

In situ temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall regimes

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Summary

- Tropical forests contribute significantly to the global carbon cycle, but little is known about the temperature response of photosynthetic carbon uptake in tropical species, and how this varies within and across forests.
- We determined *in situ* photosynthetic temperature–response curves for upper canopy leaves of 42 tree and liana species from two tropical forests in Panama with contrasting rainfall regimes. On the basis of seedling studies, we hypothesized that species with high photosynthetic capacity – light-demanding, fast-growing species – would have a higher temperature optimum of photosynthesis (T_{Opt}) than species with low photosynthetic capacity – shade-tolerant, slow-growing species – and that, therefore, T_{Opt} would scale with the position of a species on the slow–fast continuum of plant functional traits.
- T_{Opt} was remarkably similar across species, regardless of their photosynthetic capacity and other plant functional traits. Community-average T_{Opt} was almost identical to mean maximum daytime temperature, which was higher in the dry forest. Photosynthesis above T_{Opt} appeared to be more strongly limited by stomatal conductance in the dry forest than in the wet forest.
- The observation that all species in a community shared similar T_{Opt} values suggests that photosynthetic performance is optimized under current temperature regimes. These results should facilitate the scaling up of photosynthesis in relation to temperature from leaf to stand level in species-rich tropical forests.

Introduction

Currently, the terrestrial biosphere takes up $c. 123 \times 10^{15}$ g carbon from the atmosphere every year in gross photosynthesis, but respiration from plants and soils releases an almost equally large amount back into the atmosphere (Pachauri *et al.*, 2014). Both photosynthesis and respiration change nonlinearly with increasing temperature, and the small difference between these large fluxes determines the extent to which global vegetation may exacerbate or mitigate future climate change (Cox *et al.*, 2000). Current models do not accurately predict the effect of environmental change on these fluxes (Smith & Dukes, 2013) and the effect of warming on biosphere–atmosphere feedbacks remains a key uncertainty (Booth *et al.*, 2012; Piao *et al.*, 2013). This is particularly true in the tropics (Galbraith *et al.*, 2010; Ahlström *et al.*, 2012; Cox *et al.*, 2013; Huntingford *et al.*, 2013), where we lack empirical data describing the temperature response of carbon fluxes that would be important for constraining and validating the models.

Tropical forests play a large role in the global carbon cycle, accounting for more than one-third of terrestrial net primary

productivity (Saugier *et al.*, 2001) whilst occupying only $c. 15\%$ of the global land surface (Pan *et al.*, 2013). The high productivity of tropical forests is, in part, a result of the absence of cold winters, as consistently high temperatures enable tropical forests to maintain high metabolic activity throughout the year. A second factor is the extremely high species diversity, which results in greater niche occupancy and more effective resource use than in less diverse, higher latitude forests (Loreau *et al.*, 2001). However, the high temperatures put tropical forests at risk, as further warming may bring the vegetation closer to its physiological limits (Doughty & Goulden, 2008). Furthermore, the high species diversity poses a challenge to the prediction of future community dynamics if responses to warming differ among species.

Photosynthesis typically increases with increasing leaf temperature until it reaches an optimum (P_{Opt}), beyond which rates decrease, reaching zero at the high-temperature carbon-compensation point (T_{Max}). The decrease above the optimum temperature (T_{Opt}) is caused by three major factors: stomatal closure in response to increased leaf-to-air vapor pressure deficit (VPD), changes in photosynthetic biochemistry, and increasing rates of respiration in the light (e.g. Wise *et al.*, 2004; Sage &

Kubien, 2007; Lin *et al.*, 2012). T_{Opt} in tropical forest plants appears to be close to current ambient daytime temperatures (Doughty & Goulden, 2008; Slot *et al.*, 2016), but studies to date are based on very few species. Given the diversity of tropical forests, surprisingly little is known about the variation in photosynthetic temperature optima and maxima across species and plant functional groups.

Species may differ in their temperature–response traits in accordance with their position on the slow–fast continuum based on the leaf economic spectrum (Wright *et al.*, 2004). Among tropical tree seedlings, fast-growing, shade-intolerant species associated with high-light environments have higher thermal optima than slow-growing species that are associated with closed-canopy forest (Slot *et al.*, 2016). Because ‘fast’ species have higher photosynthetic rates, we would expect a positive correlation between T_{Opt} and P_{Opt} , and a directional shift in the response curves if the observed pattern holds across a larger number of species (Fig. 1). The regeneration niche of ‘fast’ species is a sunny, warm environment typically associated with early succession in forest gaps, whereas ‘slow’ species regenerate in the cooler, shaded forest understory. Physiological adaptation towards optimized performance under these contrasting conditions would yield the differences in photosynthetic traits observed for seedlings. However, in the upper canopy, where most of the stand-level gas exchange occurs, ‘fast’ and ‘slow’ species experience the same sunny and warm environment, and it is currently unknown whether the temperature–response traits diverge across species in the canopy in the same way as they do in seedlings.

Even under similar environmental conditions in the canopy, physiological parameters that play a role in shaping the temperature response of photosynthesis differ enormously among co-occurring ‘slow’ and ‘fast’ species. Species differ systematically in maximum stomatal conductance (Reich *et al.*, 1995), stomatal responsiveness to drought (Huc *et al.*, 1994), respiratory capacity (Slot *et al.*, 2014b), photosynthetic biochemistry as determined from CO_2 –response curves (Norby *et al.*, 2017) and the temperature optima of Rubisco carboxylation and photosynthetic electron transport rates (Vårhammar *et al.*, 2015). These systematic differences could lead to higher T_{Opt} in ‘fast’ than in ‘slow’ species, consistent with the observations in seedlings (Slot *et al.*, 2016). For example, photosynthesis at high temperature is commonly limited by electron transport (Wise *et al.*, 2004; Sage & Kubien, 2007): ‘fast’ species have higher electron transport capacity than slow species (Norby *et al.*, 2017), which may enable the maintenance of higher photosynthesis rates at high temperature than in ‘slow’ species. Among tropical montane trees, ‘fast’ species also have higher T_{Opt} of electron transport (Vårhammar *et al.*, 2015), which may further favor their performance at high temperature.

The shape of the temperature–response curves may also change with increasing T_{Opt} (Fig. 1c). Curves could widen or narrow with increasing T_{Opt} , depending on whether higher T_{Opt} is associated with higher or lower physiological plasticity. A recent theory linking carbon economics and leaf temperature regulation proposes that ‘fast’ species have wider temperature–response curves, and thus greater plasticity, than ‘slow’ species, and data

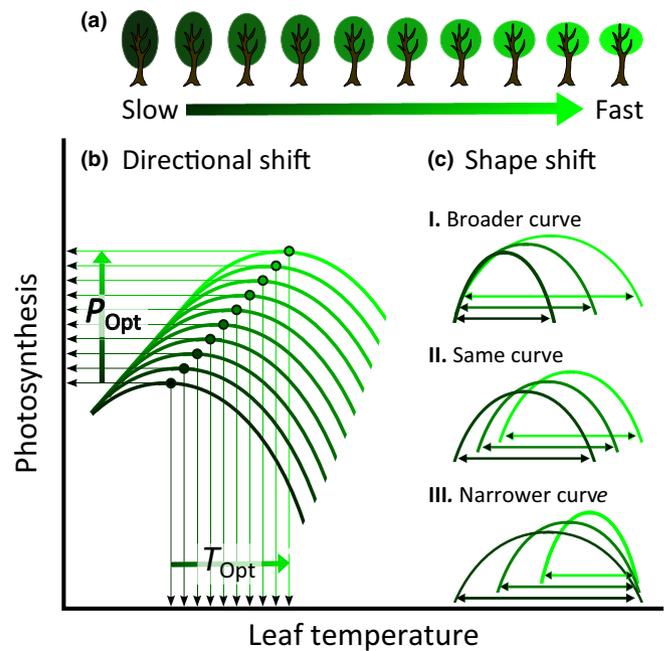


Fig. 1 Illustration of the hypothesized effects of (a) the location of a species on the slow–fast continuum associated with the leaf economics spectrum (a) on: (b) the position and (c) the shape of the temperature–response curve of photosynthesis. Darker colors represent ‘slow’ species – generally shade-tolerant species that maintain many layers of leaves; lighter colors represent ‘fast’ species associated with early succession or gap conditions – shade-intolerant species that maintain shallow crowns with little self-shading (a). ‘Fast’ species have higher photosynthesis rates at optimum temperature (P_{Opt}) and are hypothesized to have higher optimum temperatures for photosynthesis (T_{Opt}), thus effectively presenting a directional shift in the temperature–response curves relative to ‘slow’ species (b). Curves may broaden with increasing T_{Opt} values, if ‘fast’ species have wider temperature tolerance; they may stay the same, or they may narrow with increasing T_{Opt} (c), for example, as a result of fixed upper temperature limits.

on a mix of forbs, grasses and trees from thermally dynamic temperate environments support this theory (Michaletz *et al.*, 2016). This would be consistent with scenario I in Fig. 1(c). However, temperature–response curves could also narrow with increasing T_{Opt} if T_{Max} represents a fixed physiological limit. This could be the case if T_{Max} is controlled by the intrinsic thermotolerance of biochemical processes and constituents shared by all plants, rather than stomatal conductance, which can be highly species specific (e.g. Klein, 2014). T_{Max} may be controlled by Rubisco activase (Crafts-Brandner & Salvucci, 2000; Salvucci & Crafts-Brandner, 2004), ribulose biphosphate (RuBP) regeneration (Kubien & Sage, 2008) or photosynthetic electron transport (Wise *et al.*, 2004), and, although there are some species differences, for example, in thermally stable Rubisco activase orthologs (Scafaro *et al.*, 2016), some of these biochemical limits appear to be inflexible. For example, the temperature at which potential Photosystem II activity is irreversibly suppressed is *c.* 51–52°C for ‘slow’ and ‘fast’ tropical species alike (Krause *et al.*, 2010, 2015).

We measured the temperature response of photosynthesis of upper canopy leaves *in situ* for 30 tree species and 12 species of

liana (woody vines) at two lowland tropical forest sites with contrasting rainfall regimes in Panama. We used these data to test the hypothesis that temperature–response curves differ in relation to the position of species on the slow–fast continuum, leading to a positive correlation between the temperature optimum of photosynthesis and the rate of photosynthesis at this temperature (Fig. 1b). Our second hypothesis was that the higher the T_{Opt} of a species, the narrower will its temperature–response curve be (Fig. 1c, III). Because high-temperature effects on plant performance often interact with drought, with one exacerbating the negative effect of the other (Shah & Paulsen, 2003; Teskey *et al.*, 2015), we further evaluated the differences in temperature–response traits and the level of stomatal limitation of photosynthesis at *supra*-optimal temperatures between dry and wet forest species, and between trees and lianas – an important growth form in tropical forests with hydraulic architecture distinctly different from that of trees (Tyree & Ewers, 1991).

Materials and Methods

Study sites and species selection

The study was conducted at two lowland tropical forest sites on opposite sides of the Isthmus of Panama: a seasonally dry forest, and a wet evergreen forest. At both sites, the Smithsonian Tropical Research Institute maintains a tower crane that enables access to the upper canopy. Parque Natural Metropolitano (PNM, 8°59'41.55"N, 79°32'35.22"W, 30 m above sea level) is a seasonally dry secondary forest on the outskirts of Panama City, near the Pacific coast. Annual rainfall averages 1830 mm, >90% of which falls during the rainy season from May to December. Mean annual temperature at 25 m above the forest floor is 25.9°C, with mean daily minimum and maximum temperatures of 23.1 and 30.8°C, respectively (data from 1997–2015). The crane at PNM is 42 m tall and has a 51-m jib. Parque Nacional San Lorenzo (PNSL, 9°16'51.71"N, 79°58'28.27"W, 130 m above sea level) is a wet evergreen forest on the Caribbean coast. Annual rainfall averages 3200 mm, with a relatively short dry season from January to March with <100 mm rainfall month⁻¹. Mean annual temperature is 25.3°C, and mean daily minimum and maximum temperatures are 23.6 and 29.9°C, respectively (data from 1997–2015). The crane at PNSL is 52 m tall with a 54-m jib.

In total, 42 canopy tree and liana species belonging to 31 families were measured (Table 1) over the course of 38 crane visits between 1 February and 15 May 2016. At PNM, we selected 12 tree species and nine liana species. At PNSL, where the liana cover in the canopy is much lower (M. Slot, pers. obs.), we selected 18 tree and five liana species. Two liana species were measured at both sites. Species will henceforth be referred to by their genus names alone.

Measurement protocol

For each species, 5–10 sun-exposed terminal shoots were selected on one or more individuals (depending on availability within

reach of the crane; see Table 1). All leaves were measured at heights between *c.* 20 and *c.* 35 m. Per individual, *c.* 10–150 healthy-looking, fully expanded leaves were selected (Table 1) and photosynthesis was measured once on each leaf as the leaf temperature increased towards solar noon. On a subset of ten species, an additional 8–12 leaves were selected for repeated measurements (5–10 measurements per leaf) to evaluate whether repeated measurements would yield similar estimates of temperature–response parameters to the use of a large population of once-measured leaves. The repeated measurement approach was then employed for large-leaved species that maintained small numbers of leaves meeting our selection criteria at the time of measurement, such as *Castilla* and *Schefflera*. Repeated measurements were pooled before fitting of the temperature–response models.

Net photosynthesis was measured *in situ* with an LI-6400 portable photosynthesis system (Licor, Lincoln, NE, USA) over as wide an ambient temperature range as possible. Measurements were made between 07:30 and 13:30 h, during which period the ambient air temperature generally increased from *c.* 25 to 32°C. Sun-exposed leaves, however, frequently reached temperatures in the high 30°C or even in the low 40°C region. The cuvette temperature was set to the leaf temperature measured with an infrared thermometer (MiniTemp MT6; Raytek, Santa Cruz, CA, USA) before clamping the cuvette onto the leaf. On overcast days, the cuvette was warmed several degrees above ambient temperature for the final leaves to increase the temperature range of the measurements, in which case longer equilibration times were required (occasionally up to 10 min). In this approach, the leaf temperature is elevated above that of the rest of the plant, but this is not an uncommon situation in the forest canopy; because leaf temperature is strongly driven by solar irradiance, temperatures of neighboring leaves can differ by 10°C or more if one is angled towards the sun and the other is angled away from it. The degree of warming achieved by increasing the cuvette temperature is only a fraction of the total range of temperatures commonly observed within a single canopy (Rey-Sánchez *et al.*, 2016).

To minimize the number of changing variables during the measurements, all leaves were measured at the same reference [CO₂] and light level. Reference [CO₂] was maintained near 390 ppm, leading to a mean [CO₂] in the cuvette of 379 ± 6 ppm (SD) during maximum photosynthesis. Irradiance at the leaf surface was maintained at 1000 μmol quanta m⁻² s⁻¹. This light level may not saturate the photosynthesis of all leaves, but increases in photosynthesis above 1000 μmol quanta m⁻² s⁻¹ are small for most species, and this light level is unlikely to cause photoinhibition of photosynthesis when leaves are measured below or above their T_{Opt} .

Measurements were made *in situ*, because *ex situ* measurements are prone to artifacts, especially in the tropics, where many species produce latex that clogs up the xylem on branch excision (Santiago & Mulkey, 2003). *In situ* measurements of photosynthesis are superior for the purpose of monitoring ambient processes in the forest canopy, but environmental control during measurements is limited. For example, we utilized ambient temperature changes to determine photosynthetic temperature

Table 1 Tree and liana species studied, their family, and number of individuals ($N_{\text{Individuals}}$) and leaves (N_{Leaves}) in (a) a seasonally dry and (b) a wet tropical forest

| Growth form | Family | Species | $N_{\text{Individuals}}$ | N_{Leaves} | |
|--|-----------------|--|--|---------------------|-----|
| (a) Dry forest, Parque Natural Metropolitano | | | | | |
| Trees | Anacardiaceae | <i>Astronium graveolens</i> Jacq. | 1 | 80 | |
| | | <i>Spondias mombin</i> L. | 1 | 129 | |
| | Araliaceae | <i>Schefflera morototoni</i> (Aubl.) Maguire, Steyerl. & Frodin | 1 | 10 | |
| | | Lauraceae | <i>Nectandra cuspidata</i> Nees & Mart. | 1 | 75 |
| | Malvaceae | <i>Luehea seemannii</i> Triana & Planch | 1 | 33 | |
| | Moraceae | <i>Castilla elastica</i> ssp. <i>costaricana</i> (Liebm.) C.C.Berg | 1 | 8 | |
| | | <i>Ficus insipida</i> Willd. | 1 | 70 | |
| | Rubiaceae | <i>Macrocneum roseum</i> (Ruiz & Pav.) Wedd. | 1 | 72 | |
| | | <i>Pittoniotis trichantha</i> Griseb. | 1 | 43 | |
| | Salicaceae | <i>Zuelania guidonia</i> (Sw.) Britton & Millsp. | 1 | 27 | |
| | Sapotaceae | <i>Chrysophyllum cainito</i> L. | 1 | 57 | |
| | Urticaceae | <i>Cecropia peltata</i> L. | 1 | 45 | |
| | Lianas | Aristolochiaceae | <i>Aristolochia tonduzii</i> O.C.Schmidt | | 45 |
| Bignoniaceae | | <i>Amphilophium paniculatum</i> (L.) Kunth | | 56 | |
| | | <i>Bignonia corymbosa</i> (Vent.) L.G.Lohmann | | 86 | |
| Convolvulaceae | | <i>Bonamia trichantha</i> Hallier f. | | 53 | |
| Dilleniaceae | | <i>Dolioscarpus major</i> J.F.Gmel. | | 122 | |
| Malpighiaceae | | <i>Stigmaphyllon lindenianum</i> A.Juss. | | 100 | |
| Passifloraceae | | <i>Passiflora vitifolia</i> Kunth | | 56 | |
| Polygalaceae | | <i>Securidaca diversifolia</i> (L.) S.F.Blake | | 102 | |
| Sapindaceae | | <i>Serjania mexicana</i> (L.) Willd. | | 73 | |
| (b) Wet forest, Parque Nacional San Lorenzo | | | | | |
| Trees | | Anacardiaceae | <i>Anacardium excelsum</i> (Bertero ex Kunth) Skeels | 1 | 64 |
| | | | <i>Tapirira guianensis</i> Aubl. | 1 | 78 |
| | | Annonaceae | <i>Guatteria dumetorum</i> R.E.Fr. | 2 | 189 |
| | Boraginaceae | <i>Cordia bicolor</i> A.DC. | 1 | 103 | |
| | Bursaraceae | <i>Protium panamense</i> (Rose) I.M.Johnst. | 2 | 112 | |
| | Clusiaceae | <i>Garcinia madruno</i> (Kunth) Hammel | 1 | 43 | |
| | Combretaceae | <i>Terminalia amazonia</i> (J.F.Gmel.) Exell | 1 | 116 | |
| | Humiriaceae | <i>Vantanea depleta</i> McPherson | 1 | 10 | |
| | Leguminosae | <i>Tachigali versicolor</i> Standl. & L.O.Williams | 2 | 148 | |
| | Malvaceae | <i>Apeiba membranacea</i> Spruce ex Benth. | 1 | 73 | |
| | Meliaceae | <i>Carapa guianensis</i> Aubl. | 1 | 58 | |
| | Melastomataceae | <i>Miconia minutiflora</i> (Bonpl.) DC. | 1 | 71 | |
| | Moraceae | <i>Brosimum utile</i> (Kunth) Oken | 1 | 85 | |
| | Myristicaceae | <i>Virola multiflora</i> (Standl.) A.C.Sm. | 1 | 151 | |
| | Rubiaceae | <i>Tocoyena pittieri</i> (Standl.) Standl. | 1 | 68 | |
| | Sapotaceae | <i>Manilkara bidentata</i> (A.DC.) A.Chev. | 2 | 42 | |
| | Simaroubaceae | <i>Simarouba amara</i> Aubl. | 2 | 245 | |
| | Vochysiaceae | <i>Vochysia ferruginea</i> Mart. | 1 | 45 | |
| | Lianas | Bignoniaceae | <i>Bignonia corymbosa</i> (Vent.) L.G.Lohmann | | 56 |
| | | Celastraceae | <i>Tontelea ovalifolia</i> (Miers) A.C.Sm. | | 73 |
| Dilleniaceae | | <i>Dolioscarpus major</i> J.F.Gmel. | | 64 | |
| Malpighiaceae | | <i>Adelphia platyrachis</i> (Triana & Planch.) W.R.Anderson | | 80 | |
| | | Olacaceae | <i>Heisteria scandens</i> Ducke | | 89 |

$N_{\text{Individuals}}$ is not provided for lianas, the canopies of which are difficult to assign to individuals.

responses, but the reversibility of the observed patterns could not be assessed because leaf temperatures in the canopy generally do not drop below T_{Opt} until the early evening (e.g. Rey-Sánchez *et al.*, 2016), and cooling leaves using the cuvette of the LI-6400 is not feasible. Likewise, as leaf temperature increases, so does the leaf-to-air VPD, an important variable for physiological processes, such as stomatal conductance. We allowed VPD – as calculated from leaf temperature and relative humidity by the LI-6400 – to stabilize during the measurements, but did not try

to control it for two reasons. First, with currently available field-compatible equipment, the maintenance of a stable VPD over a broad temperature range is extremely challenging, if not impossible. Second, because of their interrelatedness, elevated temperature without elevated VPD – although of great interest from a physiological and modeling perspective – does not represent realistic conditions for the plants. Site-specific relationships between leaf temperature, VPD, stomatal conductance and net photosynthesis are presented in Supporting Information Fig. S1.

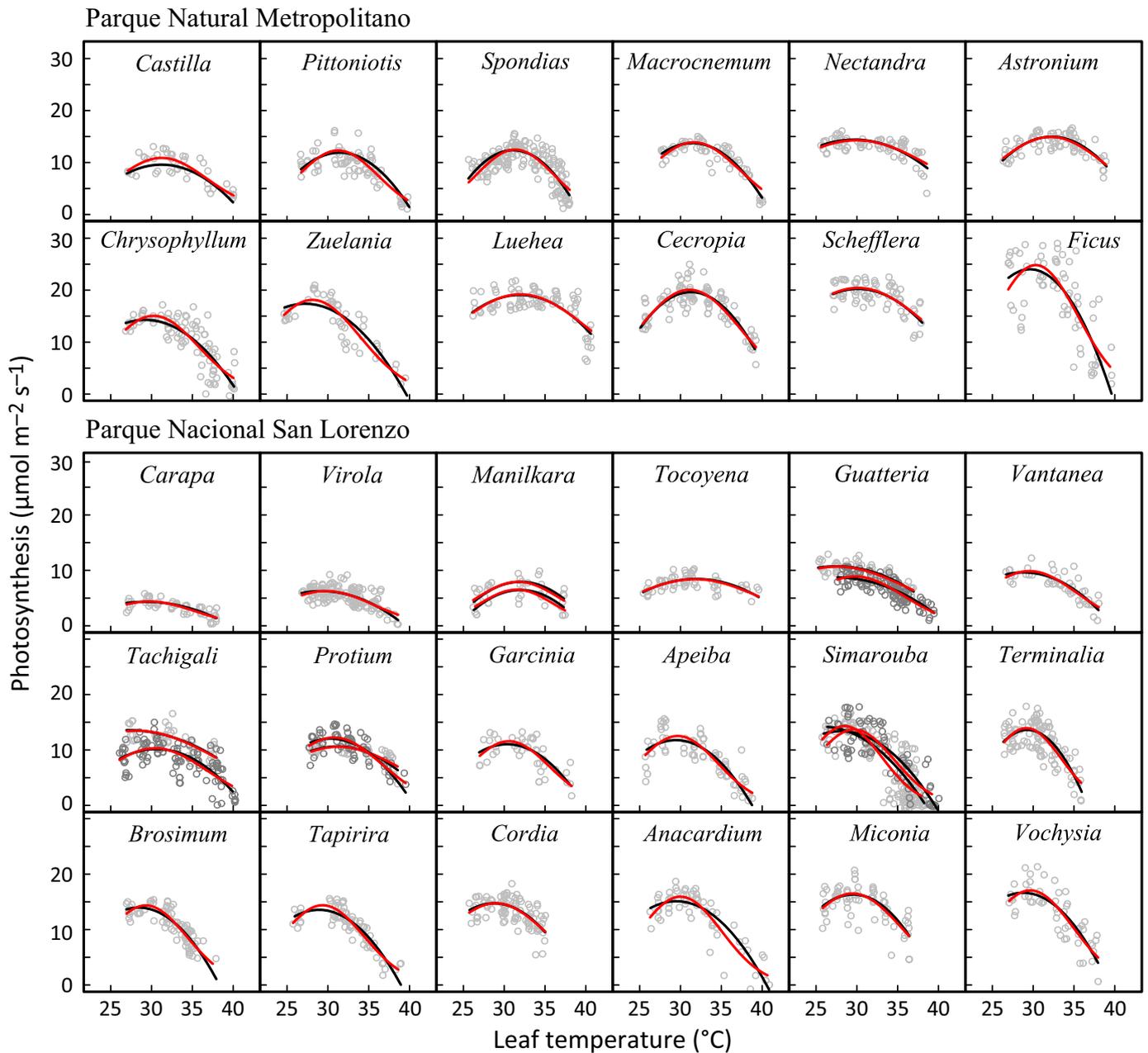


Fig. 2 Light-saturated photosynthesis as a function of leaf temperature for 12 tree species at Parque Natural Metropolitano and 18 tree species at Parque Nacional San Lorenzo. Red lines are fitted according to Eqn 1 and were used to calculate T_{Opt} and P_{Opt} ; black lines are fitted according to Eqn 2 and were used to calculate T_{Max} . Replicate curves are fitted to data for a second individual measured on a different day (dark gray data points). Within each site, species are ordered from 'slow' to 'fast' based on their P_{Opt} . See Table 1 for full species names and Supporting Information Table S1 for parameter values derived from the curves shown here.

Measurements were taken in the dry season, which is much sunnier than the wet season, and thus leaves more often experience the very high temperatures associated with direct irradiance. We plotted mean stomatal conductance and the ratio of intercellular to ambient CO_2 concentration ($c_i : c_a$) at different set temperatures, as well as the calculated parameters P_{Opt} and T_{Opt} , against the day of the year to test whether the progression of the dry season affected our response variables. No significant trend in any of the parameters was found. The dataset is publicly available (Slot & Winter, 2017).

Data analysis

Photosynthesis per unit leaf area (P) at temperature T was fitted according to June *et al.* (2004) as:

$$P(T) = P_{\text{Opt}} \times e^{-\left(\frac{T_{\text{leaf}} - T_{\text{Opt}}}{\Omega}\right)^2}, \quad \text{Eqn 1}$$

where Ω is the difference in temperature between T_{Opt} and the temperature at which P drops to e^{-1} (37%) of its value at T_{Opt} .

that is, it describes the sharpness or width of the curve's peak. Curves were fitted using the nonlinear least-squares function 'NLS' in the 'STATS' package in R v.3.1.3 (R Development Core Team, 2015), and standard errors were determined for all parameters. This equation generated curves that fitted the data very well (see Figs 2, 3), being superior to simple polynomial fits where few data points below T_{Opt} were available. However, because these curves asymptote towards zero rather than becoming negative, as happens with net CO₂ exchange in reality, Eqn 1 cannot be used to estimate the high-temperature carbon compensation point (T_{Max}). We therefore also fitted the data following Cunningham & Read (2002) as:

$$P(T) = b \times (T_{Leaf} - T_{Min}) \times (1 - e^{c \times (T_{Leaf} - T_{Max})}), \quad \text{Eqn 2}$$

to estimate T_{Max} . In Eqn 2, T_{Min} is the theoretical low-temperature carbon compensation point, and b and c are species-specific constants. T_{Min} is an extrapolated value not suitable for biological interpretation as it was, on average, at least 10°C lower than the lowest temperature at which leaves were measured. Eqn 2 yielded very similar curves to Eqn 1 (Figs 2, 3), but described the high-temperature behavior of net photosynthesis more realistically.

The maximum rate of RuBP carboxylation (V_{cMax}) was estimated using the one-point method as described in De Kauwe *et al.* (2016a,b). This approach makes use of the fact that, at current ambient atmospheric CO₂ concentration, light-saturated photosynthesis is generally limited by the rate of RuBP carboxylation, rather than by the maximum rate of RuBP regeneration (J_{Max}). The apparent V_{cMax} , or \hat{V}_{cMax} , was calculated using the biochemical model of photosynthesis of Farquhar *et al.* (1980). The temperature dependences of the Michaelis–Menten constants for CO₂ and O₂, and the CO₂ compensation point (Γ^*), were taken from Bernacchi *et al.* (2001). The rate of respiration in the light (R_{Light} , non-photorespiratory mitochondrial respiration in the light) was assumed to be 1.5% of the apparent V_{cMax} in accordance with De Kauwe *et al.* (2016a). With increasing temperature, RuBP regeneration becomes increasingly limiting (e.g. Sage & Kubien, 2007), and it is thus increasingly likely that the carboxylation limitation assumption of the one-point method is violated. Furthermore, at low stomatal conductance, the error of V_{cMax} estimation is proportionally larger than at high stomatal conductance (De Kauwe *et al.*, 2016a; Notes S1). We therefore only report \hat{V}_{cMax} at T_{Opt} (mean \hat{V}_{cMax} over the $T_{Opt} \pm 2^\circ\text{C}$ range) in the main text, and refer to the Supporting Information for \hat{V}_{cMax} at all temperatures.

We calculated the degree of stomatal limitation of net photosynthesis according to Farquhar & Sharkey (1982) by comparing the observed net photosynthesis with what the net photosynthesis would be without any stomatal limitation. The intercellular CO₂ concentration (c_i) was set equal to the CO₂ concentration in the cuvette (c_a), and net photosynthesis in the absence of stomatal restrictions was then back-calculated from \hat{V}_{cMax} using the Farquhar *et al.* (1980) model:

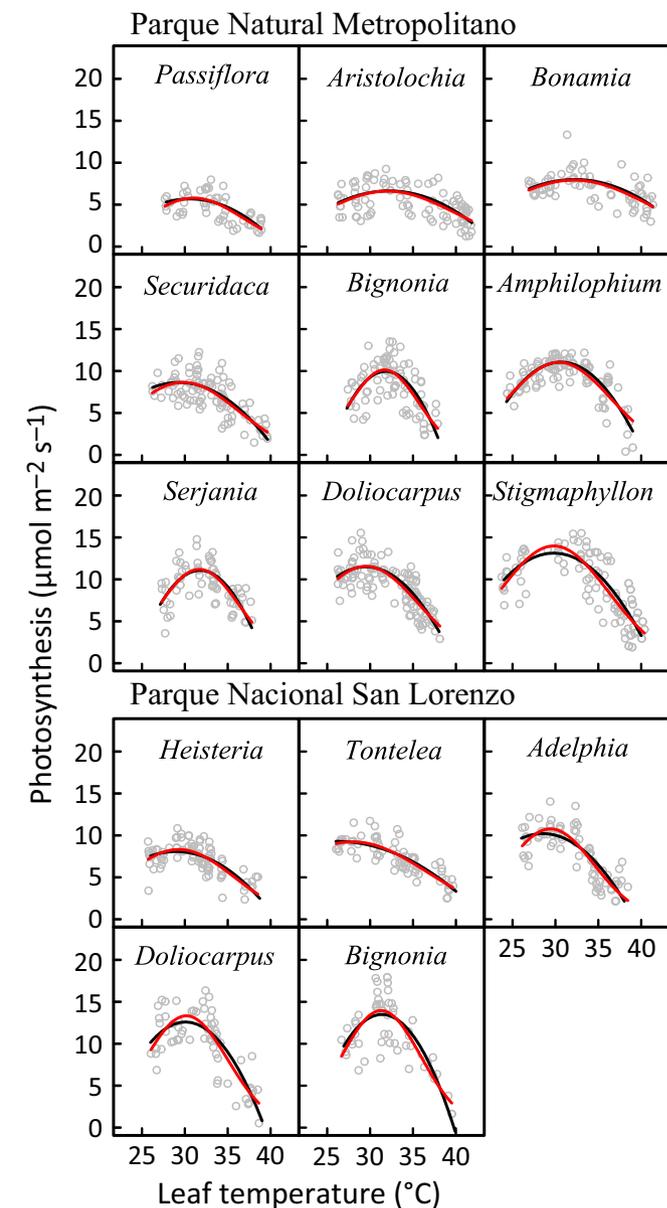


Fig. 3 Light-saturated photosynthesis as a function of leaf temperature for nine liana species at Parque Natural Metropolitano and five species at Parque Nacional San Lorenzo. Red lines are fitted according to Eqn 1 and were used to calculate T_{Opt} and P_{Opt} ; black lines are fitted according to Eqn 2 and were used to calculate T_{Max} . Within each site, species are ordered from 'slow' to 'fast' based on their P_{Opt} . See Table 1 for full species names and Supporting Information Table S1 for parameter values derived from the curves shown here.

$$V_{cMax} = \frac{A_g \times (c_i + K_m)}{c_i - \Gamma^*}, \quad \text{Eqn 3}$$

where A_g is the gross photosynthesis, K_m is the Michaelis–Menten constant and Γ^* is the CO₂ compensation point. As before, R_{Light} was assumed to equal 1.5% of V_{cMax} , and K_m and Γ^* were taken from Bernacchi *et al.* (2001).

The stomatal limitation parameter ‘*l*’ was then calculated as:

$$l = 1 - \frac{A_{\text{observed}}}{A_{\text{without stomatal limitation}}} \quad \text{Eqn 4}$$

Differences in temperature–response traits among species and between sites and growth forms were determined using analysis of variance with Tukey honestly significant difference (HSD) *post hoc* tests carried out in R with the ‘AOV’ and ‘TUKEYHSD’ functions. To evaluate relationships among the calculated temperature–response traits, simple linear regression analyses were used (‘LM’). Differences in the slopes of linear regressions were assessed with analysis of covariance. All analyses were performed in R v.3.1.3 (R Development Core Team, 2015).

Results

Photosynthesis temperature–response curves

Figure 2 shows the rates of photosynthetic carbon uptake in relation to leaf temperature for 30 tree species at PNM (seasonally dry forest) and PNSL (wet evergreen forest), where species within each forest are ranked from ‘slow’ to ‘fast’ according to their maximum photosynthesis rate. The temperature–response curves based on Eqn 1 and on Eqn 2 both describe the measured data very well, and are similar across most of the temperature range. As indicated previously, the curves based on Eqn 2 describe the trends in photosynthesis as temperature approaches T_{Max} more realistically. Figure 3 shows similar data for 12 liana species, two of which (*Bignonia* and *Dolioscarpus*) were measured at both sites. \hat{V}_{cMax} calculated from these photosynthesis data and its relation to leaf temperature are shown in Fig. S2 (trees) and Fig. S3 (lianas).

Site and growth form differences in temperature–response traits

At 30.8°C (± 1.0) (mean ± SD), the site-average temperature of optimum photosynthesis (T_{Opt}) was significantly higher ($F_{1,40} = 11.4$, $P = 0.002$) in the dry forest than in the wet forest

(29.8 ± 0.9°C) (Table 2), with no significant difference between trees and lianas. Photosynthesis rates at T_{Opt} were significantly higher in trees than in lianas in the dry forest, but not in the wet forest ($F_{1,40} = 5.8$, $P = 0.02$ for the growth form-by-site interaction effect), and they did not differ significantly between sites (Table 2). The high-temperature carbon compensation point (T_{Max}) was significantly higher at the dry site, without differences between trees and lianas (Table 2). \hat{V}_{cMax} at T_{Opt} was higher in the dry forest than in the wet forest, and was higher in trees than in lianas (Table 2). The two liana species that were measured in both forests had very similar response curves at both sites (Table S1). *Bignonia* had T_{Opt} values of 31.7 and 31.3°C in the dry and wet forest, respectively, whereas *Dolioscarpus* had T_{Opt} values of 29.5°C in the dry forest and 30.2°C in the wet forest. T_{Max} values were similarly consistent, differing by < 1.2°C between sites. P_{Opt} values were, however, higher at the wet forest site for both species (Table S1; Fig. 3). For several families, multiple species were measured (Table 1), but there was no apparent clustering of trait values to reflect this relatedness.

Temperature–response traits along the slow–fast continuum

To evaluate whether ‘slow’ and ‘fast’ species differ systematically in their photosynthetic temperature response, we plotted all the fitted curves per site on one graph, ranking species from ‘slow’ to ‘fast’ based on their P_{Opt} values (Fig. 4a,b). There was no directional change in T_{Opt} along the slow–fast continuum at either site (Fig. 4a,b), and there was no discernible relationship between T_{Opt} and P_{Opt} across species (Fig. 4c,d; Table S2). The different forest sites were plotted separately because community mean T_{Opt} values were significantly different, but, when all 44 species-by-site combinations were plotted in a single graph, there was no relationship between T_{Opt} and P_{Opt} either. Consistent with this absence of a relationship between T_{Opt} and the position of a species on the slow–fast continuum based on P_{Opt} , T_{Opt} did not correlate with other leaf functional traits that are associated with the slow–fast continuum (Table S2), such as P_{Opt} expressed per unit leaf mass, leaf mass per unit leaf area, dark respiration rate (area- or mass-based), foliar nutrient content (area- or mass-

Table 2 Temperature–response traits of 42 tropical canopy species summarized by forest type (seasonally dry forest, Parque Natural Metropolitano (PNM), and wet forest, Parque Nacional San Lorenzo (PNSL)) and growth form (trees and lianas)

| Forest | Growth form | <i>n</i> | T_{Opt} (°C) | P_{Opt} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Ω (unitless) | T_{Max} (°C) | \hat{V}_{cMax} at T_{Opt} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) |
|--------------------|-------------|----------|--------------------------|--|------------------------|--------------------------|---|
| Dry (PNM) | Tree | 12 | 30.7 ± 1.1 | 16.2 ± 4.3 | 9.5 ± 2.5 | 41.8 ± 2.1 | 134 ± 45 |
| | Liana | 9 | 30.9 ± 1.0 | 9.6 ± 2.6 | 8.9 ± 2.2 | 41.5 ± 2.6 | 99 ± 28 |
| Wet (PNSL) | Tree | 18 | 29.8 ± 0.9 | 11.9 ± 3.6 | 8.3 ± 1.7 | 40.1 ± 1.8 | 95 ± 24 |
| | Liana | 5 | 29.6 ± 1.2 | 11.1 ± 2.5 | 8.4 ± 2.4 | 40.7 ± 1.6 | 79 ± 30 |
| Site | | | $P = 0.002$ | ns | ns | $P = 0.021$ | $P = 0.008$ |
| Growth form | | | ns | $P = 0.001$ | ns | ns | $P = 0.020$ |
| Site × growth form | | | ns | $P = 0.019$ | ns | ns | ns |

Means ± SD for *n* number of species are given for the optimum temperature of photosynthesis (T_{Opt}), the photosynthesis rate at optimum temperature (P_{Opt}), the curve ‘steepness’ parameter (Ω), the high-temperature carbon compensation point (T_{Max}) and estimated V_{cMax} at T_{Opt} . *P* values indicate significant effects on physiological traits of site and growth form and their interaction (ANOVA); nonsignificant effects are indicated with ‘ns’.

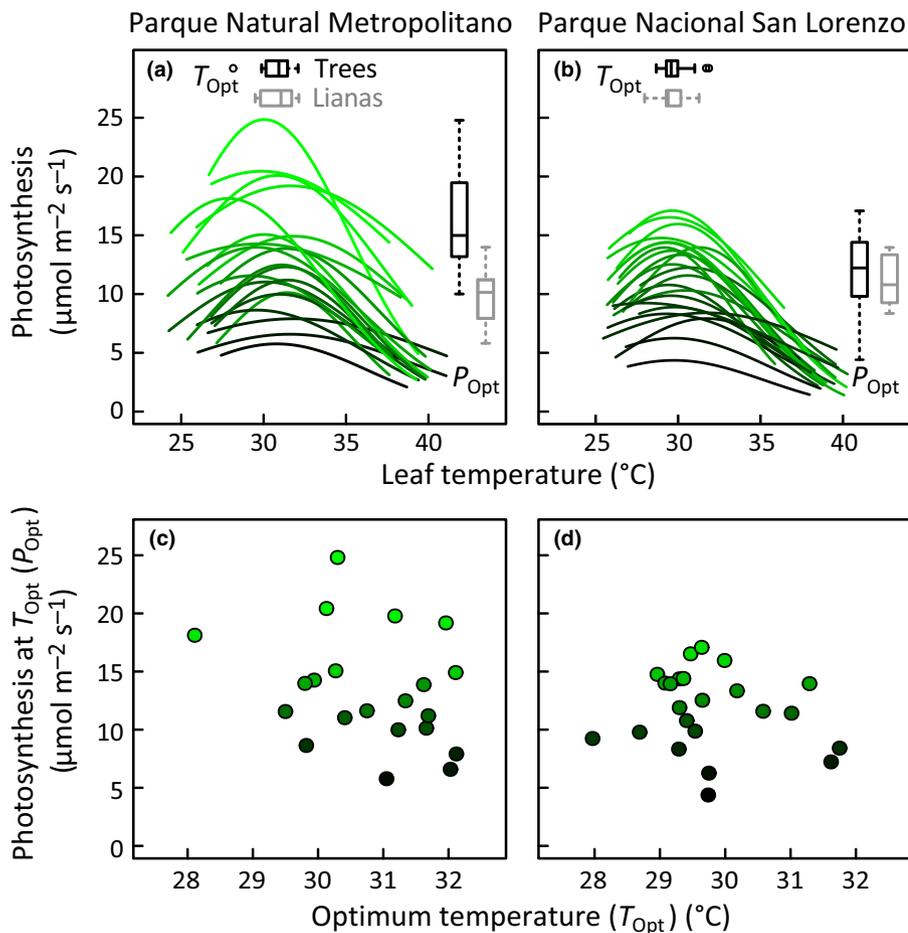


Fig. 4 Temperature–response curves of photosynthesis fitted according to Eqn 1 for (a) all 21 species in the dry forest and (b) all 23 species in the wet forest. The color scale represents the ‘slow’ to ‘fast’ ranking of the species with the black line representing the ‘slowest’ species and the light green line representing the ‘fastest’ species. Horizontal box-and-whisker plots indicate variation in the optimum temperature of photosynthesis (T_{Opt}) among trees (black) and lianas (gray) with outliers shown as open circles, and vertical box-and-whisker plots show the variation in photosynthesis rates at T_{Opt} (P_{Opt}) among trees (black) and lianas (gray). The absence of patterns between T_{Opt} and P_{Opt} across species is illustrated in (c, d), where colors correspond to those in (a, b).

based) or leaf lifespan, nor did it correlate with wood density or with the temperature sensitivity of dark respiration (previously published in Santiago & Wright, 2007; Chave *et al.*, 2009; Zanne *et al.*, 2009; Wright *et al.*, 2010; Slot *et al.*, 2013, 2014b; respiration data for PNSL species were taken from an unpublished dataset by M. Slot). Most species, regardless of growth form, optimum photosynthesis rate and associated leaf functional trait values, had T_{Opt} values near 30°C and T_{Max} values in the low 40°C region (Table S1).

The curve width, expressed as Ω , did not decrease with increasing P_{Opt} . Nor were curves for species with relatively high T_{Opt} narrower than those for species with low T_{Opt} . Ω did not decrease with increasing T_{Opt} because T_{Max} increased with increasing T_{Opt} ($P = 0.009$, $r^2 = 0.15$). T_{Max} was not highly constrained across species (range 36.7–46.6°C; Table S1).

Stomatal and nonstomatal limitations of high-temperature photosynthesis

Photosynthesis rates above T_{Opt} correlated with stomatal conductance in a log-linear fashion (Figs 5, S4, S5). Stomatal conductance decreased with increasing leaf temperature above T_{Opt} as VPD increased exponentially (Fig. S1). In all species for which measurement temperatures approached T_{Max} , stomatal conductance approached zero, suggesting that photosynthesis near T_{Max}

was limited by stomatal conductance. However, species differed considerably in their $c_1 : c_a$ ratios above T_{Opt} and the correlations between $c_1 : c_a$ and leaf temperature, VPD and net photosynthesis. For both trees and lianas, there was an overall positive correlation between photosynthesis above T_{Opt} and $c_1 : c_a$ in the dry forest ($P < 0.001$), but not in the wet forest (Fig. 5). At the species level, a positive correlation between $c_1 : c_a$ and photosynthesis above T_{Opt} was significant in 11 of 12 tree species and five of nine liana species in the dry forest, and only in five of 18 tree species and two of five liana species in the wet forest (Figs S6, S7). These results suggest that limitation of photosynthesis by stomatal processes was greater in the dry forest than in the wet forest. Stomatal limitation of photosynthesis calculated according to Eqn 4 significantly increased with increasing temperature above T_{Opt} at both sites, but the rate of increase was greater in the dry forest (significantly steeper slope, $P < 0.01$ for trees and lianas, ANCOVA) and temperature explained a greater proportion of the variance in stomatal limitation (Fig. 6; for species-level data see Figs S8, S9).

Discussion

Similarity in temperature–response traits across species

We hypothesized systematic differences in the temperature response of photosynthesis across co-occurring species because

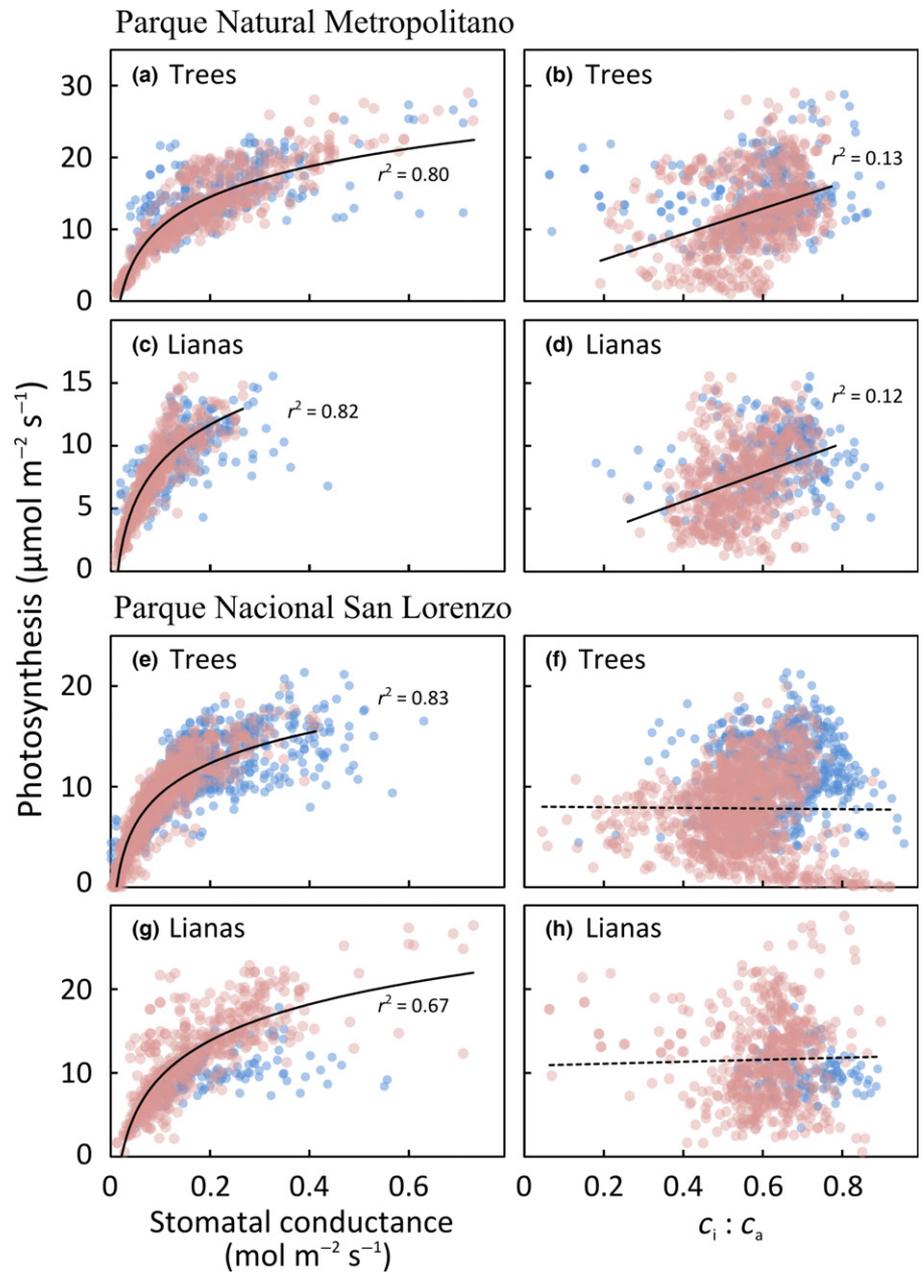


Fig. 5 Photosynthesis in relation to stomatal conductance and $c_i : c_a$ below (blue) and above (pink) the optimum temperature of light-saturated photosynthesis (T_{Opt}) for (a, b) trees and (c, d) lianas at Parque Natural Metropolitano, and for (e, f) trees and (g, h) lianas at Parque Nacional San Lorenzo. Photosynthesis above T_{Opt} is fitted as a function of log-transformed stomatal conductance and as a linear function of $c_i : c_a$. Solid lines indicate significant correlations; dashed lines are non-significant. See Supporting Information Figs S4–S7 for species-level data.

both stomatal and nonstomatal processes underlying the temperature response vary across species, often in relation to their position on the slow–fast continuum. By contrast, we found remarkably consistent thermal optima of photosynthesis across species, regardless of the position of the species on the slow–fast continuum, and no systematic differences between trees and lianas. These species differ enormously in their architecture, phenology, leaf display traits, photosynthetic parameters such as V_{cMax} and J_{Max} , and capacity for transpirational cooling, but, nonetheless, *c.* 90% of the T_{Opt} values fall within a 3°C range between 29 and 32°C. T_{Opt} is determined by the interaction of a series of processes, including stomatal conductance, R_{Light} , photosynthetic electron transport and Rubisco activation (Crafts-Brandner & Salvucci, 2000; Salvucci & Crafts-Brandner,

2004; Wise *et al.*, 2004; Kubien & Sage, 2008; Lin *et al.*, 2012) and, although the rates at which many of these processes operate differ among species, it is advantageous for all species that net photosynthesis is optimized at the ambient temperature to which they are exposed.

The small range of T_{Opt} values leaves limited space for patterns to emerge in relation to P_{Opt} variation, but we may need to exercise some caution when ranking species according to the measured photosynthesis rates. We selected healthy-looking, mature leaves, but, because leafing phenology differs among species, leaf age varied, which can affect photosynthetic capacity (Kitajima *et al.*, 1997). For example, *Castilla* was a ‘slow’ species here, because its P_{Opt} was amongst the lowest in the dry forest (*c.* 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$), but it is a dry season deciduous species with light-saturated

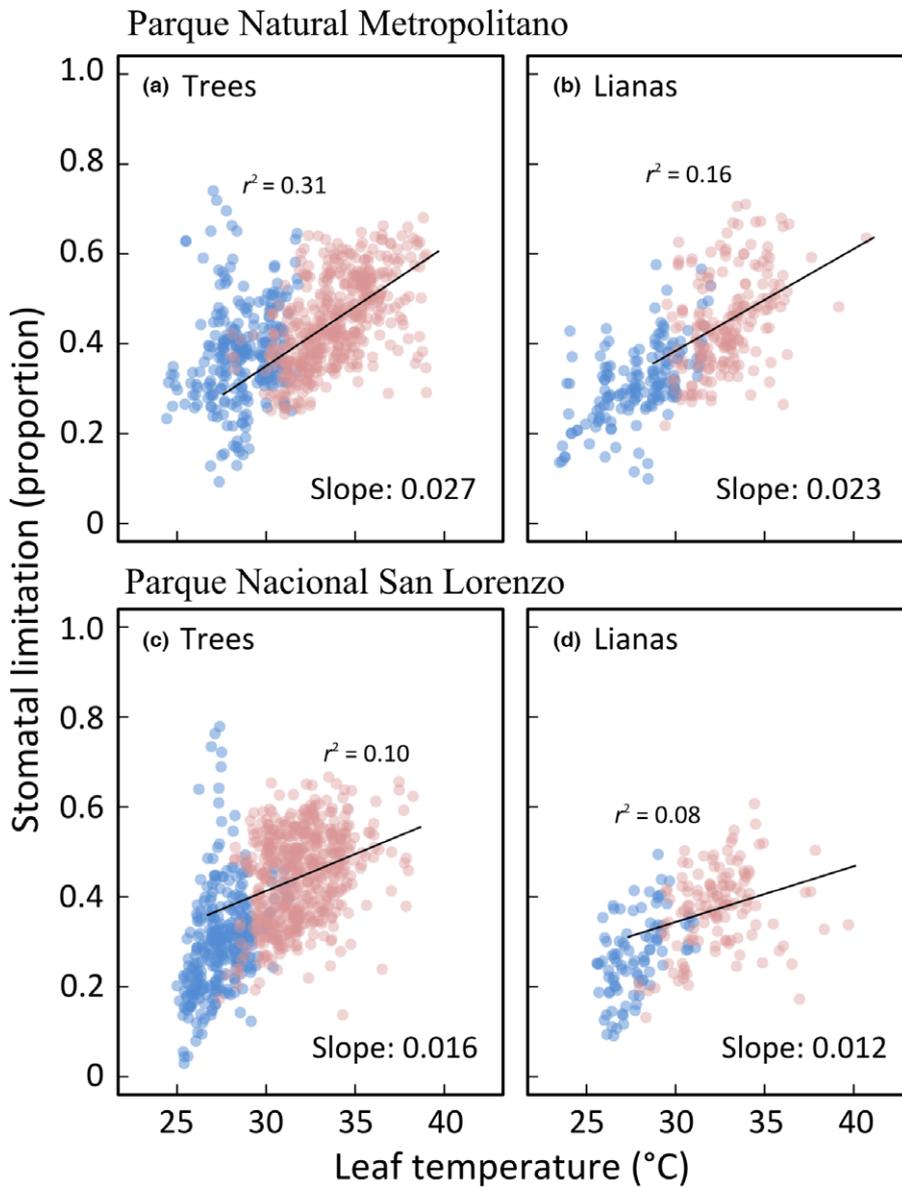


Fig. 6 Stomatal limitation in relation to leaf temperature below (blue) and above (pink) the optimum temperature of light-saturated photosynthesis (T_{Opt}) for trees and lianas at (a, b) Parque Natural Metropolitano and (c, d) Parque Nacional San Lorenzo. Significant linear correlations are shown between stomatal limitation above T_{Opt} and leaf temperature. See Supporting Information Notes S1 for data selection criteria and Figs S8 and S9 for species-level data.

photosynthesis rates of $c. 19 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the wet season (Slot *et al.*, 2013). However, consistent with the results derived from the P_{Opt} -based ranking used here, no patterns in T_{Opt} and T_{Max} emerged when ranking species on the basis of dark respiration rate at 25°C (R_{25}), leaf mass per area, and leaf nitrogen and phosphorus content – all traits associated with the leaf economics spectrum (Wright *et al.*, 2004) – or based on wood density. Variation in wood density across species similarly reflects trait-offs in plant economics strategies (Chave *et al.*, 2009), but unlike most leaf traits, wood density is not affected by the timing of the measurements (Table S2). Thus, the absence of patterns in T_{Opt} in relation to the position of the species on the slow–fast continuum is not an artifact of our measurement protocol.

Our results show that, in the absence of predictable variation in T_{Opt} and T_{Max} , trait-based models – in which traits rather than plant functional types are used to reduce the complexity of diverse ecosystems (van Bodegom *et al.*, 2012; Verheijen *et al.*,

2013) – do not require traits associated with the temperature dependence of photosynthesis. Rather, the strong convergence of community mean T_{Opt} values on mean ambient temperature across forests with contrasting precipitation regimes and with ecologically divergent species, allows the use of a single, community-level T_{Opt} value when scaling carbon fluxes from leaf to ecosystem. However, it has yet to be determined whether temperature–response traits differ in relation to canopy position. Because of differences in light regime and hydrostatic pressure, physiological and morphological traits tend to vary greatly throughout the canopy (e.g. Cavaleri *et al.*, 2010; Niinemets *et al.*, 2015) as do leaf temperature regimes (Rey-Sánchez *et al.*, 2016). Different thermal properties between sun and shade leaves could translate into differences in community-level effects of high temperature, as ‘slow’ species maintain more layers of shaded leaves than do ‘fast’ species (see Fig. 1a) (e.g. Kitajima *et al.*, 2005).

Similarity in temperature–response traits between growth forms

Trees and lianas had similar temperature–response characteristics, despite the apparently larger role of stomatal conductance limiting high-temperature photosynthesis in the dry forest and the distinctly different hydraulic architecture of lianas (Tyree & Ewers, 1991). Liana abundance appears to be increasing across many tropical forests (Schnitzer & Bongers, 2011), which can have a strong, negative impact on forest carbon stocks (Durán & Gianoli, 2013; van der Heijden *et al.*, 2016). Consequently, there is an increasing interest in including lianas as a distinct plant functional type in dynamic global vegetation models (Verbeek & Kearsley, 2016). Our results suggest that, in such models, the temperature response of photosynthesis of lianas can be considered to be similar to that of trees. This is consistent with previous observations indicating that the temperature response of respiration of lianas is similar to that of trees (Slot *et al.*, 2013, 2014a,b).

High T_{Opt} does not lead to narrower temperature–response curves

We did not find support for our second hypothesis, as the width of the temperature–response curves did not decrease with increasing T_{Opt} . Our hypothesis was based on the assumption that T_{Max} would represent a fixed upper limit of physiological performance, consistent with scenario III – ‘narrower curve’ – in Fig. 1(c). However, species with higher T_{Opt} were not ‘fast’ species *per se*, and T_{Max} did not appear to represent a fixed upper limit. T_{Max} values were much lower than those determined for seedlings in the laboratory (Slot *et al.*, 2016), which approached 50°C, a temperature very close to the temperature at which irreversible damage occurs in most species (Krause *et al.*, 2010, 2015). The fact that T_{Max} values were much lower than critical thermal thresholds of irreversible damage probably explains why T_{Max} was not as inflexible as we had hypothesized. The variability in T_{Max} probably also reflects the fact that it is calculated from curves that were not equally well constrained near T_{Max} for all species. Instead of a fixed T_{Max} and narrowing curves with increasing T_{Opt} , our results lend some support for scenario II in Fig. 1(c) – no change in curve width – albeit that the curves with higher T_{Opt} did not exclusively represent ‘fast’ species. We did not find evidence that ‘fast’ species have wider curves than ‘slow’ species, as is the case in temperate species (Michaletz *et al.*, 2016).

Temperature responses in dry and wet forests

On average, species in the seasonally dry forest (PNM) had higher thermal optima of photosynthesis than species in the evergreen wet forest (PNSL), despite stronger apparent control of stomatal conductance over photosynthesis at high leaf temperatures. The higher T_{Opt} and T_{Max} values are thus unlikely to be the result of adaptation to seasonal drought and stomatal properties associated with such adaptation. Rather, they may reflect adaptation to higher ambient temperatures at the dry forest site.

The T_{Opt} values in the two forests were strikingly similar to the mean daily maximum temperatures at each site; at PNM, the mean daily maximum temperature was 30.8°C and T_{Opt} was 30.8°C, whereas, at PNSL, the mean daily maximum temperature and T_{Opt} were 29.9 and 29.8°C, respectively. T_{Opt} of *Ficus insipida* at PNM has been shown previously to be almost identical to the most commonly observed leaf temperature (Slot & Winter, 2016; Slot *et al.*, 2016). Together, these results strongly suggest that physiological performance is optimized at the current mean maximum daytime temperatures.

Photosynthesis at *supra*-optimal temperatures correlated strongly with stomatal conductance in all species. This strong indirect effect of temperature on photosynthesis is consistent with model simulations by Lloyd & Farquhar (2008), which showed that – when ignoring rising atmospheric [CO₂] – the negative effect of rising temperatures on the photosynthesis of tropical canopy leaves is almost entirely driven by stomatal processes. Similarly, Wu *et al.* (2017) showed that short-term changes in light-saturated photosynthesis of Amazon forest – derived from eddy covariance data – were more strongly driven by VPD (and thus stomatal conductance) than by temperature *per se*. Nonetheless, the degree of stomatal limitation of photosynthesis appeared to be greater in the dry forest than in the wet forest. In the dry forest, $c_1 : c_a$ generally decreased in parallel with decreasing stomatal conductance, suggesting that the supply of CO₂ to the chloroplasts became increasingly limiting. By contrast, in the wet forest, most species did not show a decline or even showed a small increase in $c_1 : c_a$ despite decreasing stomatal conductance (e.g. *Terminalia*, Fig. S8). The fact that photosynthesis nevertheless decreased suggests that the adverse effect of high temperature on leaf biochemistry is the main factor limiting photosynthesis (e.g. Eamus, 1999; Sage & Kubien, 2007). Consistent with this, stomatal limitation calculated from \dot{V}_{cMax} increased more strongly with temperature in the dry than in the wet forest.

It is not clear why photosynthesis would experience stronger nonstomatal limitation in the wet forest than in the dry forest. There are several possibilities, but more detailed studies are required to fully understand the mechanisms. One possibility is that the biochemical limitation represents thermal deactivation of Rubisco. The temperature optimum of Rubisco activation increases with growth temperature (Yamori *et al.*, 2006), and so we cannot rule out reduced Rubisco activation at high temperature in the slightly cooler wet forest. Another possibility is that, at high temperature, R_{Light} affects net photosynthesis more strongly at PNSL than at PNM. However, this seems unlikely, as it would require a significantly larger temperature sensitivity of R_{Light} at PNSL than at PNM, as R_{Light} – calculated from the CO₂–response curves of canopy trees collected by Norby *et al.* (2017) – represents the same fraction of gross photosynthesis (at 27–30°C) at PNSL as at PNM (L. Gu & R. Norby, pers. comm.). It is also possible that photosynthesis in the relatively nutrient-poor forest at PNSL was more limited by the electron transport rate at high temperature than in the more fertile forest at PNM, because low nitrogen availability can reduce the electron transport capacity (June *et al.*, 2004). Furthermore, Vårhammar *et al.* (2015) found, for tropical montane trees, that T_{Opt} of J_{Max} was lower than that

of V_{cMax} . However, although leaf nitrogen content and V_{cMax} are significantly lower at PNSL, J_{Max} is not (Norby *et al.*, 2017). As a result, species at PNSL are more likely to be limited by carboxylation capacity – and its temperature dynamics – than by electron transport. Clearly, more detailed measurements of the temperature dependence of V_{cMax} and J_{Max} are needed to better understand the biochemical underpinning of the temperature response of net photosynthesis across lowland tropical forest sites and growth forms. These studies should also include measurements of the temperature dependences of Rubisco activase, Rubisco kinetics, mesophyll conductance and R_{light} , parameters that are variable among species, but are often assumed to equal published values of herbaceous model species (Busch & Sage, 2017). Such data would provide invaluable input for improving the representation of photosynthesis in Earth system models (Rogers *et al.*, 2017).

Thermal acclimation of photosynthesis and the long-term effects of warming in the tropics

Photosynthesis was optimal near current mean maximum daytime temperatures, suggesting that global warming may lower net photosynthesis and the carbon sink capacity of tropical forests. However, photosynthesis can acclimate to warming, which results in a shift in the temperature–response curves, such that T_{Opt} is closer to the new ambient conditions (e.g. Berry & Björkman, 1980; Hikosaka *et al.*, 2006; Way & Yamori, 2014). This has also been demonstrated for tropical tree species (Kositup *et al.*, 2009; Slot & Winter, 2016; Scafaro *et al.*, 2017), but there are several open questions about thermal acclimation of photosynthesis in tropical forests. First, will P_{Opt} increase or decrease when T_{Opt} increases in response to warming? P_{Opt} has been shown to decrease with increasing growing temperature in *Calophyllum longifolium* Willd. (Slot & Winter, 2016), exhibiting what Way & Yamori (2014) called ‘detractive adjustment’. Consistent with this, Doughty (2011) found that the photosynthetic capacity of leaves of six tropical forest species decreased significantly as a result of 2–3°C warming. More experiments are needed to determine whether ‘detractive adjustment’ is indeed a common tropical phenomenon. Second, will T_{Max} shift in parallel with T_{Opt} when tropical species acclimate? Upper physiological limits tend to be higher in warm-grown plants than in cold-grown plants (Salvucci & Crafts-Brandner, 2004), and in the tropics than in cooler climates (O’Sullivan *et al.*, 2017), but within the tropics they may not increase further with warming (Krause *et al.*, 2013). This inflexibility of T_{Max} significantly narrows temperature–response curves, and potentially affects the cumulative carbon uptake of canopy leaves. A third question is how variable are species in their thermal acclimation capacity; are thermal acclimation traits correlated with other plant functional traits, and do they differ among growth forms? Short-term temperature–response traits did not vary predictably in relation to the position of a species on the slow–fast continuum, but if acclimation to long-term warming does, this could have major consequences for community dynamics in forests of the future. Data on the thermal

acclimation of photosynthesis are needed across a wide range of tropical species to better predict long-term effects of warming on the photosynthetic properties of species-rich tropical forest canopies.

Concluding remarks

There is a strong need for an improved understanding of how tropical forests respond to atmospheric and climate change (Lloyd & Farquhar, 2008; Corlett, 2011; Cavaleri *et al.*, 2015; Slot & Winter, 2016). Without a solid knowledge of the environmental controls over photosynthesis under current conditions, the prediction of tropical carbon fluxes in the future will remain speculative. We have shown remarkable similarity in physiological temperature–response traits of canopy leaves of ecologically divergent tropical forest trees and lianas, despite apparent differences in controls (stomatal vs nonstomatal) over photosynthesis at *supra*-optimal temperatures. These data may provide a valuable benchmark for the validation of the performance of tropical vegetation models in relation to temperature. Further studies are required to gain insights into the biochemical underpinning of our observations. To predict long-term responses, however, we also need to evaluate whether ecologically divergent ‘slow’ and ‘fast’ species differ in their thermal acclimation potential. Acclimation will need to be described on the basis of V_{cMax} , J_{Max} and their activation energies for such research to make significant contributions to Earth system models. Furthermore, the effect of elevated CO₂ on the temperature response of net photosynthesis (Berry & Björkman, 1980) will need to be quantified for tropical forest species.

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Author contributions

M.S. and K.W. designed the study. M.S. collected the data, performed the analyses, and wrote the manuscript, and K.W. made substantial contributions to the writing.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Relationships between leaf temperature, vapor pressure deficit (VPD), stomatal conductance and photosynthesis.

Fig. S2 Estimated V_{cMax} in relation to leaf temperature for 30 tropical tree species.

Fig. S3 Estimated V_{cMax} in relation to leaf temperature for 12 tropical liana species.

Fig. S4 Photosynthesis in relation to stomatal conductance for 30 tropical tree species.

Fig. S5 Photosynthesis in relation to stomatal conductance for 12 tropical liana species.

Fig. S6 Photosynthesis in relation to the ratio of intercellular to atmospheric CO₂ concentration for 30 tropical tree species.

Fig. S7 Photosynthesis in relation to the ratio of intercellular to atmospheric CO₂ concentration for 12 tropical liana species.

Fig. S8 Stomatal limitation in relation to leaf temperature for 30 tropical tree species.

Fig. S9 Stomatal limitation in relation to leaf temperature for 12 tropical liana species.

Table S1 Species-level temperature–response traits for 42 tree and liana species.

Table S2 Regression analyses of the temperature optimum of photosynthesis and leaf functional traits.

Notes S1 Estimation of V_{cMax} at low stomatal conductance.

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