Plants originating from more extreme biomes have improved leaf thermoregulation

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Abstract

Background and Aims

Many plants have some capacity for leaf thermoregulation via stomatal conductance (g_{sw}), such that leaf temperature (T_{leaf}) is rarely coupled with air temperature (T_{air}). The difference between leaf and air temperature (thermal offset, ΔT) and the slope (thermal coupling strength, β) is mediated by interactions between the plant's immediate environment and its leaf traits. This study aimed to determine whether species originating from biomes with contrasting environmental conditions (alpine, desert, coastal temperate) would differ in their tendency to thermoregulate in a common environment.

Methods

Using benign (25°C) and high temperature (38°C) glasshouse treatments, we measured paired canopy T_{air} and T_{leaf} for 15 diverse species, five from each biome, in a common garden experiment. Instantaneous stomatal conductance and a suite of leaf traits were measured and calculated to test for associations with leaf thermoregulation.

Key Results

We found clear evidence for greater leaf cooling occurring during high temperature exposure, especially in alpine and desert species. The leaves of temperate species were largely warmer than air under both treatments. Thicker leaves with higher water content and high stomatal conductance clearly were more effective at cooling. Species originating from different biomes displayed divergent responses of thermal offset and thermal coupling with leaf traits.

Conclusions

Our findings suggest that plants originating from more extreme biomes have innately greater scope for thermoregulation, especially desert plants, which could better counter the risk of reaching excess temperatures at the cost of higher water loss. Leaf thermoregulation is a complex plant-environment interaction, and our work contributes to developing more accurate predictions of leaf temperature during heat exposure across diverse species and biomes.

Keywords: alpine, climate warming, desert, heatwave, leaf temperature, limited homeothermy, stomatal conductance, temperate, thermal coupling, thermal offset, thermal sensitivity, thermoregulation

INTRODUCTION

Extreme climatic events are major contemporary challenges to terrestrial plants (Perkins-Kirkpatrick et al., 2024). Pulse events that include periods of extremely high temperatures, such as heatwaves, are increasing in frequency, intensity, and duration in Australia and are expected to worsen in future decades (Perkins-Kirkpatrick and Lewis, 2020, Cowan et al., 2014). Against the backdrop of accelerated climate warming, heat pulses will expose plants to acute high temperatures that far exceed their typical range (Harris et al., 2018). High temperature affects many physiological and biochemical processes in plants, potentially inflicting injury to tissues and membranes that maintain homeostasis (Goraya et al., 2017). Plants have therefore developed an arsenal of mechanisms to help avoid, tolerate, or acclimate to high temperature to reduce the impact of heat on plant function (Goraya et al., 2017, Nievola et al., 2017, Geange et al., 2021, Deva et al., 2020).

Leaf temperature (T_{leaf}) is central to maintaining photosynthetic performance and metabolic homeostasis (Jones, 2014, Gates, 1968). It is now well established that plants are not necessarily poikilotherms that conform to air temperatures (T_{air}) of their environment (Michaletz et al., 2015, Mahan and Upchurch, 1988), which is apparent from individual leaves (Tserej and Feeley, 2021) to ecosystem canopies (Guo et al., 2023). T_{leaf} can markedly decouple from T_{air} under a range of environmental conditions but is typically exacerbated during periods with high sun exposure and low wind, and during heat pulses and heatwaves (Leigh et al., 2012, Leigh et al., 2017, Hüve et al., 2019, Kullberg et al., 2023, Slot et al., 2021, Kitudom et al., 2022, Manzi et al., 2024). Leaves are often warmer than air when T_{air} is cold and there is sufficient insolation, whereas leaves can be cooler than air when T_{air} is warm and water is available to the plant for transpiration (Michaletz et al., 2015). That is, plants can exhibit limited homeothermy.

The limited homeothermy hypothesis posits that plants can maintain an operative temperature by reducing T_{leaf} through active transpiration (Mahan and Upchurch, 1988). Decoupling of T_{leaf} from T_{air} occurs due to structural properties of the leaf as well as thermoregulatory behaviour (Tserej and Feeley, 2021, Lin et al., 2017, Michaletz et al., 2015). Mechanisms of thermoregulation in plants can be described simply as either passive or active via structural and physiological means (Drake, 2023). Intrinsic leaf structural traits allow plants to passively thermoregulate (e.g. leaf lamina area or width; Leigh et al., 2017) and avoid rapid excursions to temperature extremes by slowing heat transfer (e.g. leaf thickness and water content; Vogel, 2009, Leigh et al., 2012). Differences in leaf structural traits are driven by biome differences or environmental conditions (Lusk et al., 2018, Gibson, 1998); in a common environment, leaf trait differences may be less pronounced among species (Reich et al., 2003). In contrast to passive influences of leaf structural traits, plants can actively thermoregulate by dynamically adjusting stomatal conductance of water vapour (hereafter, g_{sw}) (Guo et al., 2022, Michaletz et al., 2015). Stomata can be finely regulated between closed and fully open states to optimise gas exchange and water loss, as well as to regulate T_{leaf} in the absence of photosynthesis (Matthews et al., 2017, Gates, 1968, Drake et al., 2018).

During drought stress, species differ in their stomatal behaviour and water management strategies along a continuum from avoidance (stomatal closure to limit water loss) to tolerance (stomatal opening allowing dehydration), sometimes referred to as isohydric and anisohydric (Klein, 2014, but see Hochberg et al., 2018). Under high temperature conditions, regulating T_{leaf} depends strongly on active evaporative cooling via transpiration (Marchin et al., 2022, Drake et al., 2018). During a record heatwave that exceeded 48°C, Posch et al. (2024) found dynamic patterns of T_{leaf} during a common garden experiment. T_{leaf} was typically lower than T_{air} when water was readily available, which enabled g_{sw} to be relatively high. Thereafter, a water stress treatment applied during extreme heat led to T_{leaf} exceeding T_{air} (disrupting homeothermy) when water availability was low and g_{sw} was near zero

(Posch et al., 2024). If high temperatures coincide with water limitation, many plant species are unable to transpire to dissipate heat, and therefore leaves can reach damaging temperatures (Cook et al., 2021, Marchin et al., 2022, Posch et al., 2024). By contrast, other species have recently been observed to maintain partially open stomata under high temperatures, even in droughted plants (Marchin et al., 2022).

There is a clear trade-off between water use and active thermoregulation (Fauset et al., 2018). However, species that originate from distinct biomes and/or that have different leaf traits will differ in their thresholds for when and how much stomata are opened based on their relative position on the avoidance-tolerance spectrum (Marchin et al., 2022). Leaf thermoregulation therefore involves more than the biophysical effects of structural leaf traits; stomatal strategy makes a substantive difference to leaf temperature. We therefore expect that species originating from contrasting environments would have developed divergent leaf thermoregulation tendencies or different thermal coupling responses (Blonder and Michaletz, 2018). Cooling via stomatal behaviour can be more effective than the mediating effects of passive leaf traits when sufficient water is available (Lin et al., 2017), though both contribute to thermoregulation strategy.

Two simple temperature metrics encapsulate $T_{\mathrm{leaf}} - T_{\mathrm{air}}$ coupling relationships. The thermal offset (ΔT) describes the magnitude of difference between T_{leaf} and T_{air}, and the thermal coupling strength (β) describes the slope of the relationship between T_{leaf} and T_{air} (Blonder et al., 2020, Blonder and Michaletz, 2018). In nature, leaf thermal offsets can exceed ± 15°C (Blonder and Michaletz, 2018, Fauset et al., 2018, Salisbury and Spomer, 1964, Leuzinger and Körner, 2007). Thermal coupling strength classifies plant thermoregulatory state into three categories: poikilothermy ($\beta \approx 1$), limited homeothermy ($\beta < 1$), and megathermy ($\beta > 1$) (Cavaleri, 2020, Blonder et al., 2020). Blonder et al. (2020) demonstrate that both ΔT and β can differ with environment across a range of T_{air} values in plant species from contrasting North American biomes. Specifically, at cool T_{air}, species from temperate forests and meadows exhibit limited homeothermy: they have T_{leaf} warmer than T_{air} (negative ΔT), but at warm T_{air}, T_{leaf} is cooler than T_{air} and $\beta < 1$. By contrast, those from subalpine meadows were often poikilothermic, but sometimes exhibited megathermy with positive ΔT when T_{air} was high. High desert species were more variable but frequently exhibited megathermy with generally large positive ΔT especially when T_{air} was high.

Plants from hot, arid environments like deserts are frequently exposed to very high T_{air} and may not have water available to freely transpire to reduce T_{leaf} (Cook et al., 2021), such that many desert plants tolerate rather than avoid high T_{leaf} (Curtis et al., 2016). A common adaptation in desert plants is small leaf area to minimise overheating, reduce transpiration, and increase water use efficiency, but some large-leafed desert plants can maintain much higher transpiration rates and relatively low T_{leaf} (Smith, 1978). Many leaf traits contribute to mediating large thermal offsets (Guo et al., 2022). For example, in tropical plants, T_{leaf} readily exceeds T_{air} (Manzi et al., 2024); however, structural leaf traits are not necessarily individually related to ΔT. For example, in tropical shrubs and herbs, no relation was found between ΔT and leaf area, leaf mass per area, or leaf thickness (Pedraza, 2024). Data from dry temperate and tropical trees support the idea that transpirational cooling can be a strategy used to improve net carbon gain, by avoiding leaf mortality or by maintaining temperature homeostasis near the optimal temperatures for photosynthesis (Drake et al., 2018, Slot and Winter, 2017). Alpine plants tend to have strategies that aim to retain heat since their environment is typically limited by cold temperatures, and T_{leaf} can exceed T_{air} by 15°C or more, especially in short-statured plants (Salisbury and Spomer, 1964). Thus, high temperatures that occur during heatwaves and extremely hot days will result in unequal thermal exposure among different plant species, especially those with different thermoregulation strategies.

Determining the drivers of variation in thermal coupling under high temperature conditions should therefore be a priority for understanding impacts to plant performance in the global change context. Although theoretical predictions of how leaf thermoregulation should vary with environments have been established for decades, empirical studies addressing this question are rare. A recent field study along a temperature and precipitation gradient showed that plants from hotter sites showed greater transpirational cooling and that physical leaf traits were important for maintaining thermoregulation (Zhou et al., 2023). To our knowledge, there have not been empirical studies in controlled environments that explore how common-grown species adapted to very different biomes vary in their leaf thermodynamic properties, and the structural or physiological drivers of leaf thermoregulation.

Our overarching goal was to determine how leaf characteristics facilitate or constrain leaf thermoregulation via thermal coupling. Here, we determined ΔT and β in 15 plant species, five from each of three contrasting biomes (alpine, desert, and coastal temperate) under benign and high air temperatures in a controlled-environment glasshouse experiment. We then tested whether leaf structural traits and stomatal conductance were associated with leaf thermoregulation. We hypothesised that species originating from biomes with more extreme climates (alpine and desert) would have greater thermoregulatory capacity than those from more benign climates (coastal temperate). This difference would reflect varying combinations of leaf traits with stomatal strategy. We expected that plants with relatively small and less succulent leaves (i.e. low water content, thinner) might be closer to T_{air}, and plants with conservative (i.e. lower and/or less dynamic) g_{sw} would be most limited in their ability to thermoregulate. Assessing the proximal causes of variation in plant thermoregulation in diverse species under controlled conditions will contribute to improving understanding of plant thermal sensitivity and vulnerability under heat extremes in nature.

MATERIALS AND METHODS

Species, growth conditions, and origin biome information

Five native Australian plant species that each originated from one of three contrasting biomes were chosen to be grown under common conditions in glasshouses at The Australian National University, Canberra, ACT, Australia. The 15 species cover seven families and four growth forms (Table 1). A simple phylogenetic tree of the study species is shown in Figure S1.

Plants used in the experiment were germinated between August and December 2020 from seed accessions obtained from the Australian National Botanic Gardens Seed Bank and the Australian Botanic Gardens Australian PlantBank. Seed accessions were originally collected within a 50 km radius within three distinct biomes (temperate: Wollongong, NSW; alpine: Kosciuszko National Park, NSW; desert: Bourke, NSW) and were stored in these facilities for less than 20 years. Mean climatic parameters of these origin biomes are provided in Table 2. Some species had poor seed germination rates and were purchased as seedings from Monaro Native Tree Nursery, NSW and Bodalla Nursery, NSW at approximately 3 months old, which were then acclimated and grown under the same conditions as plants grown from seed (Table 1). Additional information is available in Harris et al. (2024). The plants were grown in common garden well-watered conditions (watered to field capacity daily) in shade houses. Plants were transplanted in August 2021 to large pots (150-200 mm diameter and at least 200 mm depth) based on their individual size. The plants had grown for approximately 12-18 months prior to being moved to glasshouse conditions for this experiment in January-February 2022 (Austral summer) and ranged in size from 0.15-1.5 m in height at the time of the experiment. We used five replicate plants of each species for the temperature experiment. The plants were watered to saturation in the morning, prior to applying the temperature treatments to plants in controlled glasshouse rooms from 1200 h to 1500 h, where the initial 30-minute period from 1200 h to 1230 h was considered temperature equilibration time. Plants did not show visual signs of water stress (i.e. they did not run out of water during the treatment phase) and were re-watered following the treatments.

Temperature treatments

Two temperature treatments referred to as 'benign' and 'high temperature' were applied sequentially using controlled temperature glasshouse rooms. The benign glasshouse room was set to 25°C (0600 h-2000 h) during the day and high temperature glasshouse room was set to 38°C. The high temperature of 38°C was chosen as a temperature that would be sufficiently stressful, but not lethal, for all species (Harris et al., 2024). Both treatment glasshouses were set to and 16°C overnight (2000 h-0600 h). All plants (n = 75) were moved from their shade house to the benign room 14 days before the experiment began, to allow for acclimation to the higher light environment. Preliminary tests of high temperature treatment duration effects on plant temperatures showed that ΔT (calculated as $T_{\mathrm{leaf}} - T_{\mathrm{air}}$) of 10 test plants averaged over 2.5 h was not different from longer periods of 4 or 6 h of high temperature exposure, therefore the 2.5 h duration (i.e. 1230 h-1500 h) was used. The experiment was conducted over six separate days (three for each treatment), where 30 plants were measured at a time. T_{air} at canopy level averaged across each of the plants during the treatments over 2.5 h was approximately 23.2°C in benign and 35.7°C in high temperature treatments (Figure 1). Glasshouse conditions during the treatments were as follows for benign: temperature (T_{gh}) = 26.3±0.6°C, relative humidity (RH) = 30.5±4.5%, and vapour pressure deficit ($\mathrm{VPD}_{\mathrm{air}}$) = 2.4±0.5 kPa; and high temperature: T_{gh} = 38.5±0.4 °C, RH = 23.8±3.4%, and $\mathrm{VPD}_{\mathrm{air}}$ = 6.3±0.3 kPa (full details in Table S1).

Leaf temperature measurements

Leaf temperature (T_{leaf}) measurements were taken using data loggers (Onset HOBO UX120-014M; Onset Computer Co., MA, USA) and type-T thermocouples on mature, fully expanded, sun leaves emerging from the main stem or central part of each plant. Each thermocouple for measuring T_{leaf} was firmly attached to the underside of a leaf using porous surgical tape, and the thermocouple wire was supported by malleable wire on the stem to hold it in position without altering the natural leaf position. A second thermocouple was also anchored to the main stem of each plant, with the thermocouple tip open to air shielded from direct sunlight. This pairing enabled us to measure T_{air} immediately adjacent to the thermocouple measuring T_{leaf}. The data loggers recorded temperature at 1-minute intervals from 1200 h to 1500 h.

Plants that were wired for temperature measurements under benign conditions were then transferred to the high temperature conditions 2-4 days later at approximately 1100 h. Wherever possible, after the benign treatment the thermocouples were left in position so that the T_{leaf} and T_{air} measurements were taken from the same location in both treatments. If a leaf began to discolour or the thermocouple detached and could not be easily reattached, the thermocouple was moved to the nearest healthy, mature leaf to capture a similar microclimate. Logged measurements were trimmed to above 16°C for the benign treatment and 31°C for the high temperature treatment, to exclude data when glasshouse evaporative coolers were active as air circulation patterns during the active heating/cooling cycles introduced high variance and did not address our scientific questions (~10% of the data; Fig. 1A, B). We calculated the thermal offset (ΔT), as $T_{\mathrm{leaf}} - T_{\mathrm{air}}$ (°C) between 1230 h and 1500 h to allow for temperatures to equilibrate. Negative ΔT values occur when leaves are cooler than air and positive ΔT values occur when leaves are warmer than air (Fig. 1C, D). We also calculated thermal coupling strength (β) as the slope of the relationship between T_{leaf} and T_{air} at 30-minute intervals, following Blonder et al. (2020). Mean temperature responses per species are shown in Table S2.

Stomatal conductance

Stomatal conductance to water (g_{sw}; mol m^{-2} s^{-1}) of light-adapted leaves was measured using a porometer-fluorometer (LI-600; LI-COR Biosciences, NE, USA). Transpiration (E) correlated strongly with g_{sw} (Pearson's $r = 0.90$); therefore, we report only the g_{sw} results. g_{sw} was measured on the same leaf that had the T_{leaf} thermocouple attached wherever possible, and species with small or compact leaves had g_{sw} measured on the closest mature, similar leaf. There were 18 (out of 75) plants for which g_{sw} could not be measured due to small leaf size, therefore there were $n = 57$ plants in each temperature treatment for which there were a complete set of leaf traits for Principal Components Analysis. g_{sw} measurements were taken twice between 1330 h and 1430 h, after the plants had been exposed to the treatments for at least 1.5 h, and the mean of both measurements was used.

Leaf structural traits

After completing T_{leaf} and T_{air} measurements for both benign and high temperature treatments, the same leaves that were measured for temperature were carefully excised from the plant to measure structural traits. Leaf wet mass (mg) was measured with a precision balance (ML203T; Mettler-Toledo, OH, USA), then leaf area (LA; cm^2) using the *leafscan* app (Anderson and Rosas-Anderson, 2017), and leaf width (LW; mm) leaf thickness (LT; mm) with precision callipers. The leaves were then placed in an oven at 60°C for at least 72 h to dry completely. Dried leaves were then weighed for dry mass (mg), allowing the calculation of leaf water content (LWC; (wet mass – dry mass) / wet mass), leaf density (LD;

dry mass / (LA × LT); g cm^{-3}), leaf mass per area (LMA; dry mass / leaf area; kg m^{-2}), and leaf dry matter content (LDMC; dry mass / wet mass; kg kg^{-1}). Summary statistics for individual traits are shown in Table S3.

Thermal time constant

We calculated the theoretical leaf thermal time constant (τ; s) as a mechanistic composite trait that links leaf traits to time-dependent decoupling of T_{leaf} from ambient conditions in the absence of thermoregulation via latent heat flux (Michaletz et al., 2016, Michaletz et al., 2015, Bison and Michaletz, 2024).

$$\tau = \varphi \cdot \mathrm{LMA} \cdot \left[\frac{c_{p,w}}{\mathrm{LDMC} \cdot h} + \frac{c_{p,d} - c_{p,w}}{h}\right]$$

Values for parameters (φ, $c_{p,w}$, $c_{p,d}$) were as defined by Bison and Michaletz (2024), i.e. φ (the ratio of projected to total leaf area) was taken to be 0.5, specific heat capacities $c_{p,w}$ and $c_{p,d}$ were taken as 4181 and 2814 J kg^{-1} K^{-1}, respectively, and h is an heat transfer coefficient (W m^{-2} K^{-1}) that depends on leaf width (Michaletz et al., 2016). Small values of τ represent leaves that change temperature rapidly in response to environmental temperature changes, and large values correspond to leaves that respond slowly. For additional information see Appendix S1.

Statistical analyses

To test the nature of thermal decoupling (ΔT and β) under benign and high temperature treatments across different species originating from the three biomes, we fitted linear mixed effects regression (LMER) models. The temperate biome species and benign temperature treatment were used as reference levels and all models contained random effect (intercept) terms for growth form, species nested within taxonomic family, and plant ID to account for repeated measures on the same plants. LMER models were fitted with either ΔT or β as the response variable with treatment, biome, and their interaction as categorical fixed effects.

To determine the effects of the combined leaf traits and their interaction with biome on ΔT and β, LMER models were initially fitted to the benign and high temperature treatments separately. We generated composite leaf traits in two ways: Principal Components Analysis (PCA) and the thermal time constant (τ). For PCA, we included the five passive leaf traits (LA, LW, LT, LWC, LD) and the active leaf trait (g_{sw}), which generated two major axes of variation (PC1 and PC2; Table S4). For these models, the random effects of species and growth form explained near-zero variance due to redundancy with the leaf traits, therefore simplified linear models were fitted to the benign and high temperature treatments separately to determine the effects of composite leaf traits on ΔT and β. These models included two-way interactions between either PC1 and PC2 or τ with biome. We applied type-III analyses of variance (ANOVA) with Satterthwaite's degrees of freedom (*df*) to LMER models, followed by Tukey's Honest Significant Differences post-hoc tests with Kenward-Roger's *df* for reporting. Post-hoc tests compared pairwise differences among combinations of biome and treatment. The 95% confidence intervals were obtained using nonparametric bootstrapping with the *mean_cl_boot* function from *Hmisc* (Harrell, 2019). All data analyses were conducted in R 4.3.1 (R Core Team, 2023) using *lme4* (Bates et al., 2015), *performance* (Lüdecke et al., 2021), *emmeans* (Lenth, 2023), *factoextra* (Kassambara and Mundt, 2020), and *tidyverse* R packages (Wickham et al., 2019).

RESULTS

Leaf thermal decoupling depends on both biomes and temperature treatments

We hypothesised that species originating from the more extreme alpine and desert climates would have greater thermoregulation tendency (ΔT differing from 0 and β differing from 1, exhibiting either megathermy or limited homeothermy) than those originating from the more benign temperate climate. The overall effect of treatment on ΔT was significant (Table 3), where high temperature conditions resulted in significantly more negative ΔT (cooler leaves) than the benign treatment (Fig. 1). There was substantial variation in T_{leaf} along the T_{air} continuum both within and among biomes (Fig. 2A). On average, ΔT was positive for temperate species under both benign (1.99±1.30°C) and high temperature (0.60±0.91°C) treatments (Fig. 2B). For both alpine and desert species, ΔT was positive under benign (alpine: 0.63±1.01°C, desert: 0.50±1.05°C) and negative under high temperatures (alpine: –1.25±0.77°C, desert: –1.66±0.92°C).

The effect of biome on ΔT was significant (Table 3), with alpine and desert species having approximately 1.2°C cooler leaves than temperate species in both treatments (Fig. 2B). However, there were no significant interactions between biome and treatment (Table 3), such that the magnitude of difference in ΔT across biomes was consistent under both treatments (Fig. 2B). Post-hoc tests revealed that pairwise temperature treatment differences in ΔT were significant within each biome (Fig. 2B; Table S5). The temperate species were significantly different from desert species under either benign or high temperature, and different from alpine species under high temperature (Fig. 2B; Table S5).

Thermal coupling strength (β) was significantly higher under high temperature, but not significantly different among biomes (Table 3, Fig. 2C). Species from all biomes typically exhibited limited homeothermy ($\beta < 1$) under benign conditions, but at high temperature, on average temperate species exhibited megathermy ($\beta > 1$) while alpine and desert species exhibited poikilothermy ($\beta \approx 1$) (Fig. 2C). β differed significantly between treatments in only the temperate and desert species, and the only other significant contrast was the temperate species under high temperatures compared to desert species under benign conditions (Fig. 2C; Table S5).

Taxonomic and growth form differences explained relatively small variance proportions (in both temperature treatments, for both ΔT and β) beyond that explained by biome (Table 3). Across species, ΔT showed similar patterns under both temperature treatments (Fig. 3), with a few notable exceptions. *Acacia longifolia* (temperate) had the highest ΔT among temperate species under benign conditions but the lowest ΔT under high temperature conditions (Fig. 3). *Eucalyptus largiflorens* (desert) also shifted from positive ΔT under benign conditions to a strongly negative ΔT under high temperature conditions (Fig. 3). The most negative ΔT were achieved by two desert Acacia species, *A. salicina* and *A. aneura*. Both these species could cool their leaves below T_{air} by more than 3°C under high temperature conditions; > 1°C greater cooling than any other species tested.

Leaf traits can moderate thermoregulation

Species-level leaf traits are shown in Fig. S2, and the relationships of individual leaf traits and thermal coupling are shown in Fig. S3. Given the strong effect of temperature treatment on ΔT and β, we analysed the effects of composite leaf traits on thermal coupling in each treatment separately. Biome was accounted for in all models and was significant in all cases except β at high temperature, indicating that biome differences contributed to thermoregulatory differences indirectly (Table 4).

The composite leaf trait major axis (PC1) can be interpreted as an axis from negative values representing thick, less dense leaves with high water content, and high stomatal conductance to positive values increasing toward thin, dense leaves with low water content, and low stomatal conductance Fig. 4A,C). The other dominant composite leaf trait axis (PC2) can be interpreted as a continuum from negative values representing wider, larger leaves to positive values increasing toward narrower, smaller leaves (Fig. 4B,C). The three biomes formed generally distinct clusters in principal component space. The leaves of alpine species were defined by negative PC1 (thick, less dense, high water content, high g_{sw}) and a narrow range of slightly negative PC2 (Fig. 4C). The leaves of temperate species were defined by positive PC1 (thin, dense, low water content, low g_{sw}) but spanned a wide range along PC2 (broad and large to narrow and small) (Fig. 4C). The leaves of desert species covered a wide range of PC1, but all were positive along PC2 (small and narrow leaves) (Fig. 4C).

Thermal offset (ΔT) increased significantly as PC1 increased in both treatments (Table 4). That is, leaves that were thin, dense, had low water content, and relatively low g_{sw} characteristics tended to be warmer than air (Fig. 5A). Thermal coupling strength (β) increased significantly as PC1 increased in the high temperature treatment (Table 4). That is, leaves that were thicker, less dense, had high water content and high g_{sw} exhibited limited homeothermy while leaves that were thinner, denser, had low water content and low g_{sw} exhibited megathermy (Fig. 5B). There was a marginally non-significant interaction between PC1 and biome (Fig. 5A,C; Table 4). Neither ΔT nor β were significantly related to PC2 (Fig. 5C,D; Table 4). The relationship between ΔT and thermal time constant (τ) was not significant overall, but did significantly differ among biomes (Fig. 5E; Table 4). Desert species had a negative relationship between ΔT and τ, while temperate and alpine had a positive relationship, and these patterns were consistent in both treatments (Fig. 5E; Table 4). Thermal coupling strength (β) showed no significant relationships with τ or the interaction between τ and biome in either treatment (Fig. 5F; Table 4).

DISCUSSION

Here we have shown that these diverse plant species that originate from contrasting biomes clearly differ in their thermoregulation under both benign and high temperature conditions. Our hypotheses about the drivers of variation in plant thermoregulation were largely supported: variation in T_{leaf}, ΔT, and β during high temperatures were dependent on origin biome and composite leaf traits, especially leaf water content and g_{sw}. Different species exposed to nearly identical conditions will reach different T_{leaf} due to the unique interactions of their leaf properties with the environment (Perez and Feeley, 2020). Thus, understanding the sources of variation in T_{leaf} is essential: empirical data informs leaf energy budget theory and more accurate predictive models of T_{leaf} (Kearney and Leigh, 2024, Michaletz et al., 2015, Blonder et al., 2020).

Plants from extreme climates can thermoregulate more effectively

Our hypothesis that species originating from biomes with more extreme climates would have greater thermoregulatory tendency than those from more benign climates, was generally supported. That is, the adaptations a plant has to the environmental conditions of its biome of origin explain thermoregulation even under common conditions. Temperate species had leaves that were almost always warmer than air, whereas the leaves of alpine and desert species were equivalent to T_{air} under benign conditions but often much cooler than air at high temperatures. Species from all biomes showed limited homeothermy ($\beta < 1$) under benign conditions, but at high temperature, most exhibited poikilothermy ($\beta \approx 1$).

Leaf thermoregulation is thought to originate from selection on leaf traits to maximise carbon gain in their environment (Michaletz et al., 2016). That is, plants will maintain T_{leaf} within an optimal range for photosynthesis via variable stomatal opening to actively thermoregulate at an approximate crossover point when T_{leaf} reaches ~27-30°C and ΔT becomes negative (Michaletz et al., 2016, Dong et al., 2017). Experimental tests of the limited homeothermy hypothesis found that cotton (*Gossypium hirsutum*) exhibited poikilothermy until T_{air} reached 27°C, then switched to limited homeothermy when T_{air} was 27-40°C to maintain $T_{\mathrm{leaf}} = 27\pm2$°C, when water was available for transpiration (Upchurch and Mahan, 1988). However, recent large-scale analyses of canopy temperatures generally do not support a hypothesis of universal limited homeothermy; rather, there is evidence for a diverse range of viable thermoregulation strategies (β range: 0.7-1.3) (Guo et al., 2023, Still et al., 2022, Manzi et al., 2024). Our current study provides empirical support for these recent analyses at a smaller scale, where plants (on average) exhibited limited homeothermy under benign conditions, but a wide range of β under high temperatures.

Potential links between leaf thermoregulation and photosystem heat tolerance

A common measure of photosystem heat tolerance is T_{crit}, the critical temperature for photosystem II functional impairment and subsequent damage, which is derived from ramping assays of the temperature-dependent change in chlorophyll *a* fluorescence (Arnold et al., 2021). Many of the species in the present study are known to differ in T_{crit} from field surveys (Briceño et al., 2024) and controlled-environment experiments (Harris et al., 2024). Drawing links between T_{crit} from these studies and thermoregulation from our study returns some unexpected outcomes. Notably, *Dodonaea viscosa* was one of the least heat tolerant desert species in the aforementioned studies (controlled 25°C environment: 39.9±1.0°C, field: 45.4±0.5°C), while in the present study it had the highest T_{leaf} and $\Delta T \approx 0$°C under high temperature conditions. The relatively low heat tolerance thresholds of the alpine *Eucalyptus pauciflora* (controlled 25°C environment: 42.7±1.7°C, field: 39.0±0.8°C), and the temperate

Acacia binervata (controlled 25°C environment: 42.0±1.5°C), which both had positive ΔT values at high temperatures in the present study, is consistent with this pattern. The reverse is true for the desert *Acacia* species, which are both extremely heat tolerant (*A. salicina*: controlled 25°C environment: 46.9±0.8°C, field: 49.6±0.8°C; *A. aneura*: controlled 25°C environment: 48.6±0.9°C, field: 53.0±4.0°C), and here were found to have the lowest T_{leaf} and negative ΔT values at high temperatures.

We advocate for testing the association of thermal coupling metrics and heat tolerance as a focus of future investigations. It initially appears counter-intuitive that a species should have adaptations to avoid and tolerate high temperatures concurrently. In an extremely hot and dry environment, plants may typically avoid the worst of heat stress through their structural leaf properties and evaporative cooling via transpiration. Yet, sustained dry conditions may render evaporative cooling an unviable option for avoiding heat, and high heat tolerance would become necessary (Gong et al., 2023). A species that does not cool T_{leaf} below T_{air} (or only cools moderately), may indicate limited capacity for cooling or a high heat tolerance threshold before initiating cooling. As such, we hypothesise that the tendency to cool T_{leaf} below T_{air} could be associated with higher heat tolerance in some species, but that it will likely also depend on water use strategy.

Composite leaf traits contribute to thermoregulation at high temperature

The dominant axis of variation (PC1) was defined by three structural leaf traits: leaf thickness (LT), density (LD), water content (LWC), and the active leaf trait: stomatal conductance (g_{sw}). PC1 correlated strongly with ΔT in benign and ΔT and β in high temperature conditions. PC2, which was largely defined by leaf area (LA) and leaf width (LW) had relatively little consistent relationship with ΔT and β in either environment. LWC plays a key role in leaf thermoregulation and leaf economics (Wang et al., 2022, Michaletz et al., 2015). The specific heat capacity correlates positively with water content of leaves

(Zhang et al., 2025), and there is also a strong positive association between LWC and maximum g_{sw} (Zhou et al., 2023). Water availability to plants is generally linked to the capacity to regulate T_{leaf} (Cook et al., 2021, Lambers and Oliveira, 2019, Manzi et al., 2024), and the transport and storage of water directly in leaf tissues can reduce heat loading while facilitating greater cooling (Zhou et al., 2023). In desert species, thicker leaves (that often also have higher LWC) have slower heating response times relative to thinner leaves, resulting in lower T_{leaf} during temperature extremes, even in the absence of transpiration, but the effect is reduced for large leaves (Leigh et al., 2012). Our study shows that leaf cooling is more effective in plants that have higher LWC, LT, and lower LD under both temperature treatments.

Combinations of leaf functional and energy budget traits, and environments across 41 species and seven sites along an elevation gradient showed that regression approaches achieved relatively low predictive power for ΔT and especially for β (Blonder et al., 2020). In their study, the site environment played a more substantial role than commonly measured functional traits and energy balance traits, and interactions between traits and environment were relevant. Blonder et al. (2020) conclude that the low predictability of thermal coupling and the variation encountered at a given site indicate that a range of strategies will result in viable performance. Our results are consistent with these findings: variation in ΔT was more readily explained than β. The common environment approach we used highlights that both external environment (temperature treatment) and origin biome strongly influence ΔT, whereas only environmental conditions influence β.

The thermal time constant (τ) differed among plants from the different biomes. The alpine plants in this study had a relatively large values of τ, indicating that they respond more slowly to environmental changes than the desert or temperate plants, which could be to buffer against the rapid environmental temperature fluctuations that naturally occur in the alpine (Körner, 2003). We also found that the relationship between τ and ΔT differed among biomes, being positive for temperate and alpine plants, such that leaves that respond relatively slower to environmental changes were warmer than air or at least cooled less effectively. In contrast, the leaves of desert plants that respond relatively slower to environmental changes were nonetheless far more effective at cooling below T_{air}, especially compared to temperate plants. That is, for the same value of τ, ΔT differed by up to 4°C between desert and temperate plants, which suggests that g_{sw} was the main driver of these differences as it is not involved in the calculation of τ. The dynamic fluctuations of T_{air} in glasshouse conditions suggests that T_{leaf} may not frequently reach steady state within the range of τ, thus delays in both leaf warming and cooling may influence the relationships between traits and thermoregulation. All plants had access to adequate water throughout the heat event and could have transpired freely; however, desert plants transpired far more than temperate plants under both temperature treatments. If the desert plants with larger τ values opened their stomata earlier to achieve high g_{sw} and did so for longer than temperate plants with larger τ values, then that could explain why the leaves of these desert plants were much cooler than air and why relationships with ΔT differed between these biomes.

Inherently low stomatal conductance limits evaporative cooling

We predicted that species with inherently low g_{sw} would be most limited in their thermoregulation. Generally, high g_{sw} strongly reduced ΔT, which was consistent across biomes except for temperate species under benign conditions. Stomatal conductance and LWC both play pivotal roles in enabling leaf cooling at high temperature, thus reducing T_{leaf} on acutely hot days and during heatwaves will clearly depend on water availability and water use strategies (Marchin et al., 2022, Cook et al., 2021, Aparecido et al., 2020, Drake et al., 2018, Manzi et al., 2024). The temperate species originate from a biome that is typically not water limited, yet these species appear to be more limited in their tendency for thermoregulation via regulating stomata. One potential explanation for this is the intricate link between temperature and VPD. Increases in VPD are a major concern with climate change as it can also limit evapotranspiration by exacerbating water stress and forcing stomatal closure (Grossiord et al., 2020). While the relative humidity in our glasshouse experiment was generally low enough to enable cooling to take place (Mahan and Upchurch, 1988), VPD increased under the high temperature treatment. The lower g_{sw} in the species originating from the coastal temperate biome likely responded to the high temperature (with relatively high VPD) treatment by closing stomata more than alpine and desert species that are adapted to typically drier air.

An alternate explanation is that these coastal temperate species have intrinsically lower g_{sw} or slower stomatal response to high temperatures compared to species that originated from more extreme climates. For example, some desert and alpine species can open their stomata rapidly to optimise the trade-offs between carbon fixation, water loss, and leaf thermoregulation during narrower windows of suitable conditions in these challenging environments (Fernández-Marín et al., 2020, Knapp and Smith, 1988, 1991). Glasshouse experiments with plants originating from hot dry and hot wet habitats suggest that transpiration is greater in species from hot dry habitats that have sporadic rain (Lin et al., 2017), supporting the idea that extreme climate is a driver of thermoregulation strategy. Similar to our study, those authors found that cooling via stomatal behaviour was more effective than passive leaf traits when water was sufficient (Lin et al., 2017). We infer that high T_{air} in our high temperature treatment likely increased T_{leaf} to a point that exceeded the heat load that most of the temperate species could dissipate via transpiration.

Leaf thermoregulation is a complex plant-environment interaction

Plant species are often interpreted as being on an water stress avoidance-tolerance (isohydric-anisohydric) spectrum; however, but rather than being a simple plant hydraulic trait, isohydrocity is a complex plant-environment interaction (Hochberg et al., 2018). Leaf thermoregulation seems analogous to this complexity. There are many causes for leaf thermoregulation depending on the plant's immediate environment. For example, thermoregulation can optimise photosynthesis, but it also plays a role in hydraulic maintenance, and then at extreme temperatures, thermoregulation facilitates avoiding heat damage in the absence of photosynthesis (Drake et al., 2018, Slot and Winter, 2017, Guo et al., 2022, Fauset et al., 2018). Therefore, the balance among the available thermoregulation mechanisms depends on these dynamic plant-environment interactions (Guo et al., 2023). Contrasting patterns of leaf thermoregulatory traits and strategies among provenances across tropical trees demonstrates that warm-adapted provenances are not necessarily less vulnerable to heat stress based on their operating temperatures and heat tolerance (Middleby et al., 2024). Elucidating the mechanisms that underlie differences in thermoregulatory strategies of plants across different origin biomes will be essential empirical research for applications to plant breeding and management of wild populations. Determining the physical leaf and stem properties and the underlying genetic markers and mechanisms for stomatal responsiveness that contribute to variation in plant thermoregulation and plasticity therein could be used to identify and select on target traits (Fritz et al., 2018).

CONCLUSIONS

Advanced tools for rapidly estimating leaf size (Leigh, 2022, Schrader et al., 2021) and predicting leaf temperatures based on biophysical modelling with microclimates and energy budgets are now available (Kearney and Leigh, 2024). The accuracy of predicted leaf temperatures requires capturing and understanding the diversity of functional leaf traits and stomatal conductance behaviour, which can have a large impact on T_{leaf} predictions (Kearney and Leigh, 2024, Perez and Feeley, 2020). Our study provides empirical evidence that species from contrasting biomes that are exposed to common conditions (benign or high temperature) will respond to the conditions by regulating T_{leaf} to different extents. We also identify that composite leaf traits explain variation in leaf thermoregulation among species. Our findings suggest that, beyond simple expectations of leaf size, species from a coastal temperate biome appear to possess a suite of thermoregulatory traits more likely to increase exposure to heat stress, particularly if combined with dry conditions, than those adapted to more extreme conditions. The increasingly extreme environmental conditions that are occurring during the Anthropocene is exerting significant pressure on plants in many regions to avoid, tolerate, and acclimate to higher temperatures. Further work should evaluate interactive effects among temperature, VPD, and water availability to discern the impacts of these major global change factors on leaf thermoregulation.

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AUTHOR CONTRIBUTIONS

VFB and PAA conceptualised the study with input from AMC, ABN, and AL; MJW collected the data; PAA analysed the data and wrote the manuscript; all authors contributed to editing.

DATA AVAILABILITY

Data and R code are available from the Figshare digital repository: https://doi.org/10.6084/m9.figshare.28741331.

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Tables

Table 1. List of the 15 species studied including their biome of origin, taxonomic family, general growth form, and origin of plant material used in the experiment.

Species	**Biome**	**Family**	**Growth form**	**Plant material**
Eucalyptus pauciflora	Alpine	Myrtaceae	Tree	Nursery
Leptorhynchos squamatus	Alpine	Asteraceae	Forb	Nursery
Oxylobium ellipticum	Alpine	Fabaceae	Shrub	Seedbank
Ranunculus graniticola	Alpine	Ranunculaceae	Forb	Nursery
Xerochrysum subundulatum	Alpine	Asteraceae	Forb	Nursery
Acacia binervata	Temperate	Fabaceae	Tree-shrub	Seedbank
Acacia longifolia	Temperate	Fabaceae	Tree-shrub	Seedbank
Backhousia myrtifolia	Temperate	Myrtaceae	Tree	Seedbank
Melaleuca hypericifolia	Temperate	Myrtaceae	Tree-shrub	Nursery
Pittosporum undulatum	Temperate	Pittosporaceae	Tree-shrub	Nursery
Acacia aneura	Desert	Fabaceae	Tree-shrub	Seedbank
Acacia salicina	Desert	Fabaceae	Tree-shrub	Seedbank
Dodonaea viscosa	Desert	Sapindaceae	Shrub	Seedbank
Eucalyptus largiflorens	Desert	Myrtaceae	Tree	Seedbank
Flindersia maculosa	Desert	Rutaceae	Tree	Seedbank

Table 2. Environmental conditions of biomes of origin based on averages of down-sampled long-term (1981-2010) climate data from CHELSA v2.1 database (Karger et al., 2017) using field locations for these alpine, temperate, and desert biomes (Briceño et al., 2024).

Biome	**MAT (°C)**	**MinT (°C)**	**MaxT (°C)**	**T_{range} (°C)**	**MAP (mm)**
Alpine	4.5	–5.2	16.5	22.7	1764
Temperate	16.5	7.4	24.6	17.2	1285
Desert	20.2	4.5	36.0	31.5	332

Note: MAP = mean annual precipitation, MAT = mean annual temperature, MinT = mean minimum temperature of the coldest month, MaxT = mean maximum temperature of the warmest month, T_{range} = MaxT - MinT).

Table 3. Type III ANOVA outputs from linear mixed effects regression (LMER) models that test the contributions of temperature treatment and biome on thermal offset (Δ*T*) and thermal coupling strength (β). Bold indicates significance at $p < 0.05$. Random effects are reported from the LMER summary.

Response: Thermal offset (Δ*T*)						
Fixed effect	***F***	***df***	***p***	**Random effect**	**SD**	**Var. (%)**
Treatment	77.893	1,72	**< 0.001**	Species	< 0.001	0.0
Biome	22.332	2,45	**< 0.001**	Family	0.430	6.6
Treatment × Biome	0.543	2,72	0.584	Growth form	0.665	15.8
				Plant ID	0.667	15.9
$R^2 = 0.545$				Residual	1.313	61.7

Response: Thermal coupling strength (β)						
Fixed effect	***F***	***df***	***p***	**Random effect**	**SD**	**Var. (%)**
Treatment	27.244	1,132	**< 0.001**	Species	0.033	3.5
Biome	2.230	2,7	0.181	Family	0.052	8.7
Treatment × Biome	0.205	2,132	0.815	Growth form	0.009	0.3
				Plant ID	< 0.001	0.0
$R^2 = 0.190$				Residual	0.165	87.6

Table 4. ANOVA outputs from linear regression models that test the contributions of biome and leaf traits as principal components (PC1 and PC2) or as a composite thermal time constant (τ) on thermal offset (ΔT) and thermal coupling strength (β) separately under benign and high temperature conditions. Bold indicates significance at $p < 0.05$ and italics indicates $p < 0.1$.

	Thermal offset (ΔT)				**Thermal coupling strength (β)**			
	Benign		**High temperature**		**Benign**		**High temperature**	
Fixed effects	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Biome	6.178	**0.004**	23.349	**<0.001**	4.076	**0.023**	1.512	0.231
PC1	5.730	**0.021**	25.554	**<0.001**	1.938	0.170	4.207	**0.046**
PC2	0.489	0.488	0.847	0.362	0.787	0.380	0.061	0.807
Biome × PC1	2.934	*0.063*	0.115	0.892	1.194	0.312	0.454	0.638
Biome × PC2	0.442	0.645	1.041	0.361	1.732	0.188	0.019	0.981
Biome	6.000	**0.005**	19.845	**<0.001**	3.732	**0.031**	1.575	0.217
τ	0.225	0.638	0.015	0.902	0.067	0.797	0.006	0.940
Biome × τ	3.996	**0.024**	7.091	**0.002**	0.369	0.693	2.215	0.120

Figure legends

Figure 1. Temperature profiles and relationships between air temperature (T_{air}) and leaf temperature (T_{leaf}) in the glasshouse experiment. **A**) Canopy T_{air} and **B**) T_{leaf} profiles over time across all plants for the benign and high temperature treatments during the experiment. Coloured dashed lines represent the glasshouse set temperatures for each treatment. Data shown are means ± 95% confidence intervals across six days over measurement. Relationship between T_{air} and T_{leaf} in **C**) the benign treatment and **D**) the high temperature treatment. Black dashed lines represent an isometric relationship, and coloured solid lines are simple linear regressions ± 95% confidence intervals.

Figure 2. Canopy leaf and air temperature relationships, thermal coupling strength, and thermal offsets among species from three biomes and two temperature treatments. **A)** The overall raw data for relationships between T_{leaf} and T_{air}, where linear regressions are fitted to individual plants. **B)** Mean thermal offsets (ΔT), which is the magnitude of the difference $T_{\mathrm{leaf}} - T_{\mathrm{air}}$. **C)** Mean thermal coupling strengths (β), which is the slope of the relationship between T_{leaf} and T_{air}, calculated at 30-minute intervals. $\beta > 1$ indicates megathermy, $\beta < 1$ indicates limited homeothermy, and $\beta \approx 1$ indicates poikilothermy. Data shown are means ± standard errors. The grey lines for all panels (isometric, $\beta = 1$, $\Delta T = 0$) indicate when T_{air} and T_{leaf} are equivalent.

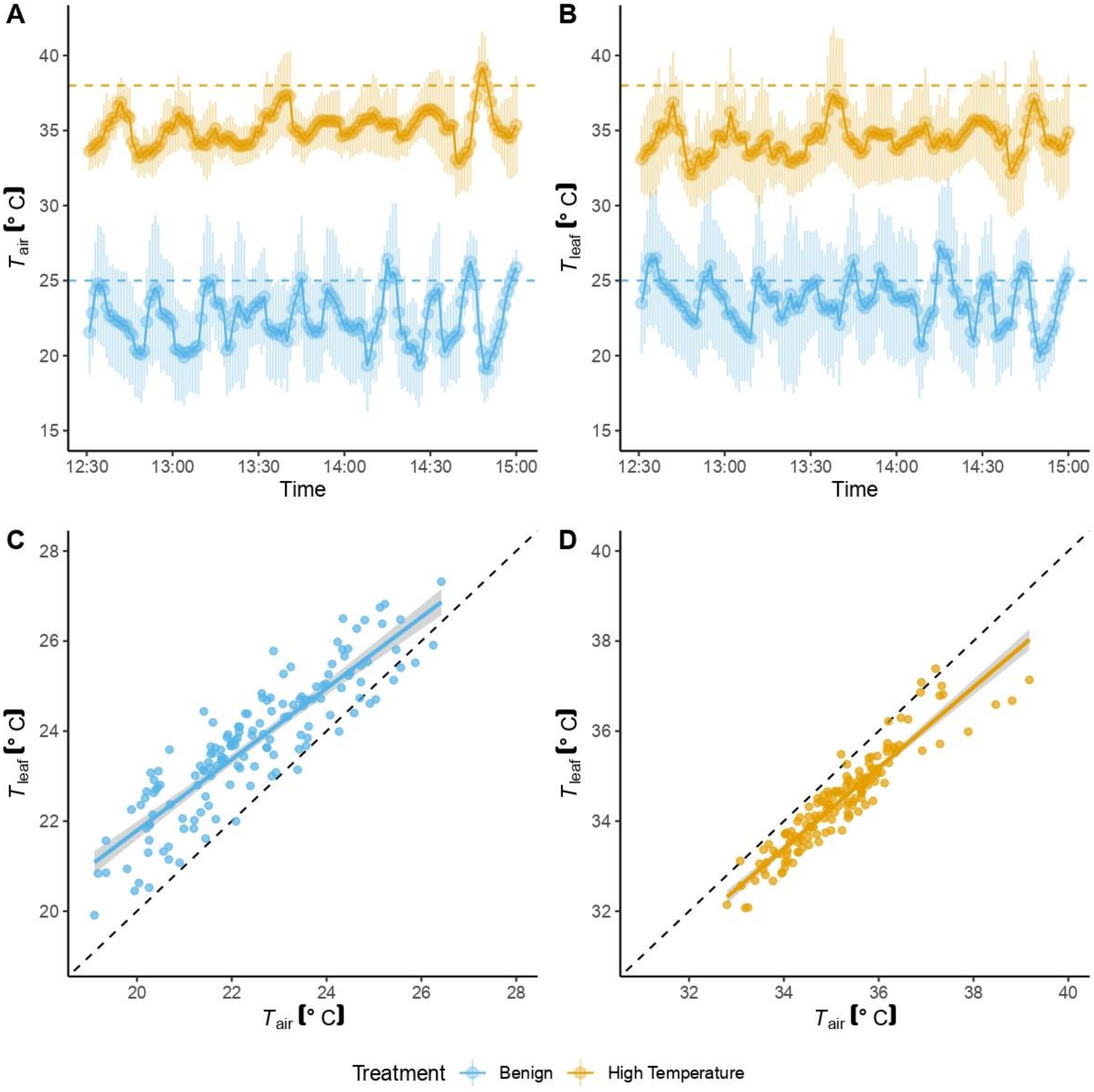
Figure 3. Thermal coupling parameters across species. **A)** Thermal offsets (ΔT) and **B)** thermal coupling strength (β) under benign (left) and high temperature (right) treatments for each of 15 species

originating from three biomes. Data shown are means ± bootstrapped 95% confidence intervals. The dashed grey line at $\Delta T = 0$ and $\beta = 1$ indicates when T_{air} and T_{leaf} are equivalent.

Figure 4. Principal Components Analysis (PCA) of six leaf traits: leaf water content (LWC), leaf area (LA), leaf thickness (LT), leaf water content (LWC), leaf density (LD), and stomatal conductance to water (g_{sw}). Contributions of each leaf trait to **A)** PC1 and **B)** PC2 major axes. Red dashed line corresponds to the expected value if contributions were uniform among traits, where grey bars that are higher than the red line indicate dominant variables to that principal component. **C)** Principal Component space of dominant PC1 and PC2 axes that together explain 75.7% of the variance in the leaf traits. Coloured ellipses represent the 95% confidence space for each biome.

Figure 5. Relationships between leaf thermal coupling and composite leaf traits from Principal Components Analysis (PC1 and PC2 axes) and thermal time constant (τ). **A)** Thermal offset (ΔT) in relation to leaf traits PC1, and **B)** thermal coupling strength (β) in relation to leaf traits PC1 under benign and high temperature treatments. **C)** ΔT and **D)** β in relation to leaf traits PC2. **E)** ΔT and **F)** β in relation to τ. Raw data are shown, and linear regressions are overlayed where relationships between trait and thermal coupling are significant (solid where $p < 0.05$ and dashed where $p < 0.1$) overall (black) or interact with biome (coloured). Corresponding model outputs are shown in Table 4. The dashed grey horizonal lines at $\Delta T = 0$ and $\beta = 1$ indicates when T_{air} and T_{leaf} are equivalent, and the dashed grey vertical lines on panels A–D show PC1 = 0 and PC2 = 0.

Figure 1



A
B
C
D
T_{air} [° C]
T_{leaf} [° C]
40
35
30
25
20
15
12:30
13:00
13:30
14:00
14:30
15:00
Time
28
26
24
22
20
T_{leaf} [° C]
T_{air} [° C]
40
38
36
34
32
Treatment
Benign
High Temperature

Figure 2

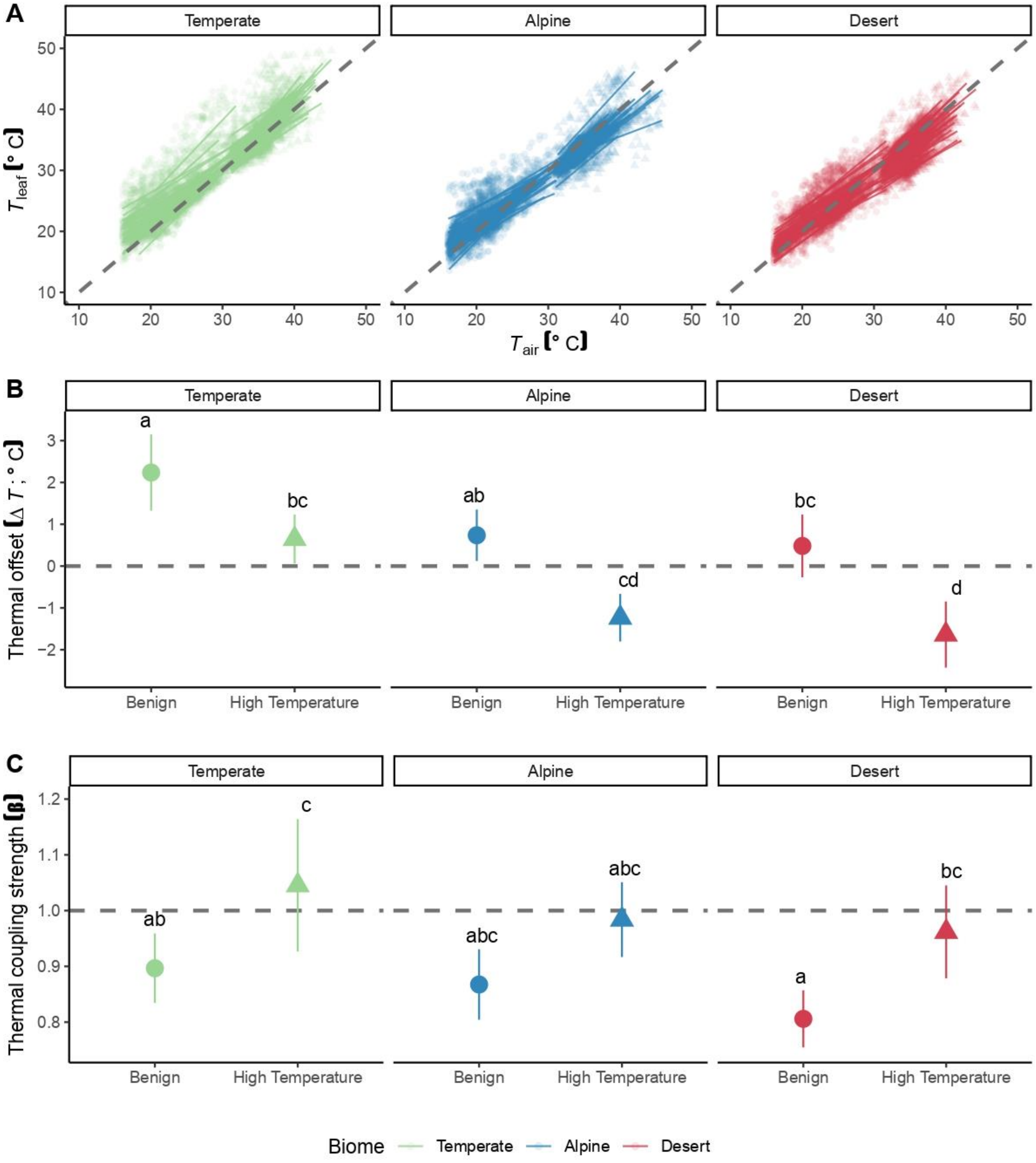

A
Temperate
Alpine
Desert
T_{leaf} [° C]
50
40
30
20
10
10
20
30
40
50
T_{air} [° C]
B
Temperate
Alpine
Desert
Thermal offset [Δ T ; ° C]
3
2
1
0
−1
−2
a
bc
ab
cd
bc
d
Benign
High Temperature
C
Temperate
Alpine
Desert
Thermal coupling strength [β]
1.2
1.1
1.0
0.9
0.8
ab
c
abc
abc
a
bc
Benign
High Temperature
Biome
Temperate
Alpine
Desert

Figure 3

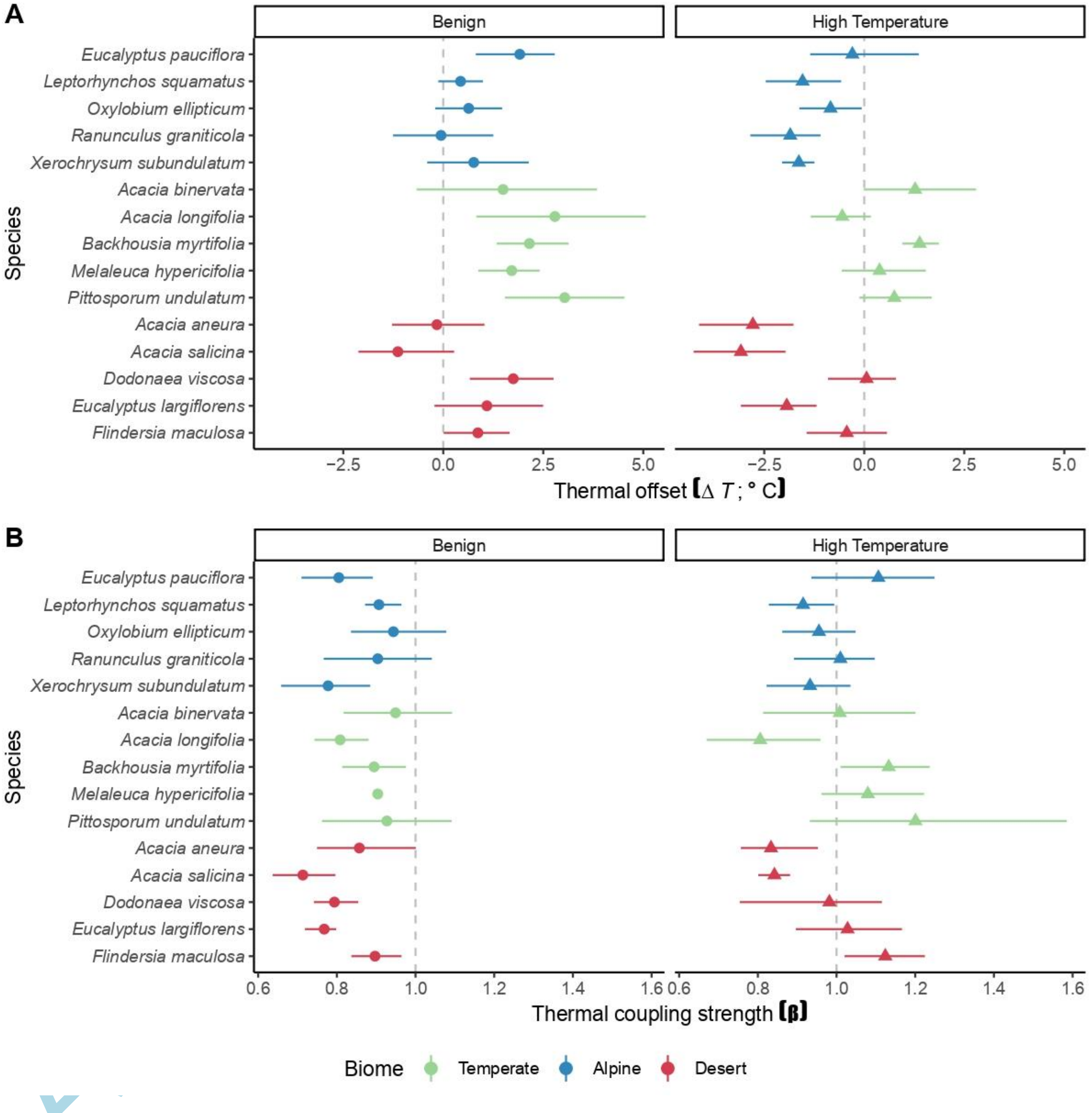
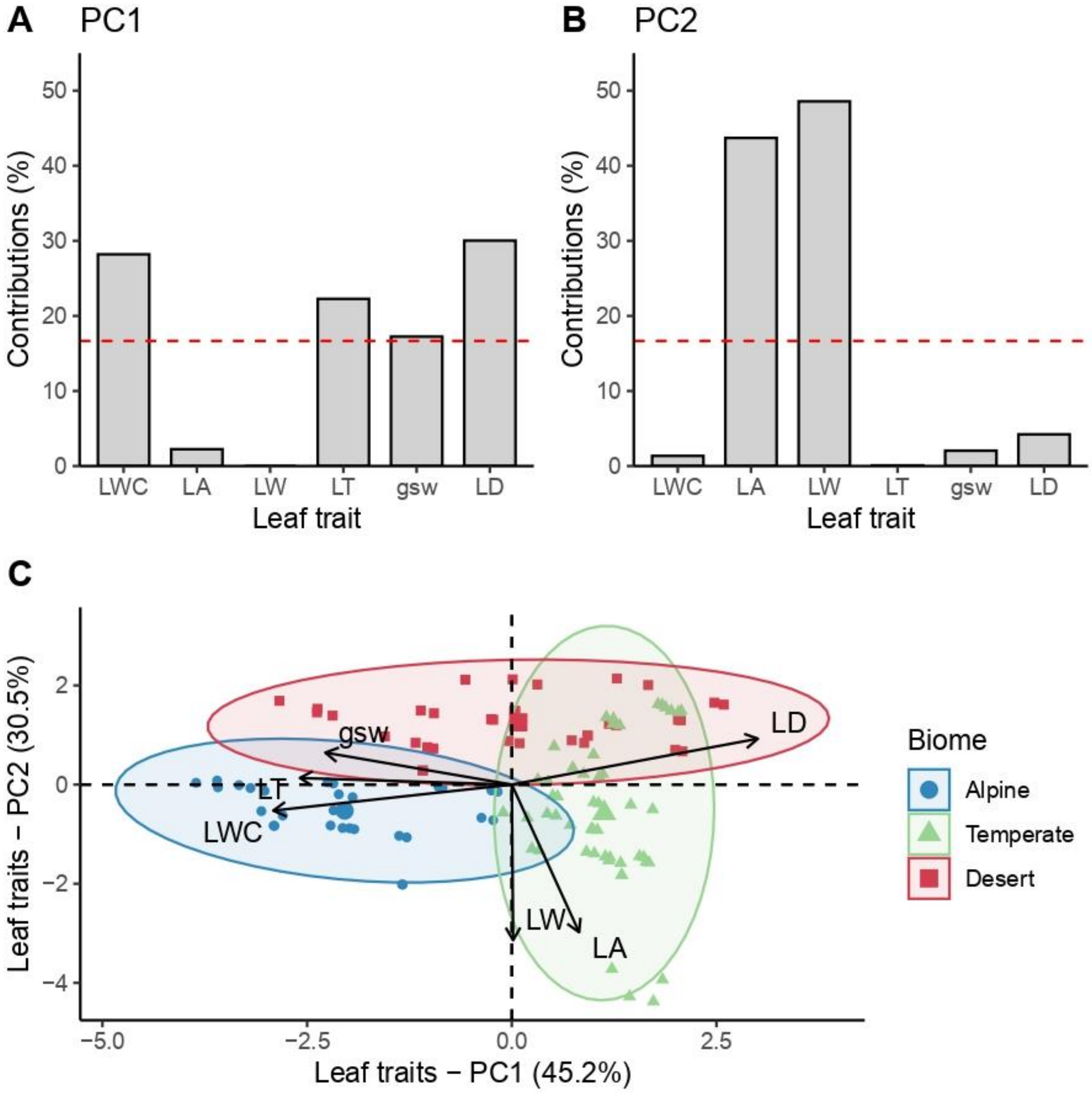
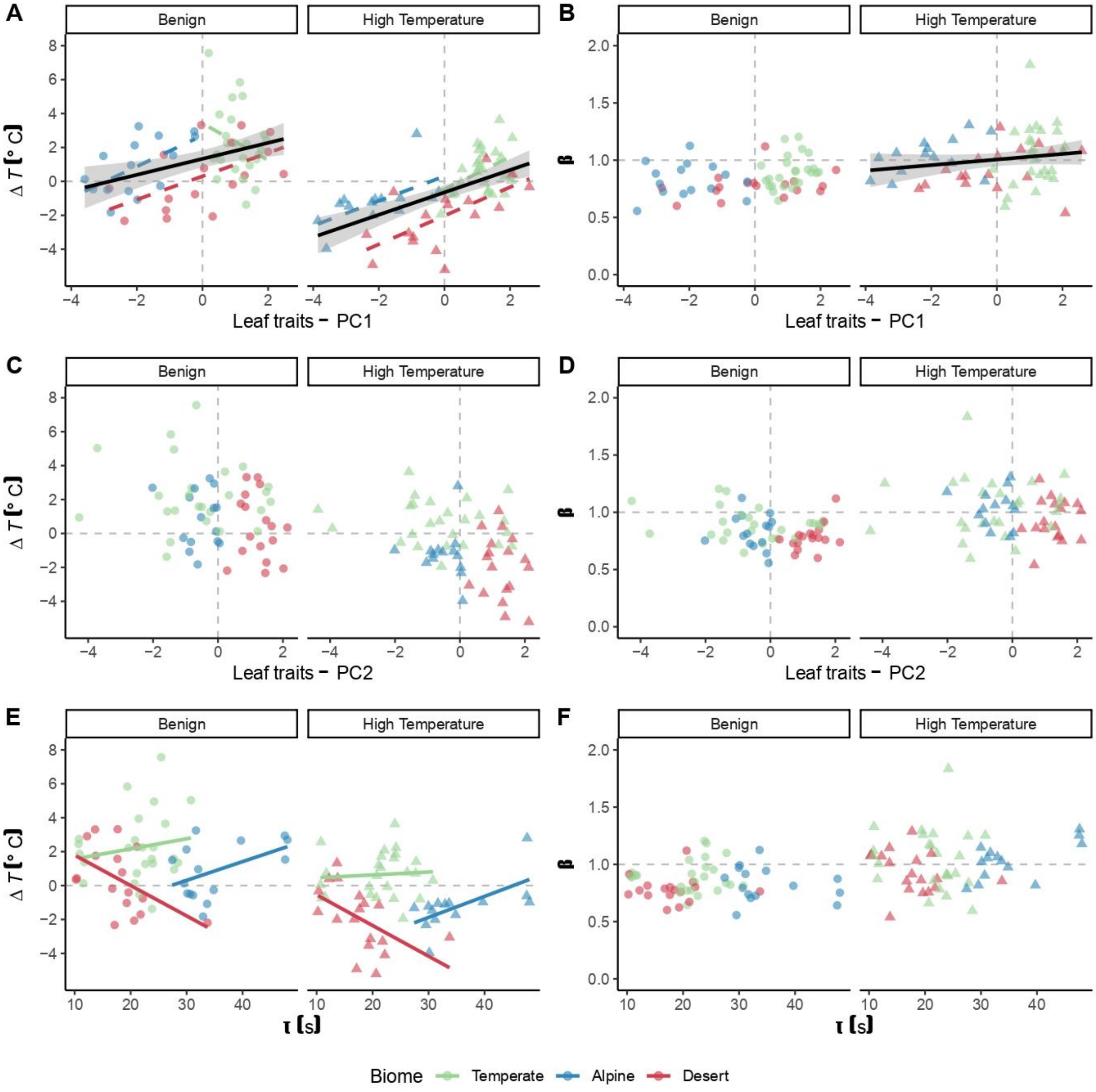

A
Benign
High Temperature
Eucalyptus pauciflora
Leptorhynchos squamatus
Oxylobium ellipticum
Ranunculus graniticola
Xerochrysum subundulatum
Acacia binervata
Acacia longifolia
Backhousia myrtifolia
Melaleuca hypericifolia
Pittosporum undulatum
Acacia aneura
Acacia salicina
Dodonaea viscosa
Eucalyptus largiflorens
Flindersia maculosa
Species
−2.5
0.0
2.5
5.0
Thermal offset (Δ T; ° C)
B
Benign
High Temperature
Species
0.6
0.8
1.0
1.2
1.4
1.6
Thermal coupling strength (β)
Biome
Temperate
Alpine
Desert

Figure 4



A
PC1
Contributions (%)
0
10
20
30
40
50
LWC
LA
LW
LT
gsw
LD
Leaf trait
B
PC2
Contributions (%)
0
10
20
30
40
50
LWC
LA
LW
LT
gsw
LD
Leaf trait
C
Leaf traits − PC2 (30.5%)
Leaf traits − PC1 (45.2%)
−5.0
−2.5
0.0
2.5
2
0
−2
−4
gsw
LT
LWC
LD
LW
LA
Biome
Alpine
Temperate
Desert

Figure 5


A
B
C
D
E
F
Benign
High Temperature
Δ T [° C]
β
Leaf traits − PC1
Leaf traits − PC2
τ [s]
8
6
4
2
0
−2
−4
2.0
1.5
1.0
0.5
0.0
10
20
30
40
Biome
Temperate
Alpine
Desert