cuvette of the LI-6400XT before the leaf was inserted, allowing readings to be taken almost immediately. The unified stomatal model of Medlyn et al. (2012; Equation 1) was then fitted to diurnal course A_n and g_s measurements in the R environment (v4.2.1; R Core Team, 2022) using the 'plantecophys' package (Duursma, 2015) to obtain the model parameter g_1

$$g_s^* \approx g_0 + 1.6\left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a} \tag{1}$$

where g_s^* is the optimal stomatal conductance to water vapour, g_0 is the residual conductance to water vapour, assumed to be zero following Lin et al. (2015), D is the leaf-to-air vapour pressure deficit (kPa), A is net photosynthesis (μ mol m^{-2} s^{-1}), and C_a is atmospheric CO_2 concentration at the leaf surface (μ mol mol^{-1}). g_1 (kPa$^{0.5}$) is proportional to the marginal water cost of carbon gain (Medlyn et al., 2011, 2012).

2.6 | Data analysis

All analyses were performed in R (v4.2.1; R Core Team, 2022). To test the hypothesis of acclimatory responses of leaf functional traits to short-term warming, we compared species-level responses (from non-fertilised trees) for individual traits expressed in absolute values, using one-way analysis of variance (ANOVA) tests from the 'stats' package and Tukey post hoc tests. We then use the same procedure to test for thermal acclimation responses by thermal affiliation (cold- or warm-affiliated), grouping the leaf trait data by their thermal affiliation. These analyses were complemented by mixed-effects ANOVAs performed with the 'nlme' package (Pinheiro et al., 2021), with temperature and species' thermal affiliation group set as the fixed effects, and individual species nested within thermal affiliation group as a random effect (Supporting Information: Table S1). As a further test, we performed the same analysis with all species being grouped according to their thermal affiliation (cold- or warm-affiliated); one-way ANOVA tests and Tukey post-hoc tests (v4.2.1; R Core Team, 2022) checked for significant temperature effects on each trait (Supporting Information: Figures S2–S4). We additionally used one-way ANOVAs to test for significant differences between non-fertilised and fertilised plants for each species, as well as mixed-effect ANOVAs using temperature and fertilisation as the fixed effects, with individual species nested within thermal affiliation group as the random effect; this enabled a check for an indirect temperature effect of soil warming on leaf traits (Rustad et al., 2001; Supporting Information: Figure S5). Before undertaking ANOVAs, residuals were checked visually for normality, with any outliers being removed.

To test the hypothesis on the relation of trait responses to short-term temperature change and species' thermal niches, species-level trait responses of non-fertilised trees were estimated as the effect of species displacement from their 'home' temperatures—defined as the site closest to the mean of each species' observed geographical thermal range (T_{mean})—on each functional trait, using linear mixed-effects models with the 'nlme' package (Pinheiro et al., 2021). To do this, we first calculated the thermal displacement index (TDI) for each species at each site (Lynn et al., 2021) using the following equation:

$$TDI = \frac{(T_{site} - T_{mean})}{\sigma(T_{mean})}, \quad (2)$$

where T_{site} is the mean temperature of the study site where trees have been planted, T_{mean} is the mean temperature of a species' observed thermal distribution and σ is the standard deviation of a species' thermal range, based on Wordlclim data from Fick & Hijmans (2017). Therefore, a positive TDI means that a species has been transplanted to a site with air temperature above its T_{mean}, and a negative TDI means that a species has been transplanted to a site with air temperature below its T_{mean}. We then scaled trait values (STV) for each species by dividing each trait value by the maximum value measured in this data set at the home elevation/temperature. This was done to have all trait values on the same scale, allowing for direct comparison among species and for them to be analysed in the

same model. An STV of '1' represents the value at home elevation/ temperature, above 1 shows an increase in the trait away from home elevation, and below 1 shows a decrease. TDI and STVs for all species and traits are given in Supporting Information: Table S1. Finally, TDI was regressed against the STVs—these show the relative increase or decrease in a trait's value with species displacement from home temperature—for each species at each site, with TDI set as a fixed factor and species affiliation set as a random factor.

3 | RESULTS

3.1 | Response of leaf functional traits to temperature change

3.1.1 | Structural traits

The simulated warming/cooling effect of our experimental set-up was used to test hypothesis 1. The effect of temperature change on leaf structural traits of non-fertilised leaves, when expressed in absolute values, was species-specific. Both LMA and LT were only significantly affected by temperature for a single species: LMA decreased by 12% with 4°C of warming in *I. marginata* compared to the value at 22°C, the site closest to its thermal mean (Table 2), and increased by 20% when exposed to its cold extreme at 14°C. LT decreased by 31% with warming at 22°C for *C. multiflora* compared to the value at 14°C, the site closest to their thermal mean (Figure 1a,b). Also, LA and LW decreased in *I. spectabilis* between 26°C, the site closest to its thermal mean, and 14°C, the site at the cold end of its thermal distribution, by 496% and 260%, respectively. LW in *I. marginata* also showed a significant reduction of 44% from 26°C to 14°C (Figure 1d,e).

Cold-affiliated species, such as *Quercus humboldtii* and *Clethra fagifolia*, were significantly affected by warming, with significant increases in LDMC for both species, and significant decreases in LW for *Q. humboldtii* between the 14°C site (closest to thermal mean) and the 22°C site (Figure 1c,e). This runs counter to the changes measured for *I. marginata* and *I. spectabilis* (Figure 1c,e). Temperature responses in absolute values were also limited when species were categorised by thermal affiliation (Table 2), with no significant change for any structural trait for cold-affiliated species, while warm-affiliated species only changed significantly for LW (Supporting Information: Figure S2d; Table S2).

3.1.2 | Nutrient traits

A greater number of significant species-level temperature effects were evident for leaf nutrients than for structural traits. N_m was most affected by warming, with three cold-affiliated species (*Andesanthus lepidota*, *C. fagifolia* and *Miconia theaezans*) having higher values (25%, 32% and 31%, respectively) at 14°C—the site closest to their thermal mean—than 22°C. In *I. marginata*, N_m was also significantly affected by
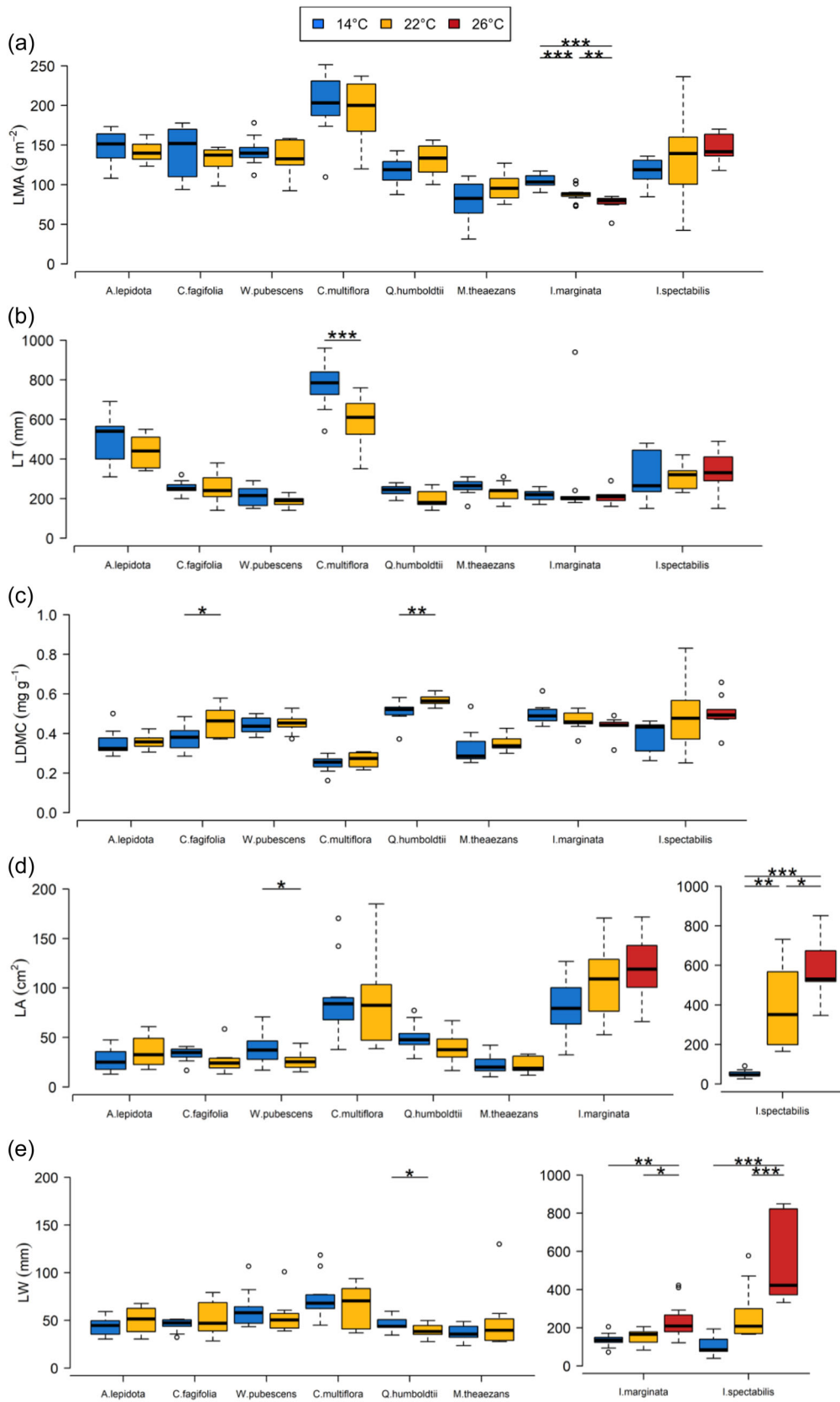
FIGURE 1 (See caption on next page).

temperature change: it increased by 24% in response to warming from 22°C—the site closest to its thermal mean – to 26°C, while cooling to 14°C from 22°C decreased N_m by 24% (Figure 2a). $I.\ marginata$ was also affected by cooling for N_a and P_a, with values at 14°C higher than 22°C by 47% and 33%, respectively, while of the cold-affiliated species, $A.\ lepidota$ and $C.\ fagifolia$ had significantly lower N_a and P_m when warmed to 22°C from their home temperature of 14°C (Figure 2b,c,d). Overall, patterns with absolute values were more evident when species were grouped by their thermal affiliation: N_m, P_m and P_a all significantly decreased when cold-affiliated species were warmed to 22°C, but increased when warm-affiliated species were cooled to 14°C (Supporting Information: Figure S3a,c,d; Table S2).

3.1.3 | Water-use efficiency traits

Of the water-use efficiency traits (non-fertilised leaves), $\delta^{13}C$ showed more thermal plasticity than g_1, with an absence of any temperature effects for g_1 (Figure 3). $I.\ marginata$ and $I.\ spectabilis$ both had significantly more negative $\delta^{13}C$ at higher temperatures: for $I.\ marginata$, values were 7% lower at home temperature (22°C) than 14°C, while $I.\ spectabilis$ decreased by 10% when cooled from 26°C to 14°C (Figure 3a). Conversely, $Q.\ humboldtii$ had more negative values at home temperature, 4% lower at 14°C than 22°C (Figure 3a). When species were categorised as either being of cold- or warm-affiliated, only warm-affiliated had their $\delta^{13}C$ affected by temperature, with values being lower at warmer temperatures closer to their T_{mean} (Supporting Information: Figure S5a). There were no significant changes in g_1 with temperature for any species (Figure 3b), and this remained true when separating species by their climatic affiliation (Supporting Information: Figure S4b; Table S2).

3.2 | Trait response to temperature change and species thermal niches

3.2.1 | Structural traits

Here, we test the hypothesis examining trait responses to short temperature change and species' thermal niches, using leaves from non-fertilised plants. When considering the relative change in trait values with species displacement from their home temperature, there was a clear influence of temperature on LDMC and LW (Figure 4c,e).

Linear mixed-effects models show significant positive relationships between TDI and the STVs of LDMC ($R^2 = 0.42$, $p = 0.033$) and LW ($R^2 = 0.54$, $p = 0.016$); in other words, transplanting species to temperatures above their home temperature generally resulted in an increase in these traits (Table 3), and vice versa when species were transplanted below their home temperatures. There was no clear relationship between TDI and LMA, LT or LA, though for LT both cold- and warm-affiliated species exhibited lower values when transplanted to temperatures outside their thermal niches (Figure 4a,b,d; Table 3).

3.2.2 | Nutrient traits

As with structural traits, temperature effects were apparent for leaf nutrients when their STVs were assessed with displacement from species thermal means. P_m and P_a displayed significant negative relationships with temperature displacement ($R^2 = 0.80$, $p < 0.001$; $R^2 = 0.55$, $p = 0.006$, respectively), while N_m showed a strong, almost significant relationship ($R^2 = 0.49$, $p = 0.097$). Transplanting species to temperatures above their thermal means decreased foliar P and N_m, while displacement below thermal means increased these values (Figure 5a,c,d; Table 3). The effect of thermal displacement on area-based leaf nitrogen content, N_a, was much weaker than on P_a, owing to low variation in N_m and no variation of LMA with TDI. N_a values remained similar in five of the eight species, even when transplanted away from their home elevation (Figure 5b; Table 3).

3.2.3 | Water-use efficiency traits

There was a highly significant relationship between TDI and the STVs of $\delta^{13}C$ ($R^2 = 0.59$, $p = 0.007$), showing that cold-affiliated species increased their $\delta^{13}C$ values with warming, while warm-affiliated species decreased values with cooling (Figure 6a; Table 3). Conversely, there was no effect of thermal displacement on g_1 STVs, with no clear pattern for either cold- or warm-affiliated species (Figure 6b; Table 3).

3.3 | Impact of fertilisation on functional traits

There was only one effect of nutrient fertilisation on trait values: this was for LA in $I.\ spectabilis$ growing at the 26°C site (its home

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FIGURE 1 Boxplots showing comparison of leaf mass per unit area (g m^{-2}; a), leaf thickness (μm; b), lead dry matter content (mg g^{-1}; c), leaf area (cm^2; d) and leaf width (mm; e) for eight species growing at home temperature and sites away from home temperature, organised by their thermal means (lowest to highest, left to right). A separate plot is given for leaf area of $Inga\ spectabilis$ due to the different scale needed for the y-axis; the same is true for leaf width for $I.\ spectabilis$ and $I.\ marginata$. Colours represent the different temperature treatments (14°C, blue; 22°C, yellow; 26°C, red); 14°C is home for the cold-affiliated species, 22°C is home for $I.\ marginata$ and 26°C home for $I.\ spectabilis$. Asterisks above boxes (*) show results from the Tukey post hoc test where there are significant differences in values with temperature for individual species (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). For (d) and (e), analysis of variances were performed independently for each subplot.
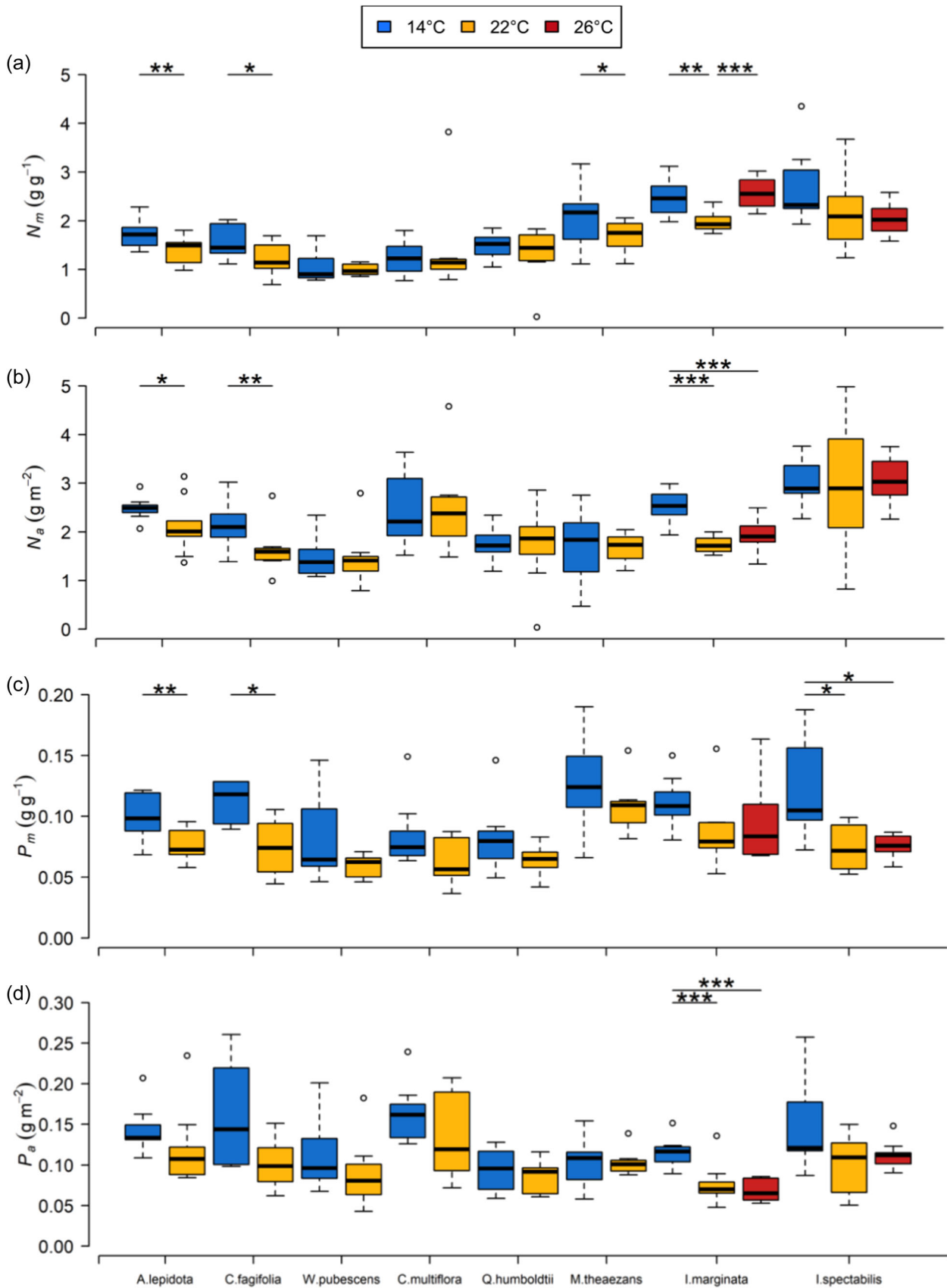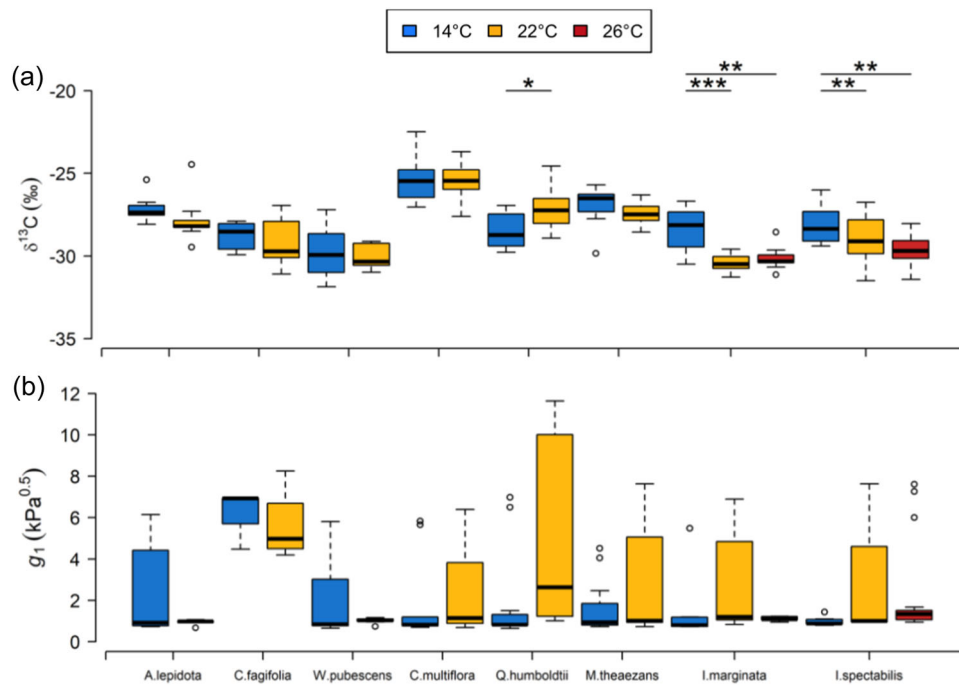
FIGURE 2 (See caption on next page).

FIGURE 3 Boxplots showing comparison of internal leaf concentration of ^{13}C (‰) and $g1$ (kPa$^{0.5}$) for eight species growing at home temperature and sites away from home temperature, organised by their thermal means (lowest to highest, left to right). Colours represent the different temperature treatments (14°C, blue; 22°C, yellow; 26°C, red); 14°C is home for the cold-affiliated species, 22°C is home for *Inga marginata* and 26°C home for *I. spectabilis*. Asterisks above boxes (*) show results from the Tukey post hoc test where there are significant differences in values with temperature for individual species (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). [Color figure can be viewed at wileyonlinelibrary.com]

temperature), where non-fertilised values were significantly higher than those of fertilised trees (Supporting Information: Figure S5). Otherwise, there were no differences between non-fertilised and fertilised plants for any other functional traits, for any other species.

4 | DISCUSSION

This study investigated the plasticity of leaf functional traits in response to a short-term temperature change (5–6 months) in eight of the most dominant TMF species found in the Colombian Andes, using a transplant approach. Variation of leaf traits along elevation gradients is commonly measured in forest plots with multiple species. These studies show a systematic shift from conservative strategies at high elevation (smaller, thicker leaves with lower nutrient concentrations and higher water-use efficiency) to acquisitive strategies at low elevation (larger leaves with higher nutrient contents and lower

water-use efficiency), reflecting community adaptations to specific environmental conditions (e.g. Feng et al., 2023; Martin et al., 2020; van de Weg et al., 2009). Our species-level study, with absolute values, shows that cold-affiliated species retain their trait values under warmer conditions, demonstrating limited plasticity in the leaf functional traits studied. On the other hand, the two warm-affiliated species studied demonstrated greater thermal plasticity: they adjusted their leaf area and width, foliar nutrients and water-use efficiency in response to cooling, switching from acquisitive to conservative strategies. When considering changes in scaled trait values for studied species with displacement from home temperature, we identified more subtle trends in how functional traits are affected by temperature change across species. Our analysis suggests that species-level responses to thermal displacement are generally determined by their climatic niches, changing from more acquisitive traits under optimal environmental conditions ('home') to more conservative traits when growing away from their home temperature;

FIGURE 2 Boxplots showing comparison of mass-based nitrogen (g g^{-1}), area-based nitrogen (g m^{-2}), mass-based phosphorus (g g^{-1}) and area-based phosphorus (g m^{-2}) for eight species growing at home temperature and sites away from home temperature, organised by their thermal means (lowest to highest, left to right). Colours represent the different temperature treatments (14°C, blue; 22°C, yellow; 26°C, red); 14°C is home for the cold-affiliated species, 22°C is home for *Inga marginata* and 26°C home for *I. spectabilis*. Asterisks above boxes (*) show results from the Tukey post hoc test where there are significant differences in values with temperature for individual species (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). [Color figure can be viewed at wileyonlinelibrary.com]
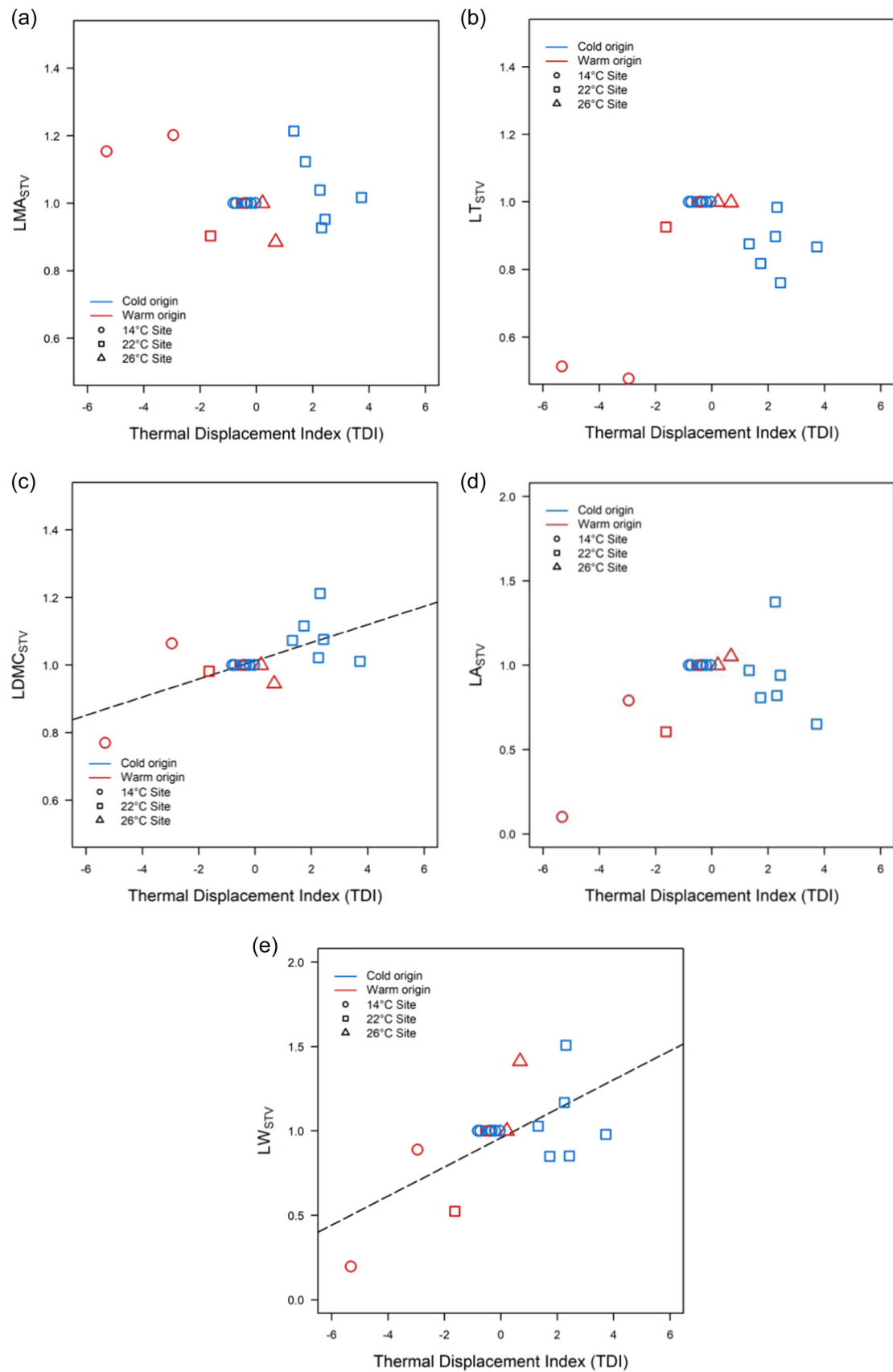
FIGURE 4 (See caption on next page).

TABLE 3 Outputs of linear mixed-effects models testing for statistically significant relationships between thermal displacement indices (TDI) and scaled trait values (STVs), where TDI and species thermal affiliation (cold/warm) were set as fixed factors, and species set as a random factor.

Trait	R^2 (conditional)	df	p-Value
LMA	0.118	1,9	0.167
LT	0.187	1,9	0.223
LDMC	0.418	1,9	**0.033**
LA	0.288	1,9	0.132
LW	0.537	1,9	**0.016**
N_m	0.492	1,9	0.097
N_a	0.400	1,9	0.197
P_m	0.797	1,9	**<0.001**
P_a	0.553	1,9	**0.006**
$\delta^{13}C$	0.587	1,9	**0.007**
g_1	0.227	1,9	0.463

Note: These results accompany Figures 4–6.

Abbreviations: LA, leaf area; LDMC, leaf dry matter content; LMA, leaf mass per unit area; LT, leaf thickness; LW, leaf width.

this reveals a greater degree of plasticity in traits than is captured by simple comparison of absolute values.

4.1 | Do acclimatory responses of leaf functional traits differ from trait variation reported along natural tropical forest gradients?

The structural trait values (LMA, LT, LDMC, LA and LW) on an absolute basis for cold-affiliated species at the 14°C site are of the same order of magnitude as those reported at high-elevation sites in adult trees along other elevation gradient studies in the Andes (Bahar et al., 2017; Llerena-Zambrano et al., 2021; Martin et al., 2020; Ochoa-Beltrán et al., 2021; van de Weg et al., 2009), and in TMF in Rwanda from both adult (Mujawamariya et al., 2018) and juvenile trees (Dusenge et al., 2021; Manishimwe et al., 2022). The much higher LT (and LMA) values for *C. multiflora* could be attributed to *Clusia*'s relation to C_3/crassulacean acid metabolism (CAM) behaviour (Grams et al., 1998; Lüttge, 2006), where water-efficiency traits, such as larger vacuoles and fewer leaf internal air spaces, have been conserved across the genus (Barrera Zambrano et al., 2014). This could also explain why *C. multiflora* has the highest $\delta^{13}C$ values of all

the cold-affiliated species. Of the two *Inga* species, the LMA and LT of *I. marginata* are akin to values reported for lowland and early-successional species in other TMF studies (Dusenge et al., 2021; Manishimwe et al., 2022; Martin et al., 2020; van de Weg et al., 2009) and mean LMA values in the lowland Amazonian study of Fyllas et al. (2009). On the other hand, *I. spectabilis* exhibits much higher LMA and LT values (69% and 52% lower, respectively) than *I. marginata* at 22°C, though this could be partly explained by the sheer size of the leaves of *I. spectabilis* (Figure 1d,e).

Trends in observed leaf $\delta^{13}C$ in this study are similar those found for structural traits: cold-affiliated species exhibit similar values to other high-elevation Andean species and do not change their values with warming, while the warm-affiliated *Ingas* have more negative values which indicate less efficient water-use, similar to those reported for lowland Andean sites and those from the Amazon basin (Fyllas et al., 2009; Martin et al., 2020; Table 4). One exception to the pattern for cold-affiliated species, however, is *Q. humboldtii*, which has significantly higher $\delta^{13}C$ at 22°C: this could be linked to the species' association with ectomycorrhizal fungi instead of arbuscular mycorrhizal fungi (Vargas & Restrepo, 2020), as the latter can encourage higher transpiration rates and thus lower WUE under warming (Zhu et al., 2011). Regarding leaf nutrients, as the soils in our study are common to all experimental sites these cannot be compared to the leaf N and P concentrations reported from trees growing in natural soils on elevation gradients (Bahar et al., 2017; Llerena-Zambrano et al., 2021; Martin et al., 2020; Ochoa-Beltrán et al., 2021; van de Weg et al., 2009). It is, however, worth noting that the N_m of the warm-affiliated species are significantly higher ($p < 0.001$) than their cold-affiliated counterparts at the 14°C and 22°C sites; this could be linked to the symbiotic relationship with N-fixing bacteria in the *Inga* genus (Franche et al., 2009). Taking these results together, our findings suggest that the cold-affiliated species in Andean TMFs are naturally more conservative in their resource-use at home temperature, whereas the warm-affiliated species are more acquisitive. The behaviour of the latter could additionally be explained by how *Ingas* are often classed as pioneer species, owing to their strong performance in high-light environments (dos Santos Pereira et al., 2019). This not only makes them ideal candidates for forest restoration projects, but suggests that they could be very capable competitors to native, cold-affiliated TMF species if these taxa struggle to acclimate to warmer conditions in the long-term.

In accordance with hypothesis 1, which tests for different trends between transplant experiments and natural elevation gradients, we suggest that natural elevation gradient studies show community level adaptations to specific conditions over long time periods (hundreds to millions of years) rather than the short-term

FIGURE 4 Relationships between thermal displacement index (TDI) and scaled trait values (STVs) of leaf structural traits: leaf mass per unit area (a), leaf thickness (b), leaf dry matter content (c), leaf area (d) and leaf width (e). Individual data points represent the mean values of each cold- and warm-affiliated species at different sites (14°C, 22°C and 26°C), while a dashed line indicates the presence of a significant relationship (see 'p-values' in Table 3). [Color figure can be viewed at wileyonlinelibrary.com]
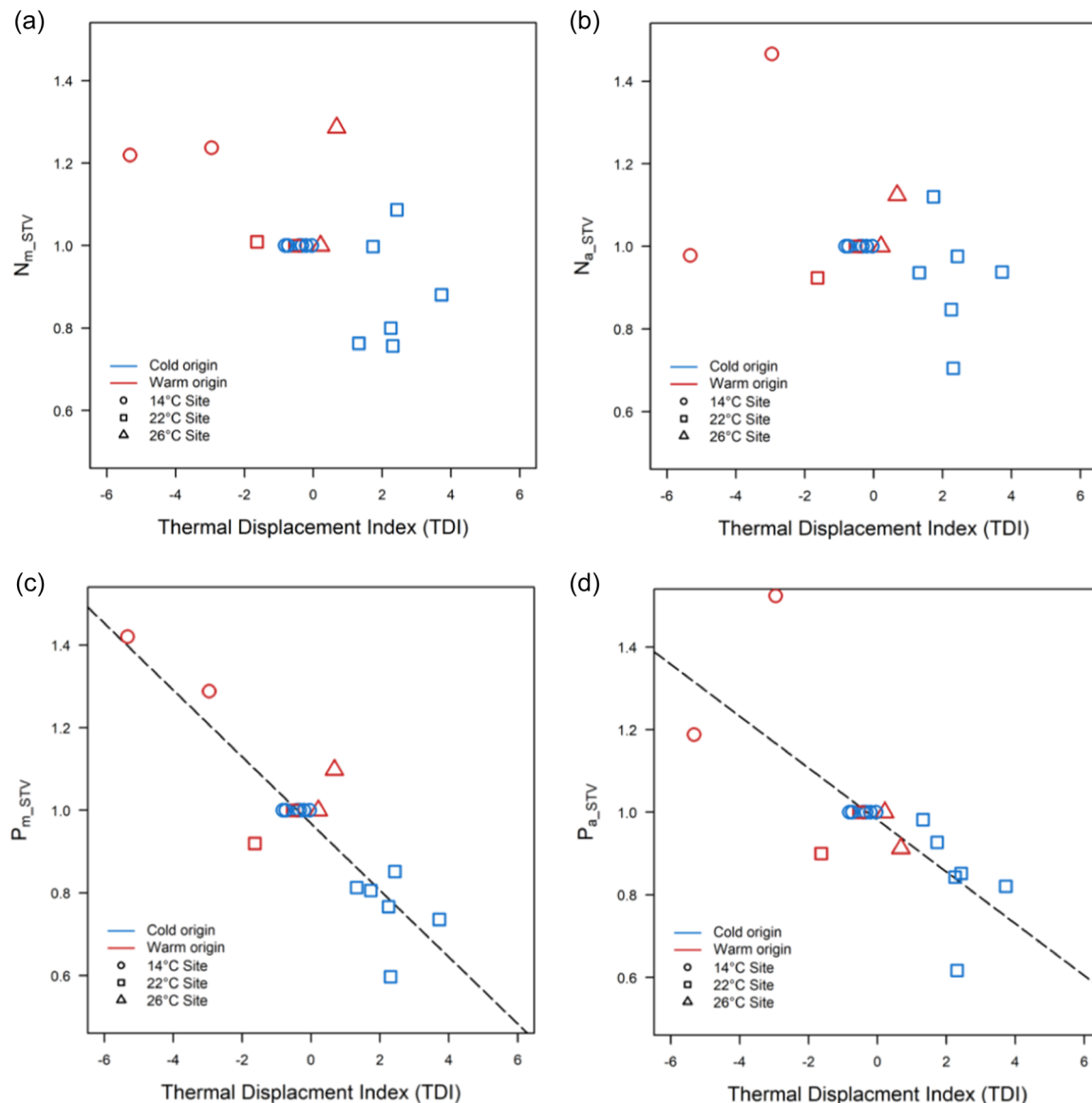
FIGURE 5 Relationships between thermal displacement index (TDI) and scaled trait values (STVs) of leaf nutrient traits: mass-based nitrogen (a), area-based nitrogen (b), mass-based phosphorus (c), and area-based phosphorus (d). Individual data points represent the mean values of cold- and warm-affiliated species at different sites (14°C, 22°C and 26°C), while a dashed line indicates the presence of a significant relationship (see '*p*-values' in Table 3). [Color figure can be viewed at wileyonlinelibrary.com]

acclimatory responses of leaf functional traits that are the focus of our study. We also argue that these observed responses might hold true in the long-term: a recent transplant experiment in Rwandan TMF found no age effect for LMA or leaf size in three out of four studied species when trait measurements were collected a year apart from the same trees (Manishimwe et al., 2022). This suggests that, counter to some previous ontogenetic studies (Brito-Rocha et al., 2016; Ishida et al., 2005), juvenile trees can provide a valuable indication of how mature trees will respond to rapid environmental change (Manishimwe et al., 2022). As such, we argue that our results may be effective for predicting how particular Andean TMF species might respond to rising temperatures in the short- and long-term.

4.2 | Thermal plasticity of functional traits in Andean TMF species

The use of scaled trait values reveals clearer patterns of how leaf functional traits respond to temperature change across our studied species than when absolute values are used, and indicate that shifts in traits can be partly explained by species' climatic niches. On the other hand, absolute values are more useful when assessing the temperature responses of individual species. For example, only *I. marginata* significantly changed its absolute LMA values in response to temperature change, and only a few species shift other structural traits (Figure 1). Conversely, our analysis using scaled traits suggests that, overall, the studied species may be more thermally plastic than
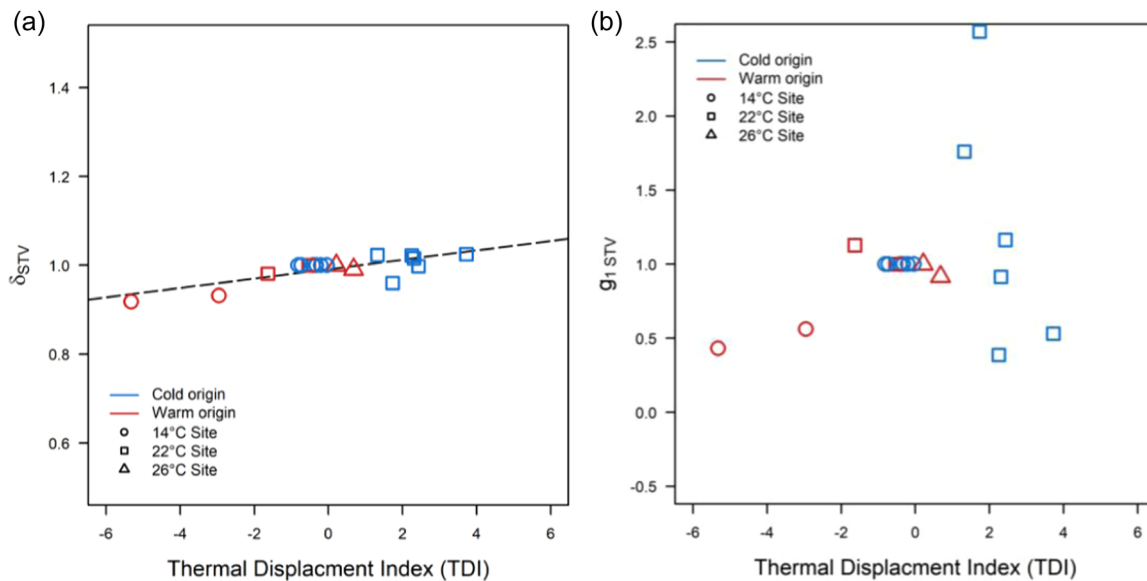
FIGURE 6 Relationships between thermal displacement index (TDI) and scaled trait values (STVs) of leaf water-use efficiency traits: internal leaf concentration of ^{13}C (a) and g_1 (b). Individual data points represent the mean values of cold- and warm-affiliated species at different sites (14°C, 22°C and 26°C), while a dashed line indicates the presence of a significant relationship (see 'p-values' in Table 3). [Color figure can be viewed at wileyonlinelibrary.com]

when observing absolute trait values for individual species; for example, some cold- and warm-affiliated species increase scaled LMA values when transplanted to warmer and cooler temperatures, respectively, which implies a shift to more conservative strategies when growing outside their usual thermal niches (Figure 4; Feng et al., 2023; Onoda et al., 2017; Poorter et al., 2009; Reich, 2014). Greater resource conservation is supported by the positive TDI relationships with LA and LW: most species exhibit lower scaled values when transplanted away from their home temperatures, with three cold-affiliated species mostly showing small reductions and the warm-affiliated species reducing LA and LW more pronouncedly (Figure 4; Table 3). The ability of *I. spectabilis*, in particular, to adjust leaf size to considerable cooling (12°C)—shown by the absolute values of LA and LW—suggests a high level of thermal plasticity, agreeing with the thermal tolerance hypothesis that species originating from warmer, wetter environments will be more able to adjust to new conditions (Anderson et al., 2021; Currie et al., 2004; Spasojevic et al., 2014). Additionally, this would enable such species to shift from conservative strategies at suboptimal temperatures to more acquisitive strategies as temperatures rise, taking advantage of warmer conditions to maximise photosynthesis and growth, with larger leaves to intercept more sunlight and with a higher number of stomata to increase their capacity for C fixation (Kundu and Tigerstedt, 1999; Wright et al., 2017). The findings of Cox et al. (2023) support this, as they report the highest photosynthetic capacities in warm-affiliated species when growing at temperatures closest to their thermal means.

Leaf nutrients exhibited clear negative relationships between scaled traits and thermal displacement (Figure 5; Table 3), while temperature-induced changes in absolute trait values were also far

more apparent than for structural traits (Figure 2 and Supporting Information: Figure S3). This suggests greater thermal plasticity of these traits across species and supports previous claims that chemical traits are more plastic than structural traits (Valladares et al., 2000). Absolute values of all nutrient traits, except N_a, were significantly higher at 14°C than 22°C in both thermal affiliation groups (Supporting Information: Figure S3), while STVs showed significant shifts in P_m and P_a when species were transplanted away from their thermal means (Figure 5). For cold-affiliated species, higher leaf nutrients coincide with higher photosynthetic capacities at their cooler, home temperatures (Cox et al., 2023); as temperatures rise, faster enzymatic reactions allow carbon assimilation to be maintained with fewer photosynthetic enzymes (Arcus et al., 2016; van de Weg et al., 2012; Wang et al., 2020). N and P are both essential in carbon fixation, with N heavily invested in Rubisco and P modulating RuBP regeneration (Bahar et al., 2017; Bar-On & Milo, 2019; Bloomfield et al., 2014; Dusenge et al., 2021), but lower concentrations of both nutrients are required at lower photosynthetic capacities. Contrastingly, a comparison of absolute values of foliar N and P showed that the two warm-affiliated species exhibit significantly higher levels of these nutrients at 14°C than their cold-affiliated counterparts; this could indicate that they are compensating for slower enzymatic reactions at lower temperatures (Dusenge et al., 2021; Smith & Keenan, 2020; Wang et al., 2020; van de Weg et al., 2014; Supporting Information: Figure S3), or driven by *Inga*'s association with N-fixing bacteria (Franche et al., 2009).

The scaled (Figure 6) and absolute (Figure 3) $\delta^{13}C$ values reflect how species' photosynthetic capacities respond to changing temperature under well-watered conditions. The *Inga* species show the most wasteful water usage at 26°C, mirroring how larger leaves with more

TABLE 4 Mean values of key functional traits (leaf mass per unit area, LMA; leaf thickness, LT; leaf dry matter content, LDMC; leaf internal ^{13}C concentration, $\delta^{13}C$), for all species in our study at sites closest to their thermal means (14°C for *Andesanthus lepidota – Miconia theaezans*; 22°C for *Inga marginata*; 26°C for *I. spectabilis*), compared with mean values from high and low elevation sites ('Highland' and 'Lowland', respectively), and from early- and late-successional ('ES' and 'LS', respectively), along other elevation gradients in the Andes (Peru[1], Ecuador[2], Colombia[3]) and Rwanda, as well as lowland sites across the Amazon.

Study	LMA (g m^{-2})	LT (μ m)	LDMC (mg g^{-1})	$\delta^{13}C$ (‰)
Andean studies				
This study:				
Andesanthus lepidota	146.57 ± 6.31	490 ± 36.61	352.54 ± 18.54	−27.16 ± 0.23
Clethra fagifolia	142.20 ± 9.93	258 ± 10.2	378.01 ± 19.77	−28.73 ± 0.26
Weinmannia pubescens	141.57 ± 4.80	213.33 ± 13.6	443.4 ± 12.53	−29.31 ± 0.55
Clusia multiflora	202.07 ± 10.78	774.17 ± 31.66	248.35 ± 10.63	−25.47 ± 0.38
Q. humboldtii	117.08 ± 4.92	243 ± 7.6	507.26 ± 15.3	−28.53 ± 0.3
M. theaezans	80.66 ± 80.66	259.17 ± 11.25	325.35 ± 23.5	−26.95 ± 0.31
I. marginata	86.68 ± 2.83	218.33 ± 14.1	465.21 ± 12.9	−30.4 ± 0.16
I. spectabilis	147.27 ± 5.85	331 ± 30.5	505.89 ± 28.31	−29.92 ± 0.36
Bahar et al. (2017)[1]:				
Highland	143 ± 39	--	--	--
Lowland	132 ± 35	--	--	--
* Llerena-Zambrano et al. (2021)[2]	79.01	373 ± 110	280.23 ± 79.01	--
Martin et al. (2020)[1]				
Highland	147.4 ± 6.9	--	--	−28.3 ± 0.3
Lowland	99.0 ± 4.9	--	--	−30.8 ± 0.3
Ochoa-Beltrán et al. (2021)[3]				
Highland	82.24	310	329.63	--
Lowland	66.40	220	344.39	--
van de Weg et al. (2009)[1]				
Highland	156.25 ± 23.4	--	370 ± 40	--
Lowland	69.39 ± 7.17	--	416 ± 17.14	--
Rwandan studies				
* Dusenge et al. (2021):				
H. montana (ES)	96.9 ± 3.1	--	--	--
S. guineense (LS)	117.7 ± 3.1	--	--	--
* Manishimwe et al. (2022):				
ES	92.2 ± 5.7	235.9 ± 13.9	410 ± 20	--
LS	121.3 ± 6.7	262.9 ± 18.4	480 ± 30	--
* Mujawamariya et al. (2018)	124.75 ± 7.27	--	--	--
Amazonian study				
Fyllas et al. (2009)	97.42			−30.86

Note: All values from other studies (besides the Amazonian study) are taken from selected sites with equivalent temperatures to the sites in our study. Highland sites in other studies all have mean annual temperatures (MATs) of 12.5–18.8°C, while Lowland sites have MATs of 23.2–26.6°C. Unless specific species are stated (e.g., Dusenge et al., 2021), trait values are averages for all species/type of species at that particular site; the LMA and $\delta^{13}C$ for Fyllas et al. (2009) are mean values for 62 sites across the Amazon basin.

*Shows where values are only shown for highland sites. Only Manishimwe et al. (2022) use field-grown trees in common soils, the others are a combination of adult trees in forest plots (Bahar et al., 2017; Llerena-Zambrano et al., 2021; Martin et al., 2020; Mujawamariya et al., 2018; Ochoa-Beltrán et al., 2021; van de Weg et al., 2009) and potted seedlings (Dusenge et al., 2021). The LMA value for from Llerena-Zambrano et al. (2021) was calculated from specific leaf area (SLA) and LA data.

stomata increase carbon uptake but simultaneously increase transpiration rates (Medlyn et al., 2017), but were then able to increase $\delta^{13}C$ at cooler temperatures (Figure 6 and Supporting Information: Figure S4); combined with smaller leaves (Figure 4d,e) and lower photosynthetic capacities (Cox et al., 2023), this indicates a shift to more conservative growth strategies. Cold-affiliated species did not change absolute $\delta^{13}C$ or g_1 values with temperature (Figure 3 and Supporting Information: Figure S4), although STVs do suggest a slight increase in $\delta^{13}C$ with warming (Figure 6). This is consistent with the approximately constant absolute values of LA and LW values and decreasing photosynthetic capacity (Cox et al., 2023) of these species under warmer conditions, as conservative water-use will limit the risk of desiccation (Cowan and Farquhar, 1977; Medlyn et al., 2017) and mortality from hydraulic failure (Rowland et al., 2015). $\delta^{13}C$ can, however, be sensitive to altitudinal variation in CO_2 partial pressure. Lower CO_2 partial pressures at high elevation (Friend & Woodward, 1990) have consistently been found to increase rates of carbon assimilation and lower leaf internal-to-external CO_2 ratio (C_i:C_a), so this must be considered when using the trait as a proxy for plant WUE. Nevertheless, the response of $\delta^{13}C$ to thermal displacement suggests that, under well-watered conditions, warm-affiliated species are more able to adjust WUE to temperature change, consistent with previous evidence that such species generally display greater thermal plasticity (Anderson et al., 2021; Currie et al., 2004; Spasojevic et al., 2014) and are more able to adopt conservative growth strategies in challenging conditions (Sartori et al., 2019). While we acknowledge the limitations of having two warm-affiliated species from the same genus in our investigation, they represent the most abundant family of neotropical lowland plants (*Fabaceae*), so may account for the behaviour of many lowland species.

4.3 | Direct vs indirect temperature effect

Although all individuals were planted in common soils at each site, the warmer temperatures of 22°C and 26°C could have increased soil decomposition and nutrient mineralisation rates, affecting nutrient availability and thus foliar nutrient content (Classen et al., 2015; Rustad et al., 2001) and related structural and water-use efficiency traits. There were, however, no significant differences in foliar traits between non-fertilised and fertilised plants at any site when species were separated by their climatic affiliation (Supporting Information: Figure S5), except LA in *I. spectabilis* at 26°C; this suggests that differences in MAT was the primary driver of observed variability in leaf traits among sites. As these plants were young (c. 6 months after planting) during the measurement period, changes to leaf nutrient content across different ontogenetic stages should, however, be monitored to separate developmental and temperature effects on leaf functional traits. This absence of any indirect temperature effects corresponds with findings for photosynthetic and respiratory traits along the same elevation gradient (Cox et al., 2023), emphasising the overwhelming influence of air temperature on foliar traits in our data set.

5 | CONCLUSION

This study has presented transplant experiments as a method for studying thermal acclimation of different leaf functional traits, as oppose to natural elevation gradient studies which show adaptation responses at the community level to prevailing environmental conditions. From this, it has highlighted the differing responses of leaf functional traits to rapid temperature change across a subset of cold- and warm-affiliated Andean TMF species. When trait values were scaled relative to the maximum observed values reported at home temperature for each trait and species, this revealed more subtle changes with thermal displacement than when absolute values were used and hence may be a more effective means of studying thermal plasticity of leaf functional traits. Our findings suggest that species maximise resource acquisition under optimal environmental conditions, but then shift to more conservative strategies if conditions become less favourable. However, the ability of species to acclimate traits to new environments will be influenced by their climate of origin. When considering absolute trait values, both warm-affiliated species demonstrated a greater ability to acclimate, becoming more conservative in their resource use at colder temperatures by decreasing leaf width (*I. spectabilis* also increased leaf area), increasing leaf nutrient concentrations and increasing water-use efficiency. On the other hand, cold-affiliated species were less able to adjust structural and water-use efficiency traits to warming, suggesting that they maintain conservative growth strategies when changing temperature. Structural traits were less plastic than nutrient or water-use efficiency traits, likely owing to their higher investment costs. The greater thermal acclimation capacity of species from warmer climates could confer upon them a competitive advantage over their cold-originating counterparts under future warming, with implications for community composition in Andean TMFs.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in [Leaf functional trait data from three experimental sites in the Colombian Andes, June-August 2019] at [DOI], reference number [EIDCHELP-63356]. The data has been submitted to and made

available via the UK Centre for Environment and Hydrology (UK CEH) Environmental Information Data Centre.

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SUPPORTING INFORMATION

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