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Land regions are warming rapidly. While in a warming world at extra-tropical latitudes vegetation adapted to higher temperatures may move in from lower latitudes this is not possible in the tropics. Thus, the limits of plant functioning will determine the nature and composition of future vegetation. The most temperature sensitive component of photosynthesis is photosystem II. Here we report the thermal safety margin (difference between photosystem II thermotolerance (T_{50}) and maximum leaf temperature) during the beginning of the dry season for four tree species co-occurring across the forest-savanna transition zone in Brazil, a region which has warmed particularly rapidly over the recent decades. The species selected are evergreen in forests but deciduous in savannas. We find that thermotolerance declines with growth temperature >40 °C for individuals in the savannas. Current maximum leaf temperatures exceed T_{50} in some species and will exceed T_{50} in a 2.5 °C warmer world in most species evaluated. Despite plasticity in leaf thermal traits to increase leaf cooling in hotter environments, the results show this is not sufficient to maintain a safe thermal safety margin in hotter savannas. Overall, the results suggest that tropical forests may become increasingly deciduous and savanna-like in the future.

1. Introduction

An increase in the frequency of extreme weather events, such as droughts and heatwaves, is expected as a consequence of climate change [1]. This is in addition to rapidly increasing temperatures. Heatwaves are defined as a period of several consecutive days with extremely high temperatures [2]. Such high temperatures may negatively affect the functioning and survival of plants [3, 4].

For most tropical tree species the intrinsic capacity to cope with extreme heat in a warming world under natural conditions is poorly known. The impact of different abiotic stressors has been investigated in experimental studies [5], however, in natural areas observations are rare [6]. Long-term exposure to excessively high temperatures can affect the ability

of essential tree physiological processes [7]. As the leaf temperature rises above the optimum temperature for photosynthesis, the activation state of Rubisco decreases [8] and net photosynthesis is reduced [9] while mitochondrial respiration rises [10]. Studies on broad bean have indicated that at temperatures above 35 °C the thylakoid membranes inside the chloroplasts undergo structural changes [11] and when the temperature exceeds 40 °C, photosystem II (PSII) can be deactivated and linear electron transport stop [12]. Above 45 °C damage to PSII may become irreversible and can lead to the death of the leaf [13]. In tropical regions, irreparable thermal damage of PSII occurs in the region of 45 °C–52 °C [14]. The impact of heat can be further increased when abiotic stresses act together (e.g. temperature, humidity, and light) [15].

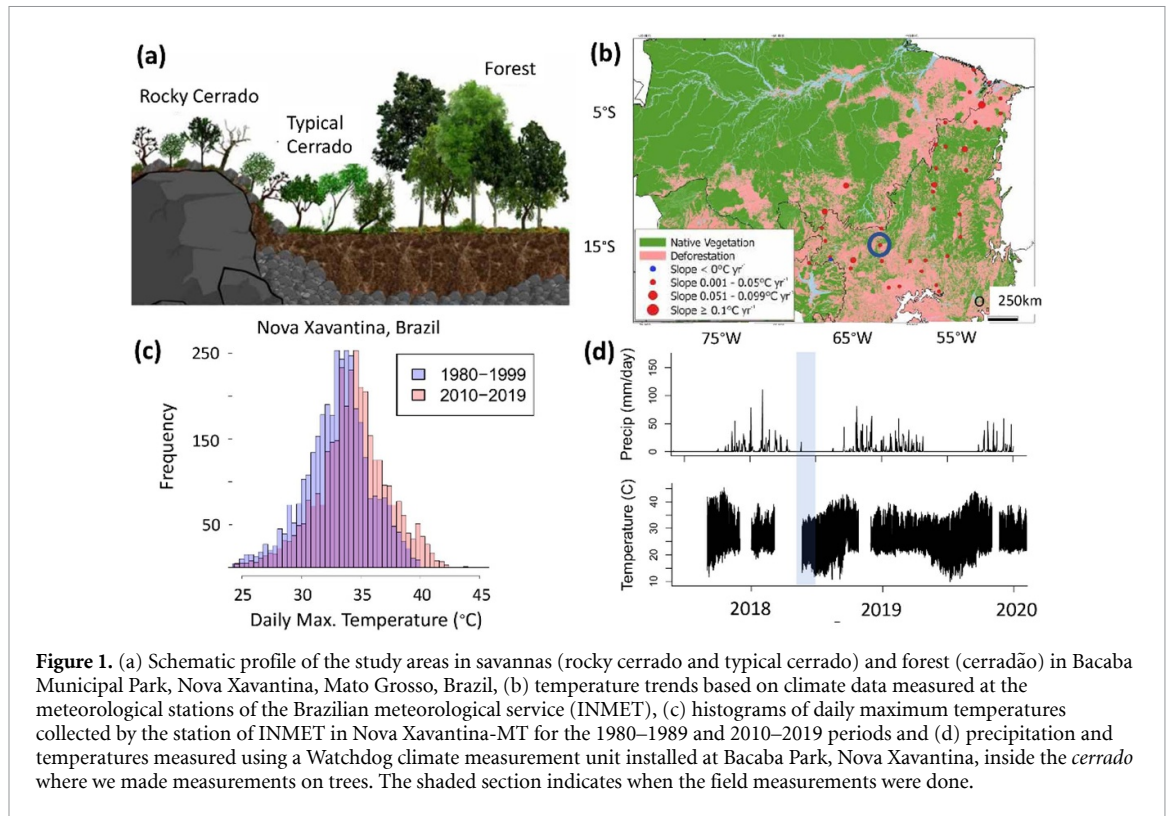


Figure 1. (a) Schematic profile of the study areas in savannas (rocky cerrado and typical cerrado) and forest (cerradão) in Bacaba Municipal Park, Nova Xavantina, Mato Grosso, Brazil, (b) temperature trends based on climate data measured at the meteorological stations of the Brazilian meteorological service (INMET), (c) histograms of daily maximum temperatures collected by the station of INMET in Nova Xavantina-MT for the 1980–1989 and 2010–2019 periods and (d) precipitation and temperatures measured using a Watchdog climate measurement unit installed at Bacaba Park, Nova Xavantina, inside the *cerrado* where we made measurements on trees. The shaded section indicates when the field measurements were done.

The thermal limits of PSII can be assessed by exposing leaves to light pulses (PAM, pulse amplitude modulation) and measuring fluorescence responses to these pulses [16, 17]. From the fluorescence signal the efficiency of PSII photochemistry, or quantum yield, can be estimated [18]. PSII chlorophyll fluorescence quantum yield as a function of leaf temperature tends to follow a sigmoidal curve. The decrease at high temperatures has been interpreted as a decrease in functioning of PSII. Once very low levels of quantum efficiency have been reached damage to PSII has been shown to be irreversible [19]. The temperature corresponding to a 50% PSII quantum yield decrease is referred to as T_{50} and is a frequently used metric of leaf thermotolerance [14, 20]. Based on T_{50} a thermal safety margin of the leaf photosynthesis apparatus has traditionally been estimated as the difference between leaf thermotolerance and air temperature [21, 22]. However, leaf temperatures differ from air temperature because heat gained by absorption of solar radiation and loss via longwave radiation, sensible heat and latent heat loss are not in balance. Thus, these limits may have been underestimated. Indeed several studies have shown that leaf temperatures can be substantially higher than air temperature [23]. A physiologically more accurate thermal safety margin of the photosynthesis apparatus is thus the difference between maximum leaf temperature and T_{50} .

In this study we evaluated for the first time the leaf photosynthetic thermal safety margin (T_{SM}), the difference between maximum leaf temperature and T_{50} , for tree species co-occurring along a gradient

of savanna and forest formations (figure 1(a)) in the Amazonia-Cerrado transition area based on *in-vivo* measured leaf temperatures and determination of T_{50} .

The region (Amazonia-Cerrado transition) has warmed rapidly over recent decades, with maximum air temperatures reaching 45 °C and is subjected to regular and increasingly hot and dry heat waves (figures 1(c) and (d)). It is a region which has experienced large rates of deforestation and conversion of vegetation to pasture and crop plantations. It is representative of a wide vegetation belt along the southern reaches of the Amazonia humid forest region characterized by a mosaic of remaining forests and agricultural land, which have similar temperature trends (figure 1(b)). We assessed T_{SM} of four tree species occurring in three common vegetation formations across the transitional zone (figure 1(a)): transitional forest (*cerradão*), typical cerrado (*cerrado típico*) and rocky cerrado (*cerrado rupestre*). These formations are in close proximity but differ in structure and microenvironment. The transitional forest (*cerradão*), which interconnect areas of cerrado with the forest, contains the tallest trees and closed canopy, lower air temperatures and radiation, and higher relative humidity and soil moisture, and with the rocky cerrado at the opposing extreme [24, 25]. In the typical cerrado, trees are spaced wider apart compared to transitional forests and have a comparably low stature [26]. In the rocky cerrado, trees are located between the rocks [27]. The species chosen *Qualea parviflora* Mart., *Pseudobombax longiflorum*

Table 1. Thermal analysis of co-occurrent trees in savanna and forest formations in the Amazonia-Cerrado transition. Loss of 50% of the PSII function (T_{50}), maximum leaf temperature (T_{Lmax}), excessive leaf temperature (ΔT_{Max}), current thermal safety margin (T_{Sm}) and future thermal safety margins ($T_{Sm+2.5\text{ }^{\circ}\text{C}}$ and $+5\text{ }^{\circ}\text{C}$). RC = rocky cerrado, TC = typical cerrado, FO = forest (*cerradão*), sd = standard deviation.

Species	Vegetations	T_{50} ($^{\circ}\text{C}$) average (min and max)	T_{Lmax} ($^{\circ}\text{C}$) average and sd	ΔT_{Max} ($^{\circ}\text{C}$) average and sd	T_{Sm} ($^{\circ}\text{C}$)	$T_{Sm+2.5\text{ }^{\circ}\text{C}}$	$T_{Sm+5\text{ }^{\circ}\text{C}}$
<i>Hymenaea stigonocarpa</i>	RC	49.06 (47.2–51.4)	47.79 \pm 2.96	1.71 \pm 0.89	1.95	−0.55	−3.05
	TC	49.84 (46.9–51.3)	42.47 \pm 2.43	4.94 \pm 0.84	−0.50	−3	−5.5
	FO	50.96 (48.5–54)	36.99 \pm 1.78	2.75 \pm 0.26	2.81	0.31	−2.19
<i>Vatairea macrocarpa</i>	RC	47.58 (45.5–49.1)	41.40 \pm 1.12	3.07 \pm 0.49	−0.89	−3.39	−5.89
	TC	47.96 (44.3–52.7)	32.42 \pm 0.52	2.76 \pm 0.63	−0.2	−2.7	−5.2
	FO	50.24 (47.6–52.8)	34.44 \pm 0.70	1.43 \pm 0.19	3.41	0.91	−1.59
<i>Pseudobombax longiflorum</i>	RC	46.74 (46.3–47.7)	44.80 \pm 1.02	5.22 \pm 2.57	−3.88	−6.38	−8.88
	TC	47.7 (45.3–50.4)	43.67 \pm 6.89	2.88 \pm 0.40	−0.58	−3.08	−5.58
	FO	48.06 (47.6–48.4)	36.12 \pm 0.98	1.27 \pm 0.39	1.39	−1.11	−3.61
<i>Qualea parviflora</i>	RC	47.08 (45.1–48.6)	36.11 \pm 1.57	2.62 \pm 0.34	−0.94	−3.44	−5.94
	TC	49.65 (48–50.6)	34.16 \pm 0.62	3.06 \pm 0.12	1.19	−1.31	−3.81
	FO	48.04 (47.2–49.7)	31.11 \pm 0.31	2.14 \pm 1.32	0.50	−2	−4.5

(Mart.) A. Robyns, *Hymenaea stigonocarpa* Mart. ex Hayne and *Vatairea macrocarpa* (Benth.) Ducke. occur in all three vegetation types, and therefore give an indication of both the interspecific variation in heat tolerance and thermal traits and the extent of intraspecific plasticity in these traits across different environments. However, their phenological status varies across vegetation types in that all species in our study are evergreen in the forest but deciduous in leaf habit in the savanna formations. April–May is not the hottest period of the year, therefore the leaf air temperature differences we measured are likely an underestimate of maximum leaf to air differences.

To better understand the thermal tolerance results, we also measured leaf morphological and physiological traits related to leaf temperature regulation. Functional traits can influence the amount of solar radiation intercepted by the leaf and leaf cooling by sensible and latent heat loss. For example, a high density of trichomes reduces the entry of radiation into the tissue, leaf angle and orientation can impact the intensity of radiation intercepted and stomatal conductance will influence transpiration rates and thus latent heat loss. In addition, leaf size also contributes to regulation of leaf temperature

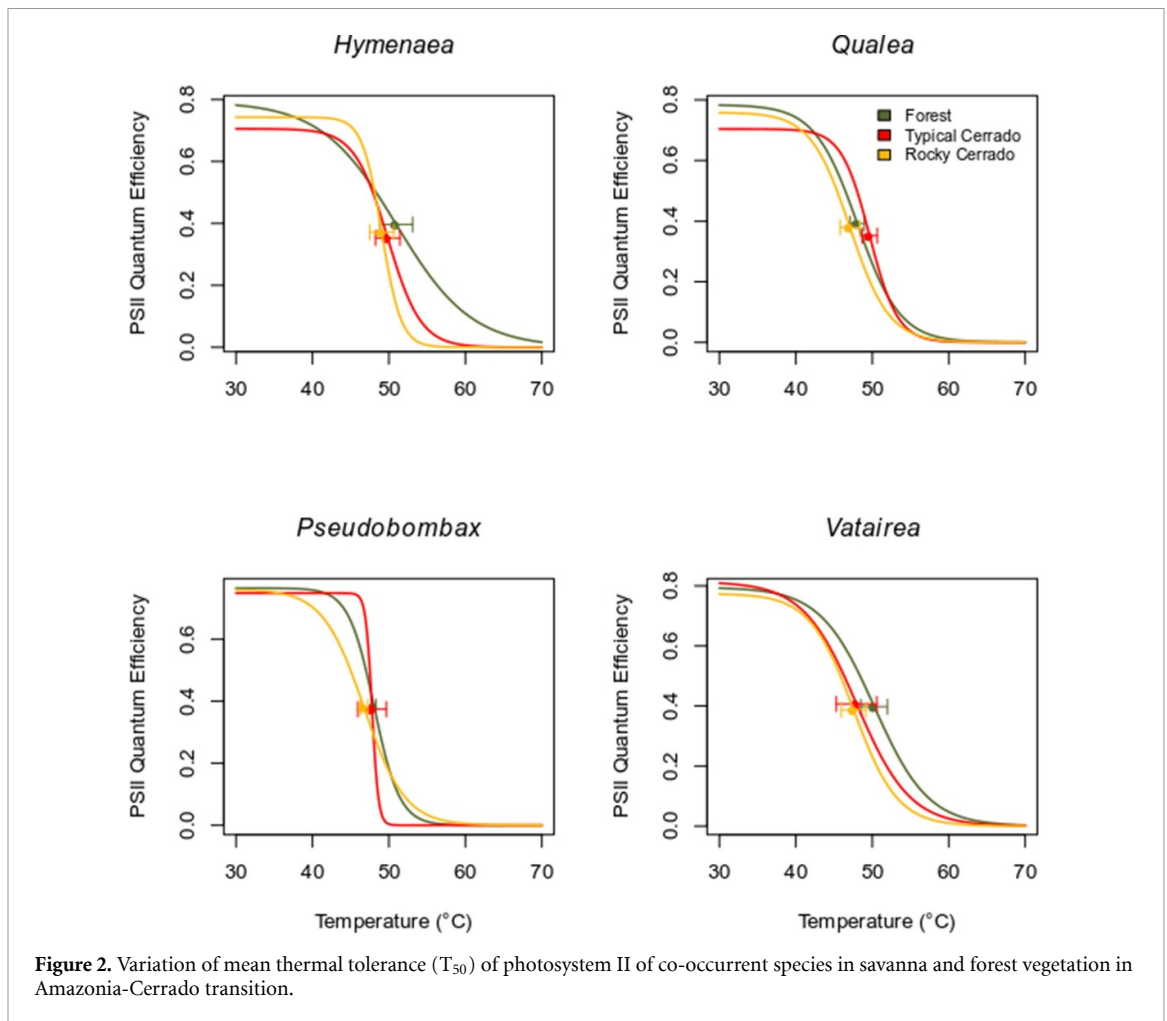
(e.g. smaller leaves have a thinner boundary layer and are more efficient at losing heat) [28, 29]. We evaluated a large set of leaf traits including leaf water mass content, specific leaf area, adaxial cuticle thickness, adaxial epidermis thickness, trichome density, stomatal density, stomatal size, maximum area of stomatal pore and leaf thickness.

2. Results

2.1. Leaf morphological and anatomical traits, maximum leaf temperature and ΔT_{MAX}

In the savannas, individuals had more efficient leaf anatomical and morphological traits: higher trichomes density, thicker epidermis and cuticle, to regulate leaf temperature, when compared to individuals in the forest (supplementary table 1 which is available online at stacks.iop.org/ERL/16/034047/mmedia). In contrast, specific leaf area of individuals in the forest was the only trait whose values were higher for forest individuals compared to the savannas (supplementary table 1).

Maximum leaf temperature (T_{Lmax}) differed significantly between savanna and forest individuals (T_{Lmax} : $P < 0.05$, table 1), but was similar



between savannas individuals (T_{Lmax} : $P = 0.41$, table 1). Individuals in forest had lower maximum leaf temperature (mean of $34.7\text{ }^{\circ}\text{C}$) than individuals in savanna (mean $42.5\text{ }^{\circ}\text{C}$), (table 1).

The maximum leaf air temperature difference (ΔT_{MAX} : difference in temperature between leaf and air) observed during the period of measurements was positively correlated with the thickness of the epidermis ($R^2 = 0.43$, $P = 0.02$) and negatively with the specific leaf area ($R^2 = -0.40$, $P = 0.04$, supplementary figure 1). We also observed that the leaves of individuals growing in the savannas (typical cerrado and rocky cerrado) with higher values of cuticle thickness and small leaves are warmer than the leaves of individuals of the same species growing in the forest (supplementary figure 1 and supplementary table 1).

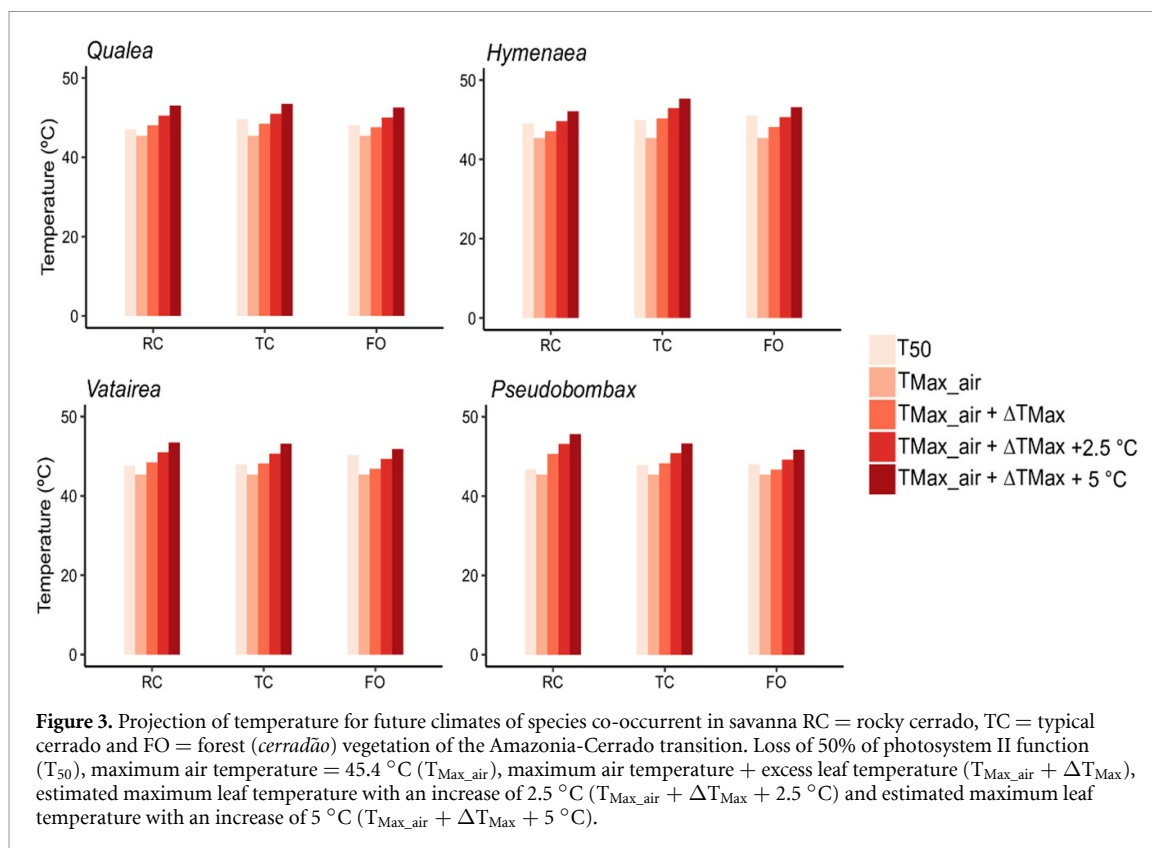
2.2. Leaf photosynthesis thermal limits (T_{50})

Thermal tolerance (T_{50}) varied significantly between savanna and forest individuals, and between species (supplementary table 2). In some cases, the quantum yield of PSII versus temperature curves varied within a species across vegetation types (supplementary figures 2–13). Combining all species, individuals in the forest were found to have higher thermal tolerance values compared to individuals in

the savannas ($P < 0.0001$; figure 2 and table 1). Within species, T_{50} also varied significantly across vegetation types, except for *H. stigonocarpa*. The T_{50} values of *Q. parviflora* were higher in the typical cerrado and lower in the rocky cerrado and in the forest, whereas for *V. macrocarpa* and *P. longiflorum*, the T_{50} values were higher in the forest and lower in the savannas (supplementary table 3).

2.3. Thermal safety margins and climate change predictions

H. stigonocarpa and *V. macrocarpa* had the highest mean thermal safety margins (T_{SM}) values, while *P. longiflorum* and *Q. parviflora* showed the lowest mean values of T_{SM} (table 1). We find that individuals growing under higher mean maximum air temperatures had lower T_{SM} (table 1). Thermal safety margins were highest for individuals in the forest (table 1) with the exception of *Q. parviflora*, with somewhat higher T_{SM} in the typical cerrado than in the forest. *H. stigonocarpa* had high T_{SM} values in both the rocky cerrado and in the forest (table 1). Surprisingly, the maximum estimated leaf temperatures already exceed T_{50} for individuals in the savannas except for *Q. parviflora* in the typical cerrado, and *H. stigonocarpa* in the rocky cerrado (figure 3). Thus, there are



already rare instances towards the beginning of the dry period when the leaf photosynthesis apparatus of these species is heavily stressed and potentially damaged (figure 3 and table 1).

To assess potential future temperature safety margins of leaf PSII operation we compare currently estimated maximum leaf temperatures plus 2.5 °C (climate change scenario RCP 4.5) and 5 °C (RCP 8.5) (figure 3 and table 1) [30]. We have chosen these temperature elevations based on a summary of climate model projections for the period 2080–2100 [30]. With the increase of 2.5 °C, the vast majority of the species evaluated showed negative thermal safety margins (figure 3 and table 1), with the exceptions of *H. stigonocarpa* and *V. macrocarpa* growing in the forest. On the other hand, with an increase of 5 °C, all species evaluated showed negative thermal safety margins (table 1). Even before the temperature elevation simulations, trees from the rocky cerrado and the typical cerrado had very low or even negative thermal safety margins, indicating that these individuals are more sensitive to changes in future climate changes (table 1 and figure 3).

3. Discussion

Our results show that the leaves of individuals growing in savanna formations had more efficient leaf morphological and anatomical traits during the onset of the dry season to regulate leaf temperature, compared to the leaves of individuals of the same species in the forest. In response to the exposure of

the leaves of savanna individuals to more extreme temperature and direct solar radiation, the individuals have developed functional strategies capable of dissipating heat more efficiently [31]. As individuals in the forest experience lower maximum leaf temperatures, they may need to invest less in strategies to increase efficiency in heat dissipation. The lower temperatures in the forest may possibly be linked to evaporative cooling or local atmospheric circulation caused by the mosaic of remaining forests and agriculturally used land. Finally, in the forest, individuals are exposed to higher air humidity, resulting in lower vapor pressure deficit (VPD) and reduced leaf transpiration, assuming stomatal conductance does not change. This would favor a higher leaf temperature for trees during times with high CO_2 assimilation rates.

Despite the more efficient morphological and anatomical traits, which should reduce leaf temperature [32], during the measurement period we observed higher leaf temperatures and ΔT_{MAX} values in the savanna formations. Plants in the savanna formations are exposed to higher air temperatures which will lead to higher leaf temperatures compared to the forest, but their traits could help limit this. However, these adaptations were not sufficient for individuals from savannas to maintain similar or lower ΔT_{MAX} compared the same species in the forest.

Plants from warmer biomes [22] which are exposed regularly to heatwaves [33] have been shown to have high thermotolerance. In contrast, we found that T_{50} declined in warmer vegetation types, suggesting that the increased stress to which

these plants were exposed has reduced their ability to cope with the heat and so at the beginning of the dry period, the savanna trees are already thermally stressed. Therefore, our study demonstrates that, for the individuals in the savannas, the critical levels of tolerable temperature for photosynthetic function is already reached at the beginning of the dry season. In particular, the T_{50} of *P. longiflorum* and *V. macrocarpa* in the rocky and typical cerrado is already being exceeded by the current maximum air temperatures, thus having a negative T_{SM} . The combination of higher leaf temperatures and lower T_{50} in savanna formations thus results in lower thermal safety margins. Such low T_{SM} would be expected to intensify as the dry season progresses. However, the deciduous nature of these species in the savannas provides an adaptation that allows for protection against dangerously high temperatures. In the forests too, thermal safety margins would be expected to become increasingly negative with dry season severity. The higher T_{50} and higher T_{SM} of forest trees provides a level of tolerance against high leaf temperatures in the peak of the dry season. However, there are limits to this tolerance, beyond which leaves cannot be sustained without damage. Beyond these limits, species persistence is likely only possible if there is an associated shift towards a deciduous habit, as observed in the savannas.

For the projected increase of 2.5 °C, the thermal safety margin of the studied species will be regularly exceeded even at the beginning of the dry season, both in savannas and in the forest, and for individuals in savannas the situation is more critical. In particular, the $T_{SM+2.5\text{ °C}}$ of *H. stigonocarpa* and *V. macrocarpa* in the forest would potentially support this temperature increase. For a future increase of 5 °C, our results indicate that during the beginning of the dry period, the PSII of all species regardless of vegetation types will be severely affected (table 1). These results demonstrate that for all these vegetation types there will be an intensification of thermal risk. This is in line with what has been found for other tropical trees [14, 34], where individuals that may be operating near and even above their thermal thresholds are more likely to be affected by the increase in heatwaves. In savanna species which are already deciduous, the increased thermal risk may alter the timing and duration of leaf loss, with potentially reducing productivity. In the forests, however, where our focal species are not deciduous, trees might be expected to become increasingly deciduous and savanna-like in the future, with important consequences for forest structure, productivity and carbon storage.

4. Conclusion

Our measurements demonstrate that the thermal limits of some tropical savanna and forest species are close to the maximum temperatures experienced, and

thus how these species function is likely to be affected by the increase in global temperature. A defence to thermal stress is deciduousness, a characteristic of those individuals growing in savannas, but not those in forests. Our results thus indicate expected shifts in deciduousness in the future and thus a trend towards savanna vegetation replacing forests in the regions in Southern Amazonia characterized by large patches of deforestation.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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Author contributions

Conceived and designed the investigation: I A, B S M, S F, M C S, M U G. Performed field and laboratory work: I A. Analyzed the data: I A, B S M, S F, M U G, M C S. Wrote the paper: I A, S F, M U G, B S M, B H M J, M C S, D R G, R T.

Conflict of interest

The authors declare they have not conflict of interests.

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