Temperature-driven PSII thermal plasticity in tropical forest trees during a non-stress seasonal window

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Abstract

We quantified seasonal plasticity in photosystem II (PSII) heat tolerance in 27 co-occurring tropical tree species across a wet-to-post-wet transition in a seasonally dry forest in the central Western Ghats, India, during a window when leaves were fully mature and water availability remained non-limiting. This transition involved a ~ 4°C increase in daytime maximum air temperature (27.5°C in the wet period to 31.6°C in the post-wet period), preceding drought-induced senescence and peak hot–dry stress, thereby isolating thermal acclimation from confounding drought and senescence effects. PSII thermal traits: damage onset (T_5), damage midpoint (T_{50}), and decline width ($DW = T_{95}–T_5$) – were quantified from Fv/Fm–temperature response curves for each species in wet and post-wet periods. Across the community, both T_5 (+ 1.7°C) and T_{50} (+ 0.9°C) increased significantly from wet to post-wet, revealing modest but consistent acclimation of PSII heat tolerance to warmer growth temperatures under non-stress conditions. However, the magnitude of this PSII thermal plasticity was strongly species-specific and was not explained by leaf habit or successional status; evergreen and deciduous trees acclimated to a similar degree. The prevention-versus-forbearance trade-off, captured by the negative $T_5–DW$ relationship, remained conserved across seasons, indicating stable underlying PSII thermal strategies despite seasonal warming. Thermal safety margins based on T_{50} were large, but T_5-based margins revealed that a subset of late-successional evergreens (e.g. *Saraca asoca*, *Ficus* spp.) and one early successional deciduous species (*Careya arborea*) already operate close to functional PSII limits under current post-wet temperatures. These results demonstrate that PSII thermotolerance in seasonally dry tropical forests exhibits real but partial acclimation to modest non-stressed warming, and that species identity, rather than broad leaf habit categories, governs the plasticity and vulnerability of photosynthetic thermal responses.

Introduction

Tropical and subtropical forests globally are approaching their operational thermal limits, with climate warming projected to push many species beyond their historical temperature thresholds within this century (Doughty et al. 2023). Photosystem II (PSII) thermal damage characterized by the loss of photosynthetic quantum yield represents a critical ecophysiological measure of tree performance, particularly in seasonally variable environments where temperature, water availability and vapor pressure deficit (VPD) vary starkly across the annual cycle (Kattge et al. 2011; Sastry & Barua 2017; Dusenge, Duarte & Way 2019). Understanding when and how tree leaves experience thermal stress, and the physiological capacity of PSII to acclimate to changing growth temperatures under field conditions, is hence essential for predicting species responses to warming.

Despite growing evidence that PSII thermal tolerance is linked to habitat and life-history strategy—such that lowland species and those with higher leaf mass per area tend to exhibit higher T50 values (Sastry & Barua 2017; Slot et al. 2021a), and thermotolerance differs between evergreen and deciduous species (Sastry & Barua, 2017) - most tropical studies remain constrained to single seasons or to contrast between phenological and stress extremes. Typically, PSII heat tolerance has been quantified either

during the wet period, when ambient temperatures are lower, soils are saturated, VPD is moderate, and leaves experience low stress, or during the peak dry season, when temperatures and VPD are at their extremes and many deciduous species are partially or fully defoliated or bearing senescing, water-stressed leaves (Nanda, Prakasha, Murthy & Suresh 2012; Sastry & Barua 2017; Sastry, Guha & Barua 2018; Dusenge et al. 2019; Silva, Espírito-Santo, Santos & Rodrigues 2020; Slot et al. 2021b; Ramos et al. 2023). This focus on cool–wet versus hot–dry comparisons limits understanding of how PSII thermal plasticity unfolds across the productive growing season, particularly in intermediate periods when temperatures are rising but drought and peak heat stress have not yet peaked.

Seasonally dry tropical forests provide a critical, underexplored window to address this gap: the post-wet (pre-senescence) period, when leaves are fully mature and capable of photosynthetic function, water availability is still favourable, and daytime maximum air temperatures are ~ 3–4°C warmer than in the wet season, but conditions remain non-extreme (Guan et al. 2015; Krishnadas, Kumar & Comita 2016; Tiwari et al. 2025). In these systems, the wet-to-post-wet transition represents the true peak canopy functional period for many species, when productivity is high yet thermal stress and dehydration risk are only beginning to accumulate. By quantifying PSII heat tolerance across this non-stress seasonal warming, rather than between wet and peak dry seasons, it becomes possible to isolate temperature-driven PSII thermal plasticity from the confounding effects of drought stress, leaf senescence, and defoliation that characterize peak hot–dry comparisons.

Leaf longevity integrates structural robustness and leaf economic strategy: long-lived leaves tend to evolve enhanced membrane stability and repair capacity under chronic exposure, whereas short-lived leaves favour high initial productivity over extreme tolerance (Russo & Kitajima 2016; Slot et al. 2021a). Across tropical forests, variation in leaf lifespan and leaf mass per area is associated with differences in photosynthetic investment, stress tolerance, and PSII stability, reinforcing the idea that leaf economic traits set a baseline for thermal performance (Kattge et al. 2011; Sastry & Barua 2017). In seasonally dry tropical forests, co-occurring tree species span a continuum from drought-deciduous heat-avoiders to species that maintain foliage through warmer conditions, implying contrasting investments in PSII thermal tolerance across the annual cycle (Tiwari et al. 2025). These differences in leaf lifespan and exposure to rising temperatures suggest that species may adopt distinct combinations of constitutive PSII robustness and seasonal acclimation, particularly during non-extreme periods when growth temperature increases but stress remains low.

A widely held but rarely tested assumption in tropical ecophysiology is that leaf habit predicts the degree of seasonal PSII thermal plasticity. Evergreen species, retaining leaves year-round and experiencing the full thermal amplitude of the annual cycle, are expected to regulate PSII thermotolerance in response to growth temperature, upregulating membrane stability, D1 turnover, and chloroplast heat-shock proteins as temperatures rise (Yamori, Hikosaka & Way 2014; Slot *et al.* 2021). Deciduous species, by contrast, are expected to invest less in physiological regulation of PSII heat tolerance because phenological avoidance – shedding leaves before peak heat stress–reduces the need to maintain PSII stability under extreme temperatures (Sastry & Barua 2017; Sastry et al. 2018). Under this trait-based framework,

seasonal plasticity in PSII tolerance should be greater in evergreens than in deciduous species, and leaf habit should serve as a functional proxy for a species' capacity to buffer warming. However, this assumption has not been directly tested across a diverse community of co-occurring species measured under matched canopy microclimates during a non-stress wet-to-post-wet transition, precisely the context needed to isolate thermally driven PSII plasticity from the confounding effects of drought stress and leaf senescence that characterize peak dry-season comparisons.

PSII heat stability, quantified by the temperatures at which F_v/F_m declines by 5% (T_5, onset of stress) and 50% (T_{50}, irreversible damage), reflects the integrity of reaction-centre proteins, thylakoid membranes, and supporting mechanisms including lipid composition, chloroplast small heat-shock proteins, and the D1 repair cycle (Schreiber & Berry 1977; Schreiber 2007; O'sullivan et al. 2017; Tiwari et al. 2021; Slot *et al.* 2021). Maintaining PSII under heat imposes energetic costs via protein turnover and repair, which acclimate to growth temperature but remain biochemically constrained, yielding modest T_{50} plasticity that rarely fully compensates seasonal thermal shifts (Yi et al. 2022). The decline width (*DW*, $T_{95} - T_5$) captures response dynamics beyond absolute thresholds: narrow DW signals abrupt PSII failure despite high T_5 (prevention-focused), whereas wide DW indicates buffered decline after onset (repair/forbearance-focused), revealing distinct PSII thermal strategies among species that can be compared across seasons (Tiwari et al. 2021).

PSII thermal tolerance is expected to be partially plastic because the integrity of the reaction centre, thylakoid membranes, and associated repair machinery are energetically and biochemically modifiable traits. Elevated growth temperature can enhance PSII heat tolerance by upregulating the synthesis and turnover of the D1 protein, stimulating chloroplast small heat-shock proteins, and adjusting lipid composition and non-photochemical quenching components, all of which stabilise PSII under heat (Yamori et al. 2014; Tiwari et al. 2021; Posch et al. 2026). However, each of these adjustments imposes costs in nitrogen, protein synthesis, and ATP that compete with investment in photosynthetic capacity and growth, implying that species will strategically balance constitutive thermal robustness against acclimation potential based on habitat thermal variability and leaf economics (Sastry & Barua 2017; Tiwari et al. 2021, 2026), particularly during non-extreme seasonal warming when growth temperatures rise but drought stress is absent.

Given the typically modest PSII thermal acclimation observed in tropical systems (Tiwari et al. 2021; Posch et al. 2026), a ~ 3–4°C seasonal warming from wet to post-wet periods in the Western Ghats (Krishnadas et al. 2016; Tiwari et al. 2025)

implies only partial compensation via T_5 and T_{50} shifts, **yet the extent of this seasonal plasticity in fully mature leaves of diverse evergreen and deciduous species under non-stress conditions has not been quantified**. Empirical field and urban garden studies across diverse biomes show that PSII heat-tolerance metrics (T_5, T_{50}) generally acclimate modestly to growth temperature and to seasonal shifts, but this plasticity is partial, species- and strategy-dependent, and rarely fully compensates for thermal regime shifts under climate warming (Sastry & Barua 2017; Slot et al. 2021a; Tarvainen et al. 2022; Kullberg &

Feeley 2024; Manzi et al. 2025). These studies also highlight that leaf habit, economic traits, and drought exposure modulate the degree of acclimation, yet most remain constrained spatially and temporally, with few datasets tracking the same individuals across seasons and under matched canopy microclimates, especially during intermediate, non-stress warming windows.

Seasonally dry forests of the central Western Ghats provide an ideal setting to address these questions, combining pronounced monsoon–post-monsoon transitions (~ 4°C warming from wet to post-wet) with co-occurring evergreen, semi-evergreen, and deciduous species spanning the slow–fast leaf economic spectrum (Krishnadas et al. 2016; Tiwari et al. 2025). Here, we quantify PSII heat tolerance (T_5, T_{50}, DW) for 27 tree species across wet and post-wet periods, outside peak hot–dry stress, to test seasonal PSII thermal plasticity during a physiologically critical, non-stress window. We specifically ask:

1) Is PSII thermal tolerance (T_5, T_{50}, DW) plastic between wet and post-wet periods under modest (~ 3–4°C) warming, and how much of this seasonal temperature increase is buffered by acclimation in fully mature leaves?

2) Does leaf habit (evergreen vs deciduous) or successional status meaningfully explain variation in PSII thermal plasticity and thermal safety margins, or is species identity the primary axis governing photosynthetic thermal responses in these forests?

Building on the trait-based expectation that leaf habit predicts PSII thermal plasticity, we hypothesised that deciduous species would show limited seasonal upregulation of T_5 and T_{50} across the wet-to-post-wet transition, consistent with an avoidance strategy in which leaf shedding reduces the need for physiological regulation of PSII heat tolerance during this non-stress window, whereas evergreen species, lacking the option of leaf shedding, would show greater seasonal plasticity as a compensatory response to rising temperatures (Sastry & Barua 2017; Slot et al. 2021a; Kullberg & Feeley 2024). Specifically, we expected PSII heat tolerance to shift upward with warmer growth temperatures, such that both T_5 and T_{50} would be higher in the post-wet period than in the wet period, and that any associated changes in DW would indicate altered dynamics of PSII failure after stress onset, even though their effects on the $T_5 \propto DW$ relationship remained unknown. Testing these predictions across 27 co-occurring species in a non-stress seasonal window, where thermal signal is not confounded by drought or senescence, provides a uniquely clean context for evaluating whether leaf habit and PSII plasticity are coupled or whether species identity emerges as the primary dimension of thermal adaptation in seasonally dry tropical forests

Materials and methods

Study site

The study was conducted in a seasonally dry tropical forest within Bhadra Reserve Forest, Shivamogga district, Karnataka, India (13.747462° N, 75.611980° E; 680 m asl). The site features predominantly

deciduous tree species interspersed with some evergreens (Krishnamurthy et al. 2010). It experiences a 5–6-month monsoon (~1200 mm rainfall), followed by a 3–4-month winter with rising daytime temperatures and declining nighttime temperatures (Fig. 1). Notably, maximum air temperatures during the wet period (June–August) average 4°C lower than in the post-wet period (October–December), when daytime highs increase while nighttime lows decrease. The wet period (June–August) had a mean maximum air temperature of 27.5 ± 0.2°C. The post-wet period (October–December) was 4.1°C warmer, with a mean maximum temperature of 31.6 ± 0.14°C. The summer period recorded the highest mean maximum temperature of 35.8 ± 0.17°C, 4.2°C higher than the post-wet period (Fig. 1).

Plant materials

We selected the most dominant canopy and subcanopy tree species spanning a spectrum of leaf longevity—from short-lived leaves that persisted only through the wet and post-wet periods to evergreens with year-round foliage, based on long-term phenological data from Nanda (2012) for the same site. This set included drought-deciduous heat-avoiders as well as typical evergreens with longer leaf longevity, thereby encompassing diverse leaf phenological and thermal adaptation strategies.

The study includes a total of 27 tree species characteristic of seasonally dry tropical forests in the central Western Ghats, Karnataka, India, spanning varied successional stages (Supplementary Table S1) (Pascal 1988). Species composition shifted from predominantly deciduous in drier stands to semi-evergreen and evergreen in wetter forest types along rainfall and topographic gradients. The site we studied is dominated by deciduous species such as *Xylia xylocarpa*, *Terminalia paniculata*, *Lannea coromandelica*, and *Careya arborea*, with *Terminalia paniculata* and *Xylia xylocarpa* jointly accounting for > 50% of basal area (Krishnamurthy et al. 2010), alongside *Tectona grandis*, *Catunaregam spinosa*, and *Terminalia anogeissiana*. Typical evergreen species include *Artocarpus heterophyllus*, *Schleichera oleosa*, *Cassine glauca*, *Ficus benghalensis*, *F. macrocarpa*, *F. religiosa*, and *Santalum album*, among others. The canopy is about 15m tall and has about two strata. Detailed taxonomy, families, and ecological attributes including succession stage and canopy properties are listed in Supplementary Table S1. For each species, we sampled five individual trees (biological replicates). The site is further characterized by an intense herbivore and carnivore fauna that strongly suppresses understorey growth.

We conducted two measurement campaigns: (a) the late summer monsoon period (mid-August to late September 2025), referred to as the ‘wet period’, and (b) the second-to-fourth week of November 2025, post-rainfall and characterized by low minimum air temperatures and rising maximum air temperatures, referred to as the ‘post-wet period’. For both campaigns, we sampled leaves representing the predominant phenological stage at each time point – we note that in all species bore mature leaves during both the campaigns. Both campaigns were conducted when soil moisture remained favourable and leaves were fully mature, ensuring that differences between periods primarily reflected changes in growth temperature rather than drought stress. Leaf samples were collected from about 4-5m from above ground using telescopic pruners. In both campaigns, leaves that were exposed to full sunlight

were collected before 9AM. Samples were transported to lab in dark polythene bags under hydrated conditions.

Heat treatment assay

We adopted Tiwari et al., (2021) and Krause (2010) protocols. We cut leaf 20 mm diameter leaf discs underwater, choosing the major lamina part of the leaf – avoiding midrib. For small leaves, we excised one disc per leaves and for the large lamina leaves, we excised 1–3 discs per leaf. Each assay consisted of at least 10 individual leaf discs from a tree. Leaf discs were randomly selected and wrapped in a layer of moist tissue paper on both sides covering the cut edge of the leaf discs. Care was taken not to touch the leaves, and the leaf discs always remained in water or covered in damp tissue paper to avoid anaerobiosis (Harris & Heber 1993). The discs were transferred into separate plastic bags (50 × 60 mm) keeping them flat and covered in a thin film of water. The bags were subjected to heat treatment in sets of at least three discs per temperature point. Heat treatment was conducted in temperature-controlled thermos flasks with pre-heated water. The water temperature was recorded in the central area of the flask using a calibrated K-type thermocouple probe. Separate sets of leaf discs were treated to one of the following temperatures points: 35, 40, 42, 44, 46, 48, 50, 52, and 60°C and a set of untreated discs were used as controls (about 25 °C). After heat treatment, the leaf discs were transferred to petri-dishes with tissue paper and water. The Petri dishes were incubated in the lab condition for 24h. After incubation period, the discs were tap-dried, wrapped in aluminium envelopes for dark adaptation followed by F_v/F_m measurements using the Multispeq v2.0 (PhotosynQ, Michigan State University, USA) (Kuhlgert et al. 2016).

Determination of PSII thermal tolerance parameters

A three-parameter logistic curve was fitted to each F_v/F_m - temperature response series using the following equation:

$$f = \frac{a}{1+e^{(b*(log\ (T)\ -log(c))}} \quad \text{Eq. 1}$$

In this equation, *T* is defined as the treatment temperature, *b* is the steepness of the curve, *a* is the upper asymptote, and *c* is the inflection point. From the fits, we extracted (i) T_5, the temperature at which F_v/F_m declines to 5% of the maximum level and (ii) T_{50}, the temperature where F_v/F_m is half of the maximum. In addition, T_{95} was determined. This parameter is defined as the temperature at which the values of F_v/F_m decrease to 95% of the maximum level. The differences between T_5 and T_{95} are henceforward referred to as the decline width ($DW = T_{95}–T_5$), which is defined as the temperature range in which F_v/F_m declined from 95% to 5% of the maximum level (Tiwari et al. 2021).

Data analysis

PSII thermal tolerance parameters (T_5, T_{50}, $DW = T_{95} - T_5$) were derived from three-parameter logistic fits to Fv/Fm-temperature response curves (Eq. 1). Species-level plasticity (ΔT_5 = post-wet – wet T_5; similarly, ΔT_{50}) was modelled using linear mixed-effects models (lmer; Bates *et al.* (Slot et al. 2021a; Kullberg & Feeley 2024)) with leaf habit (evergreen/deciduous), season (wet/post-wet), and their interaction as fixed effects, species as random intercept, (lme4 package). Type III ANOVA with Satterthwaite's degrees of freedom tested fixed effects (lmerTest), and marginal R^2 quantified habit effects (MuMIn package Bartoń (2018)) (Supplementary Table S2). Overall community means used analogous intercept-only models. Relationships among ΔT_5–ΔT_{50} and ΔT_5–DW employed SMA regression (smatr package) and concordance tests. Thermal safety margins ($TSM_{50} = \Delta T_{50} - T_{air\ (90th)}$; similarly, $TSM_5 = \Delta T_5 - T_{air\ (90th)}$) were compared via mixed models. Analyses used R 4.5.2 1 (R Core Team, 2026); figures via ggplot2 (Wickham 2009).

Results

Wet to post-wet period plasticity in PSII thermal tolerance

PSII thermal tolerance onset (T_5) increased significantly from wet to post-wet periods ($F_{(1, 241)} = 9.24$, $p = 0.0026$), indicating seasonal plasticity, though this simple model explained only 2.7% of variance (marginal R^2) (Fig. 2, A & C). A species × season interaction model revealed strong interspecific variation ($F_{(27, 215)} = 3.69$, $p < 0.0001$) and confirmed the seasonal increase ($F_{(1, 215)} = 10.14$, $p = 0.0017$), with a significant species × season interaction ($F_{(26, 215)} = 1.71$, $p = 0.021$), indicating that the magnitude of T_5 plasticity varied substantially among species (marginal $R^2 = 0.36$). These results demonstrate that while T_5 exhibits clear seasonal acclimation, species differ markedly in their plastic response to warming. Neither leaf habit nor successional status significantly modulated T_5 plasticity across seasons (habit : season $F_{(1, 240)} = 0.0025$, p = 0.96; succession : season $F_{(2, 239)} = 0.13$, $p = 0.88$), with the main seasonal effect persisting ($F_{(1, 240)} = 9.18$, $p = 0.0027$) but explaining limited variance ($R^2 < 7\%$) (Supplementary Figure S1A). Wet-to-post-wet changes in T_5, ΔT_5 did not differ between deciduous and evergreen species ($F_{(1, 240)} = 0.009$, $p = 0.93$), and leaf habit explained essentially none of the variance in plasticity (Fig. 3, A).

PSII thermal damage midpoint (T_{50}) increased significantly from wet to post-wet periods ($F_{(1, 241)} = 8.61$, $p = 0.0037$), indicating seasonal plasticity, though this simple model explained only 1.8% of variance (marginal R^2) (Fig. 2, B & D). A species × season interaction model revealed strong interspecific variation ($F_{(26, 122)} = 8.19$, $p < 0.0001$) and confirmed the seasonal increase ($F_{(1, 122)} = 9.16$, $p = 0.0030$), with a non-significant species × season interaction ($F_{(26, 115)} = 1.28$, $p = 0.19$), indicating limited species-level variation in the magnitude of T_{50} plasticity (marginal $R^2 = 0.49$). Leaf habit showed a main effect ($F_{(1, 25)} = 4.76$, $p = 0.039$) but no interaction with season (habit : season $F_{(1, 240)} = 2.60$, $p = 0.11$), while successional status marginally modulated seasonal plasticity (succession : season $F_{(2, 239)} = 2.79$, $p =$

0.064), with the main seasonal effect persisting ($F_{(1, 239)}$ = 5.04, p = 0.026) but explaining limited variance (R^2 < 10%) (Supplementary Figure S1B). These results demonstrate that while T_{50} exhibits modest seasonal acclimation, plasticity magnitude is largely consistent across species, with weak modulation by leaf habit and a marginal influence of successional status. Wet-to-post-wet changes in T_{50}, ΔT_{50} did not differ between deciduous and evergreen species ($F_{(26, 115)}$ = 2.14, p = 0.16), with leaf habit (Fig. 3, B).

PSII decline width (*DW*) showed a marginal increase from wet to post-wet periods ($F_{(1, 241)}$ = 3.10, p = 0.079), suggesting weak seasonal plasticity, with this simple model explaining only 1.0% of variance (marginal R^2). A species × season interaction model revealed strong interspecific variation ($F_{(26, 215)}$ = 3.11, p < 0.0001) and confirmed the marginal seasonal trend ($F_{(1, 215)}$ = 3.39, p = 0.067), with a significant species × season interaction ($F_{(26, 215)}$ = 1.64, p = 0.031), indicating species differed substantially in *DW* plasticity magnitude (marginal R^2 = 0.32). Leaf habit showed a main effect ($F_{(1, 25)}$ = 5.99, p = 0.022) but no interaction with season (habit : season $F_{(1, 240)}$ = 0.91, p = 0.34), while successional status showed no modulation of seasonal plasticity (succession : season $F_{(2, 239)}$ = 1.49, p = 0.23), with the main seasonal effect persisting marginally ($F_{(1, 239)}$ = 4.66, p = 0.032) but explaining limited variance (R^2 < 6%). These results demonstrate that while *DW* exhibits weak seasonal plasticity, species differ markedly in their response, though neither habit nor successional status significantly modulates this plasticity. Wet-to-post-wet changes in *DW*, Δ*DW* did not differ between deciduous and evergreen species ($F_{(26, 115)}$ = 0.65, p = 0.43), with leaf habit explaining only 0.7% of the variance in plasticity (Fig. 3, C).

Coordinated seasonal shifts in T_5 and T_{50}

Post-wet and wet period species mean seasonal changes in T_5 and T_{50} were moderately correlated (r = 0.59, 95% CI: 0.24–0.80, p = 0.0023). A sign-based test of concordance indicated that most species exhibited parallel shifts in T_5 and T_{50}. Fisher's exact test suggested that species with positive ΔT_5 (with higher valued during post-wet period) were substantially more likely to also show positive ΔT_{50} (odds ratio = 7.3, 95% CI: 0.82–106), although this association was only marginally significant (p = 0.061). These results indicate that T_5 and T_{50} tend to change in similar directions across seasons (Fig. 4).

T_5 ∝ decline width

SMA regression revealed a significant negative T_5–*DW* relationship during both wet (slope = − 0.61, 95% CI: −0.81 to − 0.46, R^2 = 0.50, p < 0.001) and post-wet (slope = − 0.52, 95% CI: −0.70 to − 0.38, R^2 = 0.43, p < 0.001) periods, with identical slopes across seasons (χ^2_1 = 0.62, p = 0.43). Linear mixed-effects modelling confirmed the strong *DW* main effect ($F_{(1, 36)}$ = 79.4, p < 0.001; marginal R^2 = 0.59) but revealed habit-specific modulation during post-wet conditions (season × habit: $F_{(1, 28)}$ = 4.71, p = 0.039; three-way: $F_{(1, 28)}$ = 5.77, p = 0.023) (Fig. 5). Thus, while high-T_5 species consistently show narrow DW (prevention-focused), evergreens and deciduous species diverge in this trade-off under warming. This extends the prevention/forbearance framework to seasonal dynamics in a diverse SDTF community.

Proximity to PSII functional limits: thermal safety margin

Thermal safety margins based on T_{50} were large for all species, such that seasonal maximum air temperatures above the 90th percentile never approached PSII damage midpoints in either period. In contrast, T_5-based margins revealed that a few species operated closer to functional thresholds: during the wet period, *Saraca asoca* and *Schleichera oleosa* had T_5 values near wet-season T_{max} > 90th percentile, and during the post-wet period *Ficus macrocarpa* and *F. religiosa* showed similarly small margins relative to post-wet T_{max}. Deciduous species generally maintained comfortable buffers, with none directly overlapping seasonal T_{max}, although Careya arborea showed a reduced margin and trended towards the post-wet upper limits. Overall, most species retained substantial separation between T_5 and realized air temperature extremes, but a small subset of late-successional evergreens and one early successional deciduous species already function near emerging seasonal heat constraints.

Discussion

Non-stressed PSII thermal acclimation is species-specific and habit-independent

A central expectation in tropical ecophysiology is that leaf habit and physiological thermotolerance regulation are coupled, with evergreens investing in year-round PSII stabilisation and deciduous species relying more heavily on avoidance through leaf shedding (Sastry & Barua 2017; Sastry et al. 2018). Our results directly challenge this expectation. Both T_5 and T_{50} increased modestly but significantly from the wet to post-wet period across the community, indicating real PSII thermal acclimation to ~ 3–4°C warmer growth temperatures under non-stress conditions, yet the magnitude of this acclimation was overwhelmingly species-idiosyncratic rather than structured by leaf habit or successional status. Physiological regulation of PSII heat tolerance and phenological heat-avoidance therefore appear to operate as largely independent axes of thermal strategy: deciduous species do not simply delegate heat tolerance to leaf shedding, and evergreens do not compensate for prolonged exposure through disproportionately greater PSII upregulation. That both groups acclimate to a similar degree suggests that species draw on combinations of constitutive PSII robustness and seasonal plasticity that reflect individual life-history trajectories rather than broad functional groupings based on leaf habit, and our repeated measurements on five trees per species across both periods provide unusually strong empirical support for these species-level patterns.

Critically, our sampling captures PSII thermal acclimation during a non-stress wet-to-post-wet transition, when leaves are fully mature, water is not limiting, and temperatures are rising but have not yet reached peak dry-season extremes. This design is deliberate and informative: by excluding the confounding effects of drought stress, leaf senescence, and defoliation that characterise peak dry-season measurements (Sastry & Barua 2017; Slot et al. 2021a), we isolate the thermal signal in PSII plasticity. The modest but significant acclimation detected here, approximately 1.7°C in T_5 and 0.9°C in T_{50} — therefore reflects genuine thermally-driven physiological adjustment rather than stress-induced or senescence-related changes in PSII integrity. This is consistent with the partial acclimation reported in

urban-garden and field studies across diverse biomes (Tarvainen et al. 2022; Kullberg & Feeley 2024; Manzi et al. 2025), but extends those findings into a community-wide, paired, non-stress context that has not previously been quantified in SDTFs. The non-stress window thus provides a cleaner baseline for understanding the limits and mechanisms of PSII plasticity than peak-season comparisons, and we suggest it should be incorporated more systematically into future thermal acclimation studies.

Deciduous species show higher T_{50} than evergreens: a leaf economics interpretation

The higher T_{50} observed in deciduous relative to evergreen species in our study contrasts with Sastry and Barua (2017), who reported the opposite pattern and interpreted it as reflecting greater constitutive membrane investment in evergreens exposed to chronic thermal stress. However, a critical contextual difference must be noted: their study was conducted in an urban garden setting where species were growing under modified microclimates, altered soil conditions, and reduced canopy competition, conditions that likely confound the expression of intrinsic thermotolerance strategies. Our study, by contrast, samples species in their natural forest context, where canopy position, interspecific competition, and seasonal microclimate interact to shape leaf traits as they would under evolutionary selection.

Within our natural forest community, we suggest the higher deciduous T_{50} reflects a leaf economics argument rooted in longevity and resource allocation. Deciduous species invest heavily in leaf construction during the brief wet-season window, producing leaves that must maximise photosynthetic returns within a constrained lifespan while tolerating rising post-wet temperatures before senescence. This compressed functional window may select for higher baseline PSII thermal robustness as an insurance strategy, not because deciduous species face greater chronic heat exposure, but because mid-season leaf replacement is not viable. This aligns with the slow-fast resource acquisition spectrum, where short-lived, high-return leaves in deciduous species are expected to show distinct thermal trait combinations relative to the more conservative investments of long-lived evergreen leaves (Russo & Kitajima 2016; Slot et al. 2021a). Evergreen species, by contrast, can spread PSII damage and repair costs across longer leaf lifespans, tolerating moderate recurring thermal perturbation through D1 turnover and incremental acclimation rather than constitutive robustness (Yi et al. 2022). Direct comparison of leaf economic traits such as specific leaf area, leaf nitrogen, and leaf lifespan across both datasets would be a productive avenue for testing this interpretation.

Conservation of the T_5–*DW* prevention-forbearance trade-off across seasons

The negative T_5 – *DW* relationship where species with higher thermal onset temperatures show narrower decline windows, was conserved across both seasons, confirming that the prevention-versus-forbearance axis represents a stable dimension of PSII thermal strategy rather than a seasonal artefact (Tiwari et al. 2021). Identical slopes in wet and post-wet periods indicate that as species shift their thermal onset upward with warming, the shape of their F_v/F_m - temperature response is maintained. However, the habit-specific divergence in this relationship under post-wet conditions is noteworthy:

evergreen and deciduous species separated along the prevention-forbearance axis as temperatures rose, suggesting that while the trade-off itself is conserved, the position species occupy along it is subtly modulated by habit under warming. This points to an interaction between phenological strategy and thermal response dynamics that warrants further investigation across the full annual cycle.

Within-habit variation and the limits of binary phenological classification

Within both evergreen and deciduous groups, individual species showed considerable variation in the direction of seasonal change: some increased T_5, T_{50}, or *DW* from wet to post-wet, others showed no detectable shift, and a subset showed modest declines. This within-habit heterogeneity reinforces the conclusion that binary leaf habit classification captures only a coarse axis of thermal strategy variation, and that the species-specific nature of PSII plasticity documented here reflects genuine biological diversity that functional groupings cannot resolve. Fine-scale phenological attributes including the duration of mature leaf retention, the timing and pace of leaf senescence and emergence, and seasonal preferences in leaf turnover are likely to explain thermal strategies more precisely than a simple evergreen-deciduous dichotomy. Among the 27 species studied, meaningful differences in these phenological attributes exist that were not captured by our binary classification. For example, while most drought-deciduous species avoid the peak summer period by shedding leaves (e.g., *L. coromandelica, C. arborea, S. oleosa*) well before temperatures peak, a small number of species in this community retain or flush leaves during the later summer months (evergreens such as *A. heterophyllus*, *N. cadamba*, and *Ficus* spp.; deciduous species such as *T. bellirica, T. paniculata, T. anogeissiana*) (Nanda et al. 2012), which corresponds to one of the hottest periods of the year. Whether these species deploy distinct thermal tolerance strategies relative to their habit-group peers remains an open question that warrants dedicated investigation. Resolving these within-habit contrasts would require fine-frequency phenological monitoring across the full annual cycle, linking leaf stage and turnover rates directly to PSII thermal metrics measured at matched time points.

Beyond phenological complexity, resource allocation to leaf heat tolerance and structural leaf traits are expected to interact with the thermal strategies observed here. Investment in membrane thermostability, D1 protein turnover, and heat-shock protein synthesis all compete with investment in photosynthetic capacity and leaf structural robustness, implying that leaf economics should modulate both constitutive thermotolerance and its seasonal plasticity (Russo & Kitajima 2016; Sastry & Barua 2017). The species-driven variation in plasticity we observe is therefore likely to reflect, at least in part, differences in how species allocate resources across these competing demands, differences that are not captured by habit alone and that would require trait-level data to disentangle. While we did not collect leaf economic trait data in this campaign, this was a deliberate choice: our aim was to first establish whether phenological strategy and PSII thermal regulation are coupled or independent before introducing the additional complexity of morphological and chemical trait variation. Future studies integrating specific leaf area, leaf nitrogen, and leaf lifespan with the seasonal PSII framework developed here would provide a more complete mechanistic account of what drives species-specific plasticity in this community and would

allow direct testing of whether the leaf economics argument proposed here to explain the higher deciduous T_{50} is supported by measured trait differences.

Vulnerable species and implications for warming in SDTFs

Despite generally comfortable T_{50}-based thermal safety margins across the community, consistent with findings from other tropical forests where T_{50} buffers remain large relative to ambient maxima (Slot *et al.* 2021; Kullberg & Feeley 2024); T_5-based margins revealed a functionally significant vulnerable subset. Late-successional evergreens including *Saraca asoca* and *Ficus* species, alongside the early-successional deciduous *Careya arborea*, showed the smallest buffers relative to post-wet temperature maxima. That these species span both habit categories and successional positions reinforces the conclusion that vulnerability is not well-predicted by broad functional grouping. Their reduced margins likely reflect distinct mechanisms: *Saraca asoca* and *Ficus* species may reflect trade-offs of shade-adapted or strangler growth strategies (Schmidt & Tracey 2006) that prioritise carbon capture over thermal robustness, while *Careya arborea*'s fire-adapted open-canopy habit (Malasiya et al. 2022) may expose it to higher leaf temperatures than closed-canopy species. As seasonal maximum temperatures continue rising under climate warming, species currently operating near T_5 thresholds face the greatest risk of crossing functional limits, not at peak dry-season extremes, but during the earlier post-wet warming transition that this study specifically captures. Trait-based frameworks that aggregate species into evergreen and deciduous functional types, risk masking this within-community heterogeneity, and our findings argue for species-resolved approaches to predicting thermal vulnerability in SDTFs.

Conclusion

Across 27 co-occurring tree species in a seasonally dry tropical forest of the central Western Ghats, PSII thermal tolerance increased modestly but significantly from the wet to the post-wet period, tracking a approximately 4°C seasonal warming during a physiologically critical non-stress window. This plasticity was real but partial, consistent with the biochemical constraints on PSII acclimation documented across tropical systems, and insufficient to fully compensate for seasonal temperature shifts. Crucially, the magnitude of this acclimation was driven by species identity rather than leaf habit or successional status, with evergreen and deciduous species acclimating to a similar degree, directly falsifying the assumption that phenological strategy predicts physiological thermotolerance regulation. The prevention-versus-forbearance trade-off along the T_5 and *DW* axis was stable across seasons, confirming it as a conserved dimension of PSII thermal strategy, while thermal safety margins based on T_5 identified a functionally vulnerable subset of species including late-successional evergreens and one early successional deciduous species already operating near seasonal heat limits during the post-wet transition rather than at peak dry-season extremes.

These results show that PSII thermotolerance in seasonally dry tropical forests exhibits real but partial acclimation to modest, non-stressed warming from wet to post-wet periods, with both T_5 and T_{50} shifting upward but not fully matching the ~ 3–4°C increase in daytime maximum air temperature. The

magnitude and form of this PSII thermal plasticity are strongly species-specific and only weakly related to leaf habit or successional status, indicating that physiological regulation of PSII heat tolerance and phenological heat-avoidance are largely independent dimensions of thermal strategy. By quantifying PSII heat tolerance in fully mature leaves across a non-stress seasonal transition, this study demonstrates that species identity, rather than broad leaf habit categories, governs both the plasticity and the emerging vulnerability of photosynthetic thermal responses in these forests, with a subset of late-successional evergreens and one early successional deciduous species already operating close to functional PSII limits under current post-wet temperatures. As the post-wet warming transition intensifies under climate change, arriving earlier in the season and reaching higher temperatures, the non-stress window characterised here is likely to progressively narrow, and the species currently operating closest to T_5 thresholds will be among the first to experience functional heat limitation during what is presently their peak productive period.

Declarations

Author contribution

RT conceived the research. RT and YK planned and designed the study. PTB, SNH, RGH, PN, JBM, SBS, MMM, SG, TN, AKS, VN, LBS, KTG, conducted thermal tolerance measurements and field data collection. YK and RT oversaw the field campaigns. NA, SBS, and MMM supported phenological characterization. RT collated and analysed the data and wrote the manuscript. All co-authors contributed to manuscript revision and approved the final version for submission.

Conflict of interest

The authors declare no conflict of interests.

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Figures

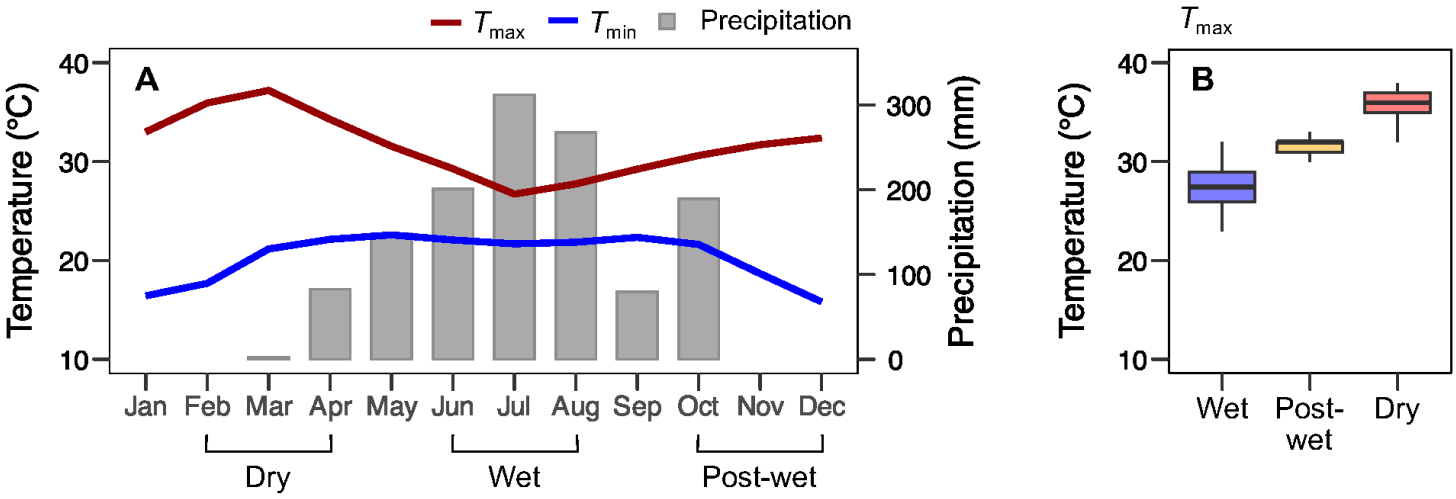

Figure 1

Panel (A) Seasonal monthly mean air temperature maxima/minima, and monthly total precipitation at Singanamane weather station (13.719217°N, 75.634778°E), located 2 km from the study site. Data cover March 2025–February 2026 (annual precipitation: 1284 mm). Panel B shows maximum air temperature ranges during the three periods.

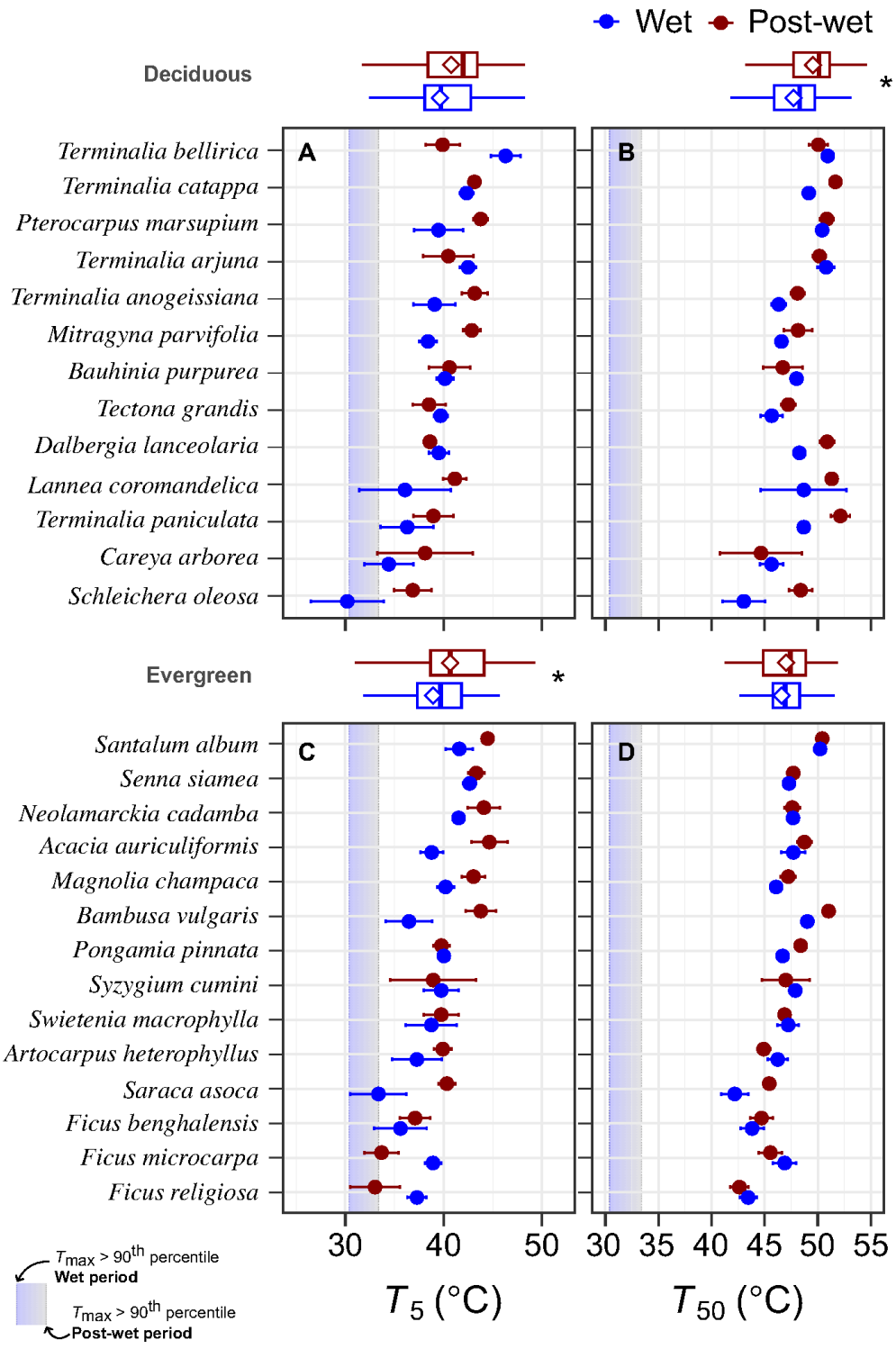

Figure 2

PSII thermal tolerance (T_5 and T_{50}) of co-occurring tree species during wet monsoon and post-wet periods, relative to seasonal air temperature maxima (T_{max} > 90th percentile) illustrating species-specific plasticity and large mid-point safety margins under modest non-stress warming. Boxplots depict T_5 (left panels, A, C) and T_{50} (right panels, B, D) thresholds for leaf heat tolerance in deciduous (top row) and

evergreen (middle row) species. T_5 marks 5% F_v/F_m decline (functional onset), T_{50} marks 50% decline (damage midpoint). Bottom panels show T_{max} distributions (30.4°C wet; 33.4°C post-wet), revealing most species retain large T_{50} buffers while select evergreens (*Saraca asoca*, *Ficus* spp.) and *Careya arborea* operate near T_5 functional limits.

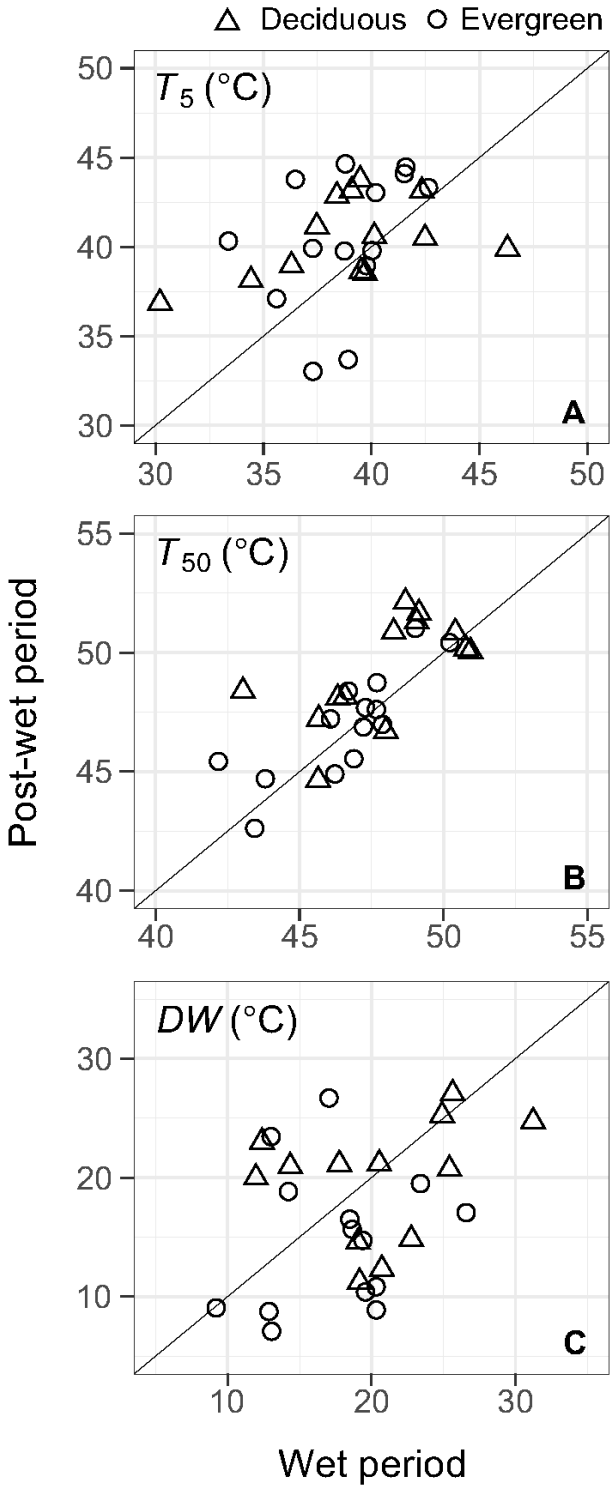

Figure 3

Wet-to-post-wet period plasticity in PSII thermal tolerance parameters (T_5, T_{50} and decline width, panels A-C) across 27 tree species in a seasonally dry tropical forest, Central Western Ghats, India. Circles represent evergreen species; triangles represent deciduous species. Each symbol shows species mean (n=5 trees). Dashed line indicates 1:1 relationship.

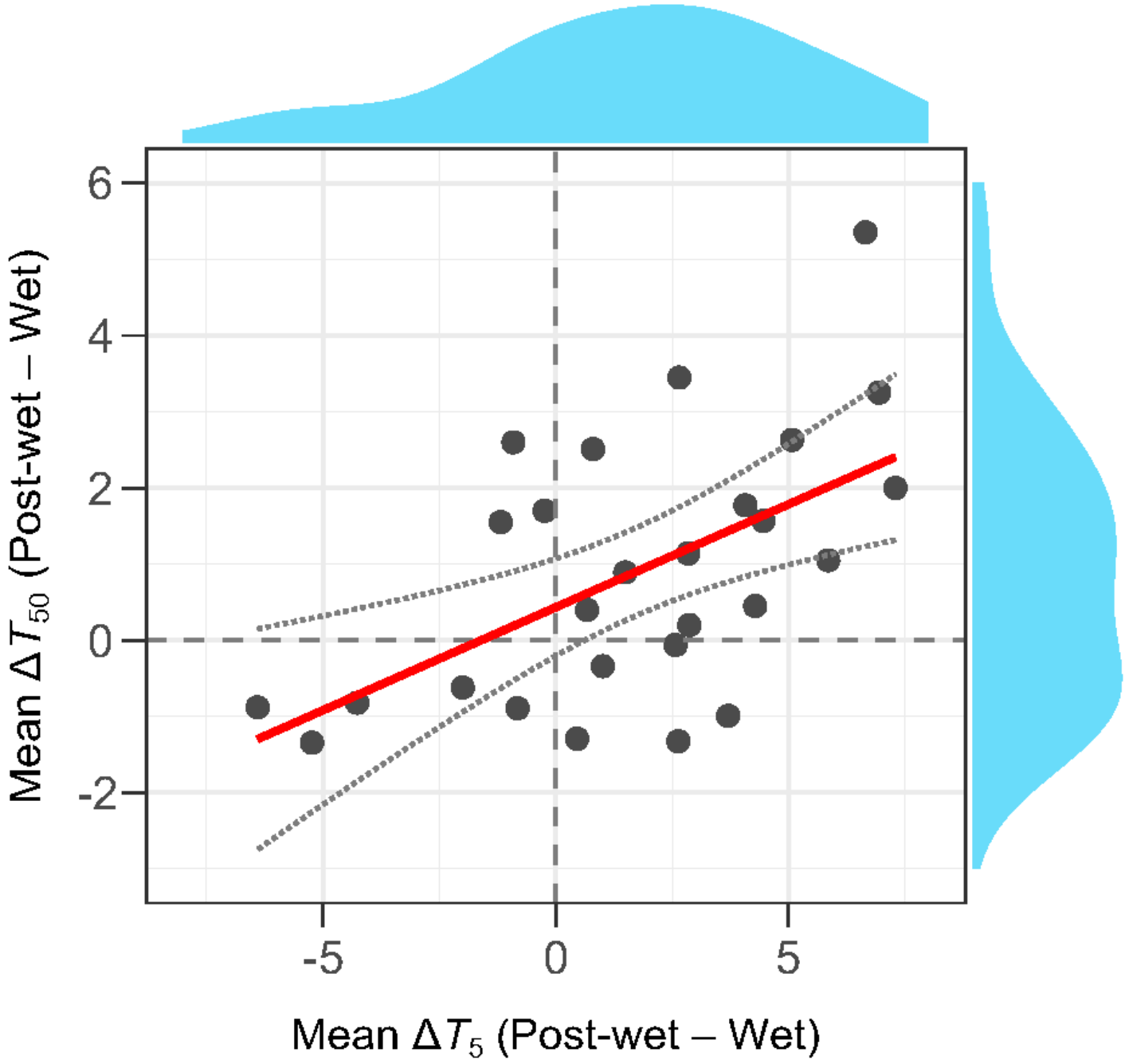

Figure 4

Coordinated seasonal shifts in T_5 and T_{50} across 24 tree species in a seasonally dry tropical forest, Central Western Ghats. Species-mean DT_5 (post-wet minus wet T_5, °C) vs. DT_{50} (post-wet minus wet T_{50}, °C) reveals positive correlation (r = 0.56, p = 0.0023), with most species showing parallel shifts (odds ratio = 7.3, p = 0.061). Standard major axis slope = 2.08, 95% CI: 1.49–2.90 (R^2 = 0.32, p < 0.01).

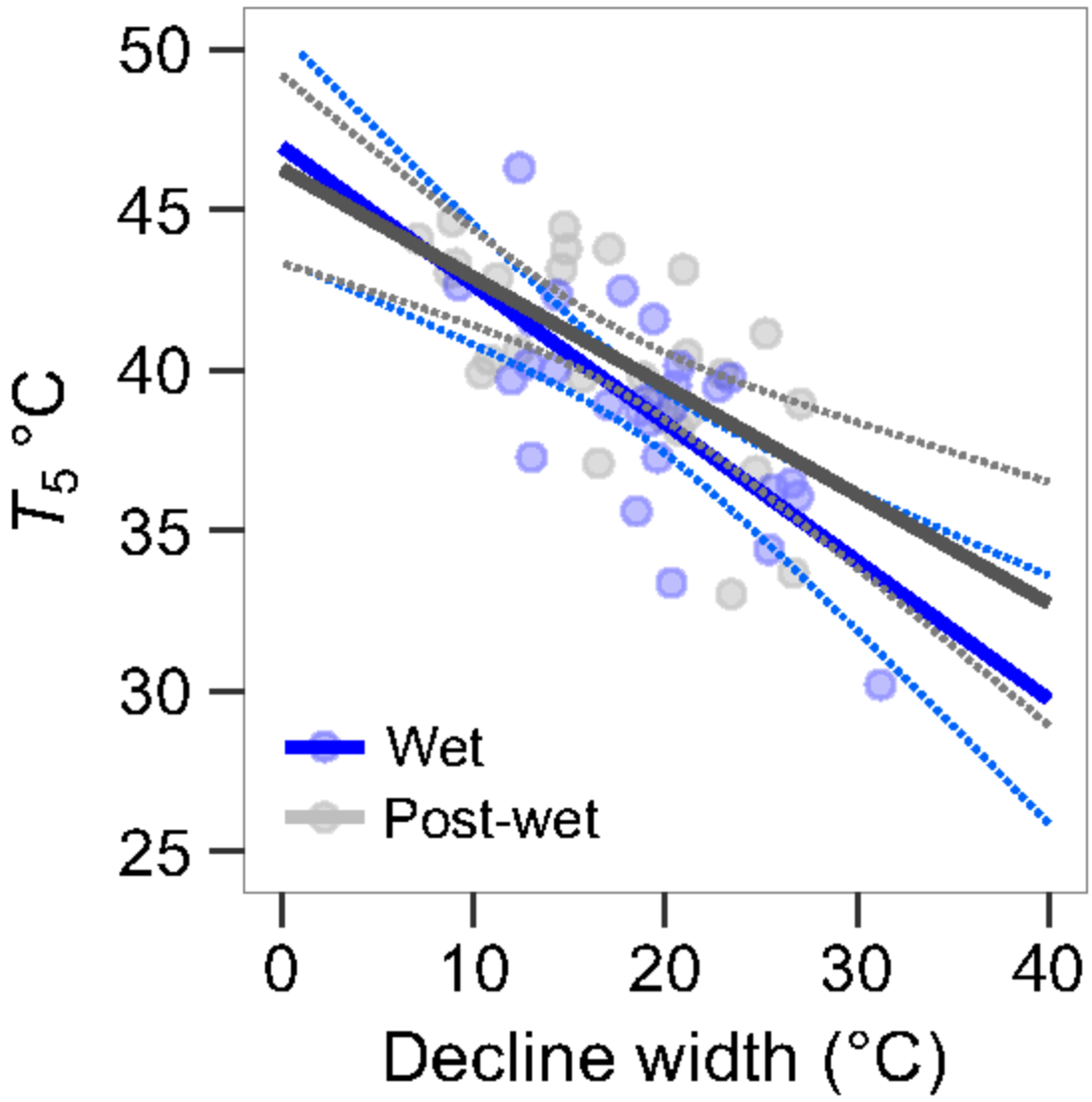

Figure 5

Relationship between temperature of PSII heat sensitivity initiation (T_5) and decline width, the temperature window from T_{95} to T_5. Standard major axis regression (linear) model fit was significant for both wet and post-wet periods the slopes were statistically indifferent.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

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