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Temperature responses of photosynthesis and respiration in evergreen trees from boreal to tropical latitudes

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Summary

Evergreen species are widespread across the globe, representing two major plant functional forms in terrestrial models. We reviewed and analysed the responses of photosynthesis and respiration to warming in 101 evergreen species from boreal to tropical biomes. Summertime temperatures affected both latitudinal gas exchange rates and the degree of responsiveness to experimental warming. The decrease in net photosynthesis at 25°C (A_{net25}) was larger with warming in tropical climates than cooler ones. Respiration at 25°C (R_{25}) was reduced by 14% in response to warming across species and biomes. Gymnosperms were more sensitive to greater amounts of warming than broadleaved evergreens, with A_{net25} and R_{25} reduced c. 30–40% with > 10°C warming. While standardised rates of carboxylation (V_{cmax25}) and electron transport (J_{max25}) adjusted to warming, the magnitude of this adjustment was not related to warming amount (range 0.6–16°C). The temperature optimum of photosynthesis (T_{optA}) increased on average 0.34°C per °C warming. The combination of more constrained acclimation of photosynthesis and increasing respiration rates with warming could possibly result in a reduced carbon sink in future warmer climates. The predictable patterns of thermal acclimation across biomes provide a strong basis to improve modelling predictions of the future terrestrial carbon sink with warming.

I. Introduction

Evergreen tree species are found at most latitudes and represent key dominant plant functional types (PFTs) employed in process-based vegetation models. Boreal forests are dominated by needle-leaved evergreen species and extensively cover the higher northern latitudes, accounting for *c.* 20% of the global aboveground biomass. The mid-latitudes contain a mixture of evergreen conifers and deciduous species, with a transition towards mostly broadleaved evergreen species in subtropical and tropical latitudes. Together, boreal and tropical forests are the strongest contributors across all biomes to the global terrestrial carbon sink; *c.* 27% each corresponding to *c.* 0.30 Pg C yr^{-1} in each biome (Beer *et al.*, 2010; Tagesson *et al.*, 2020). With a projected future warming of 2.6–5°C by the end of this century (Stocker *et al.*, 2013; Masson-Delmotte *et al.*, 2022), understanding how evergreen species will respond as the climate warms is key to estimating the strength of the future terrestrial carbon sink.

Although temperature has increased on average by *c.* 1.1°C globally, the amount of warming is not equally distributed across latitudes. Boreal regions are predicted to warm up to 10°C while tropical regions may experience warming of about 3–4°C by the end of this century (Masson-Delmotte *et al.*, 2022). Projecting evergreen tree responses to warming is complicated due to key uncertainties regarding the temperature responses of photosynthesis and respiration and their feedbacks to the global carbon cycle (Lombardozzi *et al.*, 2015; Mercado *et al.*, 2018). Importantly, small adjustments of photosynthesis and respiration in response to climate warming can have a large impact on carbon uptake and therefore the size of the future terrestrial carbon sink (Huntingford *et al.*, 2017; Dusenge *et al.*, 2019). There is extensive evidence that both photosynthesis and respiration physiologically adjust to changes in growth temperature over a timeframe of weeks to years, the so-called thermal acclimation (Atkin *et al.*, 2005a). Taking this physiological acclimation into account will result in more accurate estimates of global carbon exchange (Atkin *et al.*, 2008; Smith & Dukes, 2013; Smith *et al.*, 2016; Dusenge *et al.*, 2019).

In this review, we focus on the capacity of evergreen species to physiologically acclimate to warming and investigate how warming responses vary with biome. Evergreen tree species, and especially tropical broadleaf evergreen species, generally have formed a small component in previous analyses investigating plant physiological responses to warming across a broad set of species (Saxe *et al.*, 2001; Way & Oren, 2010; Chung *et al.*, 2013; Liang *et al.*, 2013; Dusenge *et al.*, 2019). Here we aimed to bring together an understanding of how evergreen tree physiology responds to warming. We focus on the response of photosynthesis and respiration and related variables. Whole-plant metrics or other aspects of warming responses such as growth (Saxe *et al.*, 2001; Way & Oren, 2010), phenology (Chambers *et al.*, 2013; Chung *et al.*, 2013) and environmental interactions with warming (Teskey *et al.*, 2015; Ruehr *et al.*, 2016) are beyond the scope here and are reviewed elsewhere. However, in many cases these responses are derived from the gas exchange processes affected by warming that we consider in this review.

In addition to reviewing the literature involving how evergreen species adjust to a change in growth temperatures, we collected photosynthetic and respiratory variables from warming studies on evergreen species from both the field and controlled environment experiments, which we will refer to as the 'Evergreen species in a warming environment' (ESWE) dataset. The ESWE dataset contained 101 evergreen species across two plant groups with different leaf form, that is needleleaf and broadleaf, representing a total of 23 gymnosperm and 78 angiosperm evergreen species across three biomes: boreal, temperate and tropical, based on the coordinates indicated in the study (Supporting Information Table S1). Each coordinate was linked to a mean annual temperature and a mean temperature of the warmest quarter from BioCLIM (Hijmans *et al.*, 2005), both of which corresponded well with biome (Fig. S1). The ESWE dataset represented a realistic diversity of evergreen species and leaf forms across latitudes with 13 needleleaf evergreen species in the boreal zone, a mixture of needleleaf (10 species) and broadleaf (31 species) evergreen species in the temperate zone and 51 broadleaf evergreen species in the tropical zone (Table S1). The amount of warming across the ESWE dataset spanned from 0.6°C to 16°C warming. See Appendix A1 for more details on the variables and the statistical analyses and Appendix A2 for the studies used in the analyses.

We evaluated the following questions: (1) Are there any intrinsic latitudinal patterns using ambient (i.e. control only) conditions across biomes and leaf form (Section II), (2) How do photosynthesis and respiration parameters respond to experimental warming? Is that response different across biomes and/or leaf forms? (3) How are these parameters related to the amount of warming applied? (Sections III; IV and V). Finally, we discuss whether we could use spatial gradients in the environment as a proxy for time (i.e. future projected warming) to predict temporal changes (Section VI) and consider how our review can inform land surface models (Section VII).

II. Latitudinal patterns

Examining variation across latitudinal gradients provides insight into how climate has shaped plant functioning to survive, grow and reproduce, including physiological processes (Brown *et al.*, 1996; Willig *et al.*, 2003). Evergreen species are an ideal 'model' to examine biogeographic patterns due to their wide occurrence, allowing physiological responses to be contrasted across species originating from different climates. Understanding how physiological traits are related to the current climate conditions is important to evaluate responses to warming across a large set of species (see Appendix A1 for statistical details).

Plants have been hypothesised to balance functional trade-offs to optimally utilise their available resources (Dewar *et al.*, 2009; Togashi *et al.*, 2018; Harrison *et al.*, 2021). Plants invest a lot of nutrients toward metabolism (Evans, 1989) and balance how nutrients are allocated to achieve the best resource-use efficiency at the least cost (Togashi *et al.*, 2018). Global patterns of leaf nitrogen (N) and phosphorus (P) have been related to latitude, which strongly co-varies with temperature (Reich & Oleksyn, 2004). Leaf N and P declined from high-latitudes towards the equator,

suggesting a response of declining N as average temperatures increase (Reich & Oleksyn, 2004). This trend in leaf nutrients has been supported by many studies, finding higher N in cool-grown plants and lower N observed in response to warmer growth temperatures (Strand *et al.*, 1999; Hikosaka, 2005; Yamori *et al.*, 2005; Way & Sage, 2008; Crous *et al.*, 2018). In the ESWE dataset, area-based leaf N (N_a) decreased as site temperature increased both with the mean temperature of the warmest quarter, a proxy for summer growing temperature based on latitude ($P < 0.0001$, $R^2 = 0.14$; Table 1; Figs 1a, S2) and with experimental growth temperature (Fig. S3), supporting that leaf N content declines with higher growth temperatures.

Given the global patterns of declining N and P with warmer growth temperatures in combination with the large amount of N invested in the enzymes driving photosynthetic capacity, defined as the maximum carboxylation rate, V_{cmax25} and the maximum electron transport rate measured at 25°C (J_{max25}), we expected lower V_{cmax25} and J_{max25} rates in response to warmer growth temperatures (Dusenge *et al.*, 2020; Wang *et al.*, 2020). Examining our ESWE dataset, we found that most photosynthetic variables in ambient conditions showed significant relationships with mean temperature of the warmest quarter (Table 1) and with mean annual temperature (Table S2) and differed depending on leaf form (Table 1). As N_a declined with mean temperatures of the warmest quarter (Fig. 1a), the maximum rates of carboxylation and electron transport at a common temperature of 25°C as well as their ratio all declined with increasing mean temperatures of the warmest quarter (Table 1; Figs 1, S2a). Grouped per biome,

Table 1 ANCOVA results (*F*-statistic and *P*-value) with leaf form as categorical variable and mean temperature of the warmest quarter (meanTWQ) as the covariate using the *values of the control treatments only*, transformed when necessary.

Control conditions	Total obs.	Leaf form df = 1		meanTWQ df = 1	
Variable		*F*	*P*	*F*	*P*
V_{cmax25}	69	4.32	**0.042**	8.63	**0.0046**
J_{max25}	68	9.66	**0.0028**	26.09	**< 0.0001**
$J : V_{25}$	53	8.69	**0.005**	19.95	**< 0.0001**
A_{net25}	106	0.74	0.39	7.08	**0.0091**
T_{optA}	56	0.019	0.89	20.17	**< 0.0001**
A_{growth}	54	8.48	**0.0056**	0.48	0.49
R_{growth}	126	0.068	0.79	0.84	0.36
R_{d25}	129	0.001	0.97	9.52	**0.0026**
N_a	109	0.99	0.32	19.10	**< 0.0001**

Sources of the model are the columns and variables form the rows, df is the degree of freedom for each source and the sample size for each variable is found in the second column (Total obs.). *P*-values are indicated in bold when significant < 0.05.
Variables are: the maximum carboxylation rate (V_{cmax25}); the maximum electron transport rate (J_{max25}); the ratio of J_{max25} over V_{cmax25} ($J : V_{25}$); and net photosynthesis (A_{net25}). All parameters were measured at a common temperature of 25°C, the temperature optimum of photosynthesis (T_{optA}); photosynthesis and respiration were measured at their growth temperatures (A_{growth} and R_{growth} respectively); mitochondrial dark respiration was measured at 25°C (R_{d25}); and area-based leaf nitrogen content (N_a).

V_{cmax25} and J_{max25} were $25 \pm 10\%$ and $26 \pm 8\%$ lower, respectively in the tropical biome compared to temperate/boreal biomes, but temperate and boreal biomes were not different from each other. Net photosynthesis measured at 25°C, A_{net25} slightly increased with higher mean temperature of the warmest quarter (Fig. 1e, $R^2 = 0.06$). Similar trends were observed with mean annual temperatures (Fig. S4; Table S2) and to some extent with experimental growing conditions (Fig. S3). Dark respiration rates measured at a common temperature of 25°C, R_{25} rates reduced with higher mean temperatures of the warmest quarter (Fig. S2e; Table 1), similar to Atkin *et al.* (2015), reporting lower rates in the tropics than the Arctic measured at a common temperature.

Taken together, there were clear latitudinal patterns in photosynthetic and respiratory variables (V_{cmax25}, J_{max25} and $J : V_{25}$, R_{25}) for which rates in the tropical biomes were lower compared with the other biomes, are likely to be linked to a corresponding decline in N_a. Although standardised photosynthesis and respiration declined in warmer climates, actual rates at prevailing growth temperatures (i.e. A_{growth} and R_{growth}) were similar across latitudes (Table 1). This implies that negative effects on biochemical capacities at 25°C (i.e. V_{cmax25} and J_{max25}) were balanced by positive direct effects of higher growth temperatures on enzyme reaction rates (up to the biochemical optimum temperatures, which are higher for V_{cmax25} and J_{max25} than those of A_{net}), resulting in overall similar gas exchange rates across biomes.

Leaf form also influenced the rates of V_{cmax25} and J_{max25}, in which needle-leaved evergreens had lower rates compared with broadleaf evergreen species (−19% for V_{cmax25}, −20% for J_{max25}, −8% for $J : V_{25}$; $P < 0.05$; Table 1). At prevailing growth temperatures, A_{growth} had significantly lower rates in needleleaf compared with broadleaf species (−34%, $P = 0.0056$; Table 1). Given that growth temperatures varied among studies, the A_{growth} response could reflect lower growth temperatures used in experiments with needleleaf compared with broadleaf species.

III. Acclimation of photosynthesis to warming

The temperature response of net photosynthesis is usually described as an increase in a maximum net photosynthesis rate at an optimum temperature (T_{optA}, black triangle in Fig. 2) followed by a relatively rapid decline in photosynthesis at higher temperatures (Berry & Björkman, 1980; Sage & Kubien, 2007; Yamori *et al.*, 2014). The temperature response of net photosynthesis can be empirically modelled as:

$$A_{net} = A_{opt} - b(T - T_{optA})^2 \qquad \text{Eqn 1}$$

where T_{optA} is the temperature optimum (°C) at which the highest rate of photosynthesis occurs (A_{opt}) and b represents the broadness of the parabolic curvature.

Stomatal conductance generally has a large control over photosynthesis and often declines in response to high vapour pressure deficit (VPD) associated with higher temperatures (Fig. 2b) (Monteith, 1995; Lloyd & Farquhar, 2008; Grossiord *et al.*, 2020). This decline in stomatal conductance can affect the
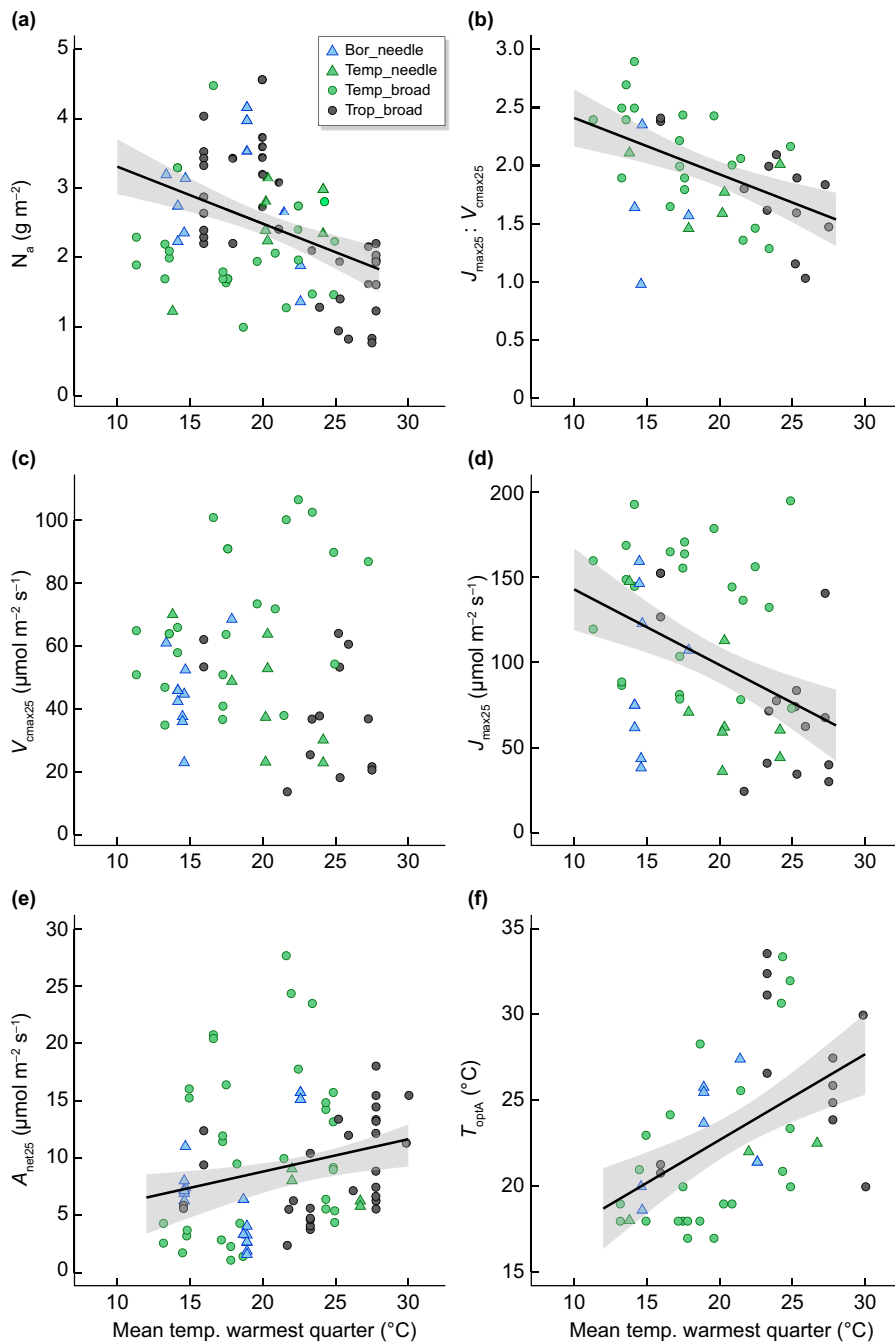
Fig. 1 Linear regression relationships with 95% confidence intervals (grey area) between several variables against mean temperature of the warmest quarter (or average summer temperatures) to test for latitudinal patterns across biomes (Bor, boreal in skyblue; Temp, temperate in green; Trop, tropical in black) in control conditions based on latitudinal information for (a) nitrogen content ($N_a = -0.0822x + 4.128$, $R^2 = 0.16$, $P < 0.0001$), (b) the ratio of maximum carboxylation rate at 25°C (V_{cmax25}) to maximum electron transport rate at 25°C (J_{max25}) ($J_{max25} : V_{cmax25} = -0.048 + 2.89$, $R^2 = 0.25$, $P = 0.0001$), (c) maximum carboxylation rate at 25°C (V_{cmax25}), (d) maximum electron transport rates at 25°C ($J_{max25} = -4.43x + 187.09$, $R^2 = 0.19$, $P = 0.0002$), (e) net photosynthesis measured at a common temperature of 25°C (A_{net25}) ($A_{net25} = 0.28x + 3.15$, $R^2 = 0.06$, $P = 0.0088$), and (f) the temperature optimum of photosynthesis (T_{optA}) ($T_{optA} = 0.499x + 12.698$, $R^2 = 0.26$, $P < 0.0001$). The partial regressions from the analyses of covariance (ANCOVA) were similar (except for V_{cmax25}) and found in Supporting Information Fig. S2. Different symbols indicate leaf form with triangles for needleleaf and circles for broadleaf species.

shape of the temperature response of photosynthesis. Lin *et al.* (2012) showed that low stomatal conductance decreased the T_{optA} of photosynthesis. One approach to examine photosynthetic biochemistry without confounding influences from stomatal limitations is to estimate photosynthesis at a common internal CO_2 concentration, C_i (or at a common chloroplastic CO_2 concentration, C_c using the Farquhar *et al.* (1980) model of photosynthesis (Vårhammar *et al.*, 2015; Kumarathunge *et al.*, 2019; Dusenge *et al.*, 2021). It is currently more common to use C_i than C_c as data on the temperature response of mesophyll conductance are rare (Von Caemmerer & Evans, 2015) and it is hard to measure accurately in the field.

The temperature response of photosynthetic biochemistry is determined by changes in the maximum rates of carboxylation of ribulose-1,5-bisphophate (RuBP) (V_{cmax}) and regeneration of RuBP (i.e. the maximum rate of electron transport, J_{max}), and mitochondrial respiration (R_d) (Farquhar *et al.*, 1980). Biochemical processes underlying photosynthesis are mechanistically independent from stomatal effects and represent the photosynthetic capacity of the plant (Farquhar *et al.*, 1980). Both V_{cmax} and J_{max} have their own temperature dependency. The instantaneous temperature responses of V_{cmax} and J_{max} each have a temperature optimum, with the optimum of J_{max} usually occurring at a lower temperature than the optimum of V_{cmax} (Fig. 2a). J_{max} is more
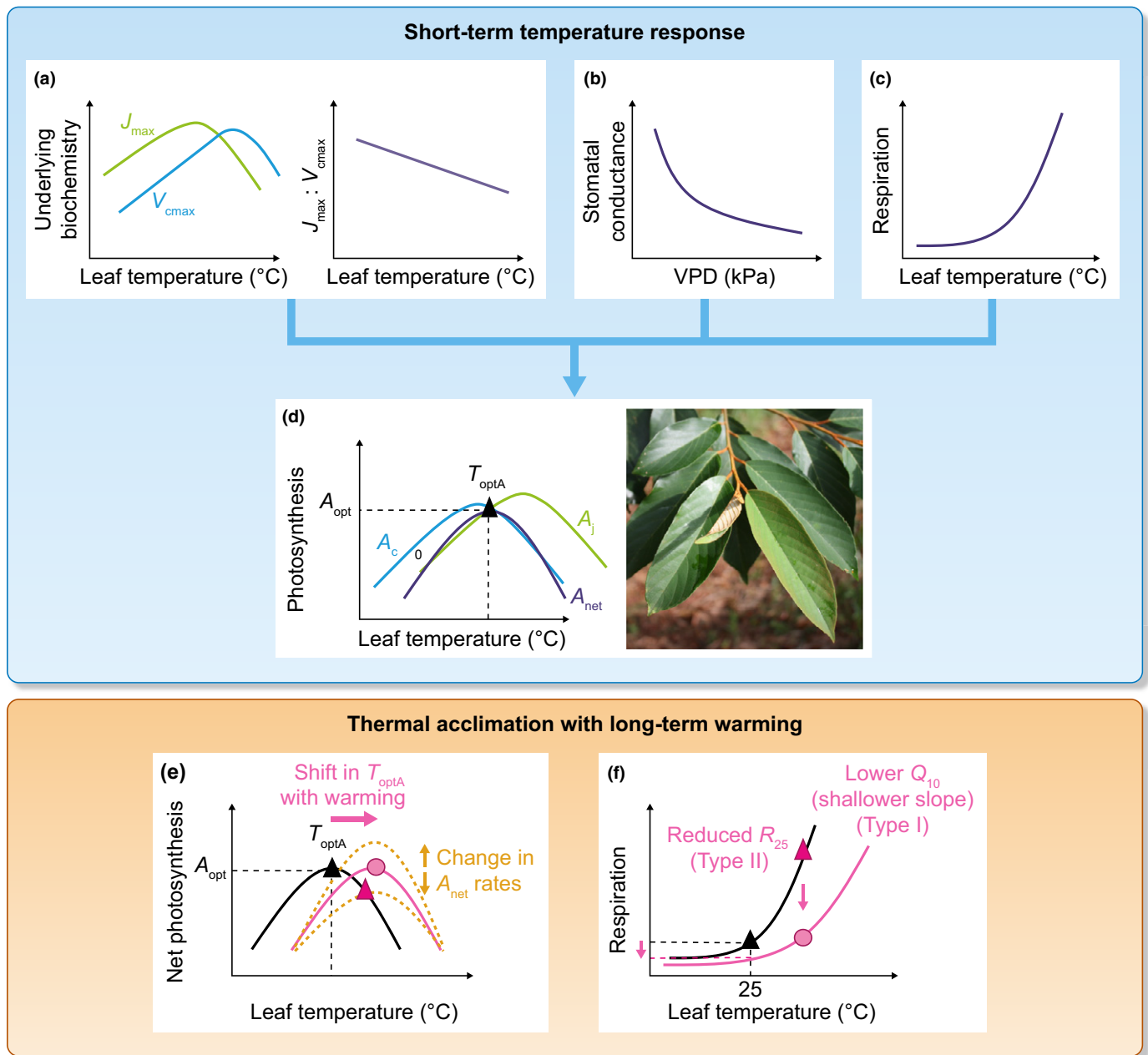
Fig. 2 The photosynthesis–temperature (T) response is governed by underlying biochemistry (maximum carboxylation rate, V_{cmax} and maximum electron transport rates, J_{max}) (a) and stomatal processes by their responses to vapour pressure deficit (VPD) (b) and leaf respiration during the day (c), each of which has their own temperature response. Together these processes result in a net photosynthesis–temperature curve with a temperature optimum of photosynthesis (T_{optA} black triangle) and a maximum photosynthesis rate at the T_{opt} (A_{opt}) (d), (curve differences emphasised for clarity). While the T_{opt} of $J_{max} < T_{opt}$ of V_{cmax}, Rubisco-limited photosynthesis (A_c) usually declines faster at high temperatures than V_{cmax}, resulting in T_{opt} of $A_c < T_{opt}$ of A_j (RuBP-limited photosynthesis). Changes in the temperature response curve of photosynthesis due to thermal acclimation is represented in (e) with a shift in T_{optA} (pink arrow) and/or changes in photosynthesis rates (orange arrows, dotted lines). Changes in the temperature response curve of respiration due to thermal acclimation is represented in (f) with a lower temperature sensitivity (Q_{10}) and reduced respiration rates at a given temperature (pink arrow). In (e, f), black lines are representing instantaneous temperature responses under current growth temperatures, whereas the pink lines represent the adjustments to long-term warming for photosynthesis and respiration. The pink triangles represent the short-term response to warming without thermal acclimation (black and pink triangles, respectively). Pink circles represent the long-term response to warming. Both lower respiration rates and similar to higher photosynthesis rates at higher temperatures due to acclimation improve the carbon gain balance compared with when these adjustments would not have occurred, compare pink triangles with pink circles in (e, f).

sensitive to high temperatures than V_{cmax} because it depends on thylakoid membrane stability to function effectively (Sage & Kubien, 2007). By contrast, Rubisco-limited photosynthesis (A_c) usually declines earlier and faster at high temperatures than V_{cmax} (Fig. 2d), as Rubisco oxygenation increases more steeply than carboxylation (Sage & Kubien, 2007; Busch & Sage, 2017).

Moreover, stomatal conductance typically constrains the CO_2 supply to carboxylation even further at high temperatures (Lloyd & Farquhar, 2008; Grossiord *et al.*, 2020). As a result, declines in A_{net} at high temperatures are usually the consequence of Rubisco limitation rather than electron transport limitation (Vårhammar *et al.*, 2015; Busch & Sage, 2017; Dusenge *et al.*, 2021). This is also the case at 25°C in most tree species globally (De Kauwe *et al.*, 2016). Alternatively, reduced photosynthesis at high temperatures (> 35°C) may be limited by reduced J_{max} rates related to reduced PSII electron flow in favour of increased cyclic electron flow by PSI (Havaux, 1996; Pastenes & Horton, 1996; Sharkey, 2005). Generally, however, at higher temperatures, there is often a rebalancing between carboxylation and electron transport in the favour of V_{cmax}, leading to a lower J_{max} to V_{cmax} ratio (Bernacchi *et al.*, 2003; Yamori *et al.*, 2005; Kattge & Knorr, 2007).

Fitting a temperature response to V_{cmax} and J_{max} with a peaked Arrhenius function requires at least four different temperatures over which V_{cmax} and J_{max} are determined. It is modelled as:

$$f(T_k) = k_{25}\exp\left[\frac{E_a(T_k - 298)}{298RT_k}\right]\frac{1 + \exp\left(\frac{298\Delta S - H_d}{298R}\right)}{1 + \exp\left(\frac{T_k\Delta S - H_d}{T_kR}\right)} \qquad \text{Eqn 2}$$

where k_{25} is the value of V_{cmax} or J_{max} at 25°C, R is the universal gas constant (8.314 J mol^{-1} K^{-1}), T_k is leaf temperature in °K, E_a (J mol^{-1}) is the activation energy describing the exponential rise in enzyme activity with increasing temperature, H_d (J mol^{-1}) is the deactivation energy describing the rate of decline above the temperature optimum, and ΔS is the entropy term (J K^{-1}). When only four different temperature points are used, H_d is usually held constant at 200 kJ mol^{-1} (Medlyn *et al.*, 2002; Kattge & Knorr, 2007). Even with five different temperature measurements, H_d is often fixed to avoid overfitting. An in-depth analysis by Medlyn *et al.* (2002) has shown that keeping H_d constant does not meaningfully affect the mathematical description of the function, recently supported by Yin (2021). Because the parameters from the peaked Arrhenius curve strongly co-vary, they cannot be evaluated independently, regardless of whether H_d is fixed or not.

Based on the fitted parameters from a peaked Arrhenius function, the temperature optimum (T_{opt}) of V_{cmax} or J_{max} can be calculated as:

$$T_{opt} = \frac{H_d}{\Delta S - R\log_e\left[\frac{E_a}{(H_d - E_a)}\right]} \qquad \text{Eqn 3}$$

where $\log_e$ represents the natural logarithm and T_{opt} is expressed in K.

Based on biochemical theory, photosynthetic capacity at a common temperature is predicted to increase with warming in plants grown under low-to-moderate growth temperatures, due to faster enzyme kinetics at these warmer temperatures (Kattge & Knorr, 2007; Sage & Kubien, 2007; Fig. 2a). However, at higher growth temperatures, relatively less enzyme is needed to achieve similar rates at warmer temperatures, thereby allowing less nutrient

investment in the photosynthetic apparatus (Smith & Keenan, 2020; Wang *et al.*, 2020). Recent literature has observed decreased photosynthetic capacity (i.e. V_{cmax25} and J_{max25}) with warmer growth temperatures. This observation may be related to latitudinal patterns, which have shown lower leaf N concentrations at higher growth temperatures (Reich & Oleksyn, 2004), consistent with lower rates of photosynthetic capacity in the tropics (Fig. 1). Overall, however, it remains unclear what causes reduced photosynthetic capacity at higher growth temperatures. It is expected that plants exposed to warming adjust in such a way to increase or maintain photosynthesis (Way & Yamori, 2014) including a higher temperature optimum of photosynthesis (T_{optA}) with warmer temperatures. These physiological adjustments to warming are likely to occur through changes in one or several parameters describing the temperature response curves of photosynthesis (Eqn 2). In the following sections, we used the ESWE dataset to evaluate the adjustment of the temperature optimum of photosynthesis, and changes in photosynthetic parameters both at common and prevailing growth temperatures by their response ratio to warming (i.e. values at warming over ambient treatment) (Appendix A1).

1. Temperature optimum of net photosynthesis: a sensitive indicator

The shift in temperature optimum of net photosynthesis (T_{optA}) is a sensitive indicator as to how much the temperature response curve of photosynthesis can adjust to maximise carbon uptake under warming (Berry & Björkman, 1980). The T_{optA} in C$_3$ species typically increases by 0.3–0.6°C for each 1°C shift in growth temperature (Berry & Björkman, 1980; Yamori *et al.*, 2014). Recent studies have clarified the relationship between T_{optA} and the underlying biochemical parameters of photosynthesis. An increased T_{optA} with warming is usually related to increased temperature optima of V_{cmax} and J_{max} (Fig. 2a) (Medlyn *et al.*, 2002; Onoda *et al.*, 2005; Hikosaka *et al.*, 2006; Kattge & Knorr, 2007; Crous *et al.*, 2018; Dusenge *et al.*, 2020). The increased optima of V_{cmax} can reflect a more temperature tolerant form of Rubisco activase (Salvucci & Crafts-Brandner, 2004) while increased thylakoid membrane stability at higher temperatures is important to increase the T_{opt} of J_{max} (Sharkey, 2005; Sage & Kubien, 2007). However, T_{optA} can also be increased either by an increase in activation energy of V_{cmax} or J_{max} (Hikosaka *et al.*, 2006) or a lower entropy term (ΔS) without a change in the activation energy parameter, E_a (Kattge & Knorr, 2007). Moreover, changes in the balance between RuBP carboxylation and RuBP regeneration described by the $J_{max} : V_{cmax}$ ratio (Hikosaka *et al.*, 2006) can also affect T_{optA}. A low $J_{max} : V_{cmax}$ ratio has been related to a higher temperature optimum of photosynthesis (Hikosaka *et al.*, 2006; Kumarathunge *et al.*, 2019; Dusenge *et al.*, 2020). When $J_{max} : V_{cmax}$ is low, RuBP regeneration has greater control over photosynthesis (i.e. less Rubisco limitation compared with when $J_{max} : V_{cmax}$ is high). As photosynthesis is usually carboxylation limited at high temperatures, this adjustment leads to a higher T_{optA} in warmer growth temperatures (Hikosaka *et al.*, 2006). Therefore, there are several adjustments occurring in

the underlying biochemical component processes (J_{max} : V_{cmax}, E_a and/or ΔS) that can result in a higher temperature optimum of photosynthesis, which is beneficial to plants growing in warmer temperatures (Kumarathunge *et al.*, 2019).

We explored the T_{optA} responses to warming in evergreen tree species in the ESWE dataset with the following hypotheses: (1) warming increases T_{optA} as the absolute shift by the temperature difference between warming and control and (2) the relative shift (i.e. temperature shift per °C warming) in T_{optA} with warming is similar across biomes, between 0.3 and 0.6°C per °C increase in growth temperature (Berry & Björkman, 1980). To test the effect of warming on the absolute shift in T_{optA}, an analysis of covariance (ANCOVA) approach was used with warming amount and leaf form as factors and mean temperature of the warmest quarter as a covariate to represent the fact that measurements are usually taken under growing season conditions (see Appendix A1 for more details). Our analyses of the ESWE data indicated that T_{optA} increased with higher growth/summer temperatures, from boreal to tropical biomes ($R^2 = 0.28$; $P < 0.001$; Figs 1f, S2, S3) consistent with Kumarathunge *et al.* (2019) and with higher experimental warming (Fig. 3a; $R^2 = 0.28$; $P < 0.0001$; Table 2). Further support for the sensitivity of T_{optA} to a change in surrounding growth temperatures, is provided by temperature gradients, even within tree canopies where the T_{optA} is often higher at the top of the canopy than in more shaded parts lower in the canopy (Carter *et al.*, 2021).

In contrast with an increased T_{optA} with warming (Fig. 3a), there was no relationship between the relative shift in temperature optimum and the amount of warming applied ($P = 0.94$; Fig. 3b). The shift of 0.34°C per °C warming in evergreen species remains the same, regardless of the amount of warming applied and is within the range given by Berry & Björkman (1980) and Way & Yamori (2014). This consistent finding across biomes, leaf form and a broad range of experimental warming (up to +16°C) in the ESWE dataset delineates a limit to photosynthetic temperature optimum adjustment in evergreen species in a predictable manner.

2. Rates at a standard temperature: negative warming responses in warmer climates

Measurements of photosynthesis or photosynthetic capacity at a common temperature (e.g. 25°C) allowed us to compare the degree of thermal acclimation between different warming treatments or among biomes (i.e. 'set temperature method'; Mooney, 1963; Hikosaka *et al.*, 1999; Medlyn *et al.*, 2002; Bernacchi *et al.*, 2003; Atkin *et al.*, 2005a; Onoda *et al.*, 2005; Sage & Kubien, 2007; Ghannoum *et al.*, 2010). The degree of thermal acclimation is interpreted as the relative change in a physiological process that a plant can make in response to a growth temperature change, expressed in the ESWE dataset by the response ratio of the values of the warmed treatment compared with the values in the control treatment for a given variable (Appendix A1). Here we review the literature and analyse the response ratio of several photosynthetic variables (V_{cmax25}, J_{max25}, J : V_{25}, N_a, A_{net25} and A_{growth}) to warming amount, leaf form and summer growth temperature (i.e. mean temperature of the warmest quarter) (Table 2).

The increase in T_{optA} with warming can be accompanied by an increase or decrease in photosynthesis rates at a common, standard temperature (dotted lines in Fig. 2e). This acclimation of photosynthesis rates is often reflected in the underlying biochemical components of photosynthesis (i.e. V_{cmax25} and J_{max25}). Photosynthetic capacity may increase through enhanced V_{cmax25} or J_{max25} at higher growth temperatures in some studies (Hikosaka *et al.*, 1999; Medlyn *et al.*, 2002; Bernacchi *et al.*, 2003; Onoda *et al.*, 2005; Sage & Kubien, 2007; Ghannoum *et al.*, 2010) while other studies on evergreen trees reported decreased V_{cmax25} or J_{max25} with warming (Ferrar *et al.*, 1989; Wertin *et al.*, 2011; Crous *et al.*, 2013; Aspinwall *et al.*, 2016; Dusenge *et al.*, 2021). It is currently unclear whether photosynthesis rates measured at a standard temperature generally increase or decrease with warming and whether there are patterns in these responses related to prevailing growth temperatures or the biome where these species grow.

Across the ESWE dataset, we found both positive (i.e. response ratio (RR) > 1, $n = 26$–27) and negative (i.e. RR < 1, $n = 36$–41)
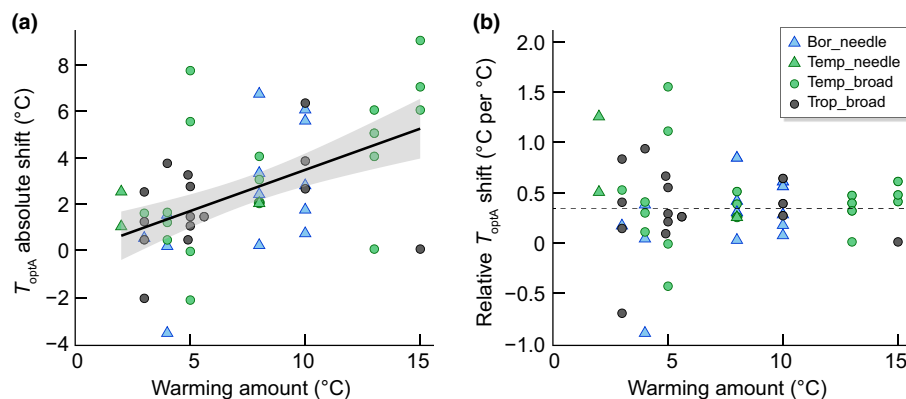
Fig. 3 (a) Positive linear relationship with 95% confidence intervals (grey area) of the absolute temperature shift of the temperature optimum of photosynthesis (T_{optA}) (°C, i.e. the temperature difference of T_{optA} between warmed and control conditions) as a function of warming amount ($T_{optA\text{-}abs} = 0.355x - 0.083$, $R^2 = 0.28$, $P < 0.0001$) across biomes (Bor, boreal in skyblue; Temp, temperate in green; Trop, tropical in black) and leaf form (triangles are needleleaf and circles are broadleaf species) and (b) no relationship between the relative shift in temperature optimum (°C per °C warming) and the amount of warming, but with a significant intercept of 0.342°C per °C ($P = 0.006$, dashed line).

Table 2 ANCOVA results (*F*-statistic and *P*-value) with warming amount, biome and leaf form as categorical variables and mean temperature of the warmest quarter as covariate (a proxy for biome) *on the response ratios to warming* (RR) to test the effects of warming, except for T_{optA} for which the absolute shift and the shift per °C warming was evaluated.

| Response ratio (RR)	Total obs.	Warming amount (binned) df = 2		meanTWQ (cov) df = 1		Leaf form df = 1		Warming amount × leaf form df = 2	
Variable		*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
T_{optA}_abs. shift	56	6.62	**0.0032**	0.79	0.38	0.09	0.92	1.36	0.27
T_{optA}_shift per °C	56	0.06	0.94	0.24	0.63	1.18	0.28	0.54	0.59
RR_V_{cmax25}	69	0.13	0.88	5.93	**0.018**	0.02	0.89	1.95	0.15
RR_J_{max25}	68	0.72	0.49	1.50	0.23	0.002	0.99	1.48	0.24
RR_$J:V_{25}$	53	0.040	0.96	6.78	**0.013**	0.36	0.55	0.63	0.54
RR_A_{net25}	106	0.03	0.97	4.76	**0.032**	9.93	**0.0022**	6.33	**0.0027**
RR_A_{growth}	54	1.55	0.22	0.004	0.94	12.45	**0.0011**	1.96	0.17
RR_R_{growth}	126	1.85	0.16	6.62	**0.012**	3.71	0.057	0.36	0.70
RR_R_{d25}	129	0.88	0.42	2.21	0.14	1.77	0.19	5.28	**0.0064**
RR_Q_{10}	27	4.05	**0.035**	0.09	0.77	1.31	0.27	0.21	0.81
RR_N_a	109	3.08	0.051	4.57	**0.035**	0.036	0.85	0.49	0.62

Sources of the model are the columns and variables form the rows, df is the degree of freedom for each source and the sample size for each variable is found in the second column (Total obs.). *P*-values are indicated in bold when significant < 0.05.
Variables are: the absolute shift in temperature optimum of photosynthesis (T_{optA}_abs. shift); the relative shift in T_{optA} per °C warming (T_{optA}_shift per °C); the maximum carboxylation rate (V_{cmax25}); the maximum electron transport rate (J_{max25}); the ratio of J_{max25} over V_{cmax25}, ($J:V_{25}$); and net photosynthesis (A_{net25}). All parameters were measured at a common temperature of 25°C, Photosynthesis and respiration were measured at their growth temperatures (A_{growth} and R_{growth} respectively), the mitochondrial dark respiration was measured at 25°C (R_{d25}); the temperature sensitivity of respiration (Q_{10}); and area-based leaf nitrogen content (N_a). The response ratios of these variables are indicated with RR and all are log-transformed to meet normality assumptions.

responses of V_{cmax25} and J_{max25} to warming, indicating that V_{cmax25} and J_{max25} generally acclimated to warming, although without a consistent direction. There were no significant overall effects of warming amount on the RRs of V_{cmax25}, J_{max25} or $J:V_{25}$ across biomes (Table 2; Fig. 4). The same result has been reported for a broader range of species and functional groups in Way & Oren (2010). Therefore, while absolute rates of photosynthetic capacity (V_{cmax25}, J_{max25}) were lower in the tropical biome compared with higher latitudes (Fig. 1; Table 1), the response to experimental warming amount was similar across biomes (Table 2), suggesting

that all species can acclimate to warming, regardless of where they originated.

Several studies have found similar acclimation capacity of photosynthesis to warming among species within boreal (Reich *et al.*, 2015; Sendall *et al.*, 2015) and tropical climates (Slot & Kitajima, 2015; Slot & Winter, 2017b). However, across biomes, it has been hypothesised that tropical species would have less acclimation capacity than temperate species and therefore less ability to adjust to new temperature conditions (Janzen, 1967; Cunningham & Read, 2002). Our analyses showed reduced RRs
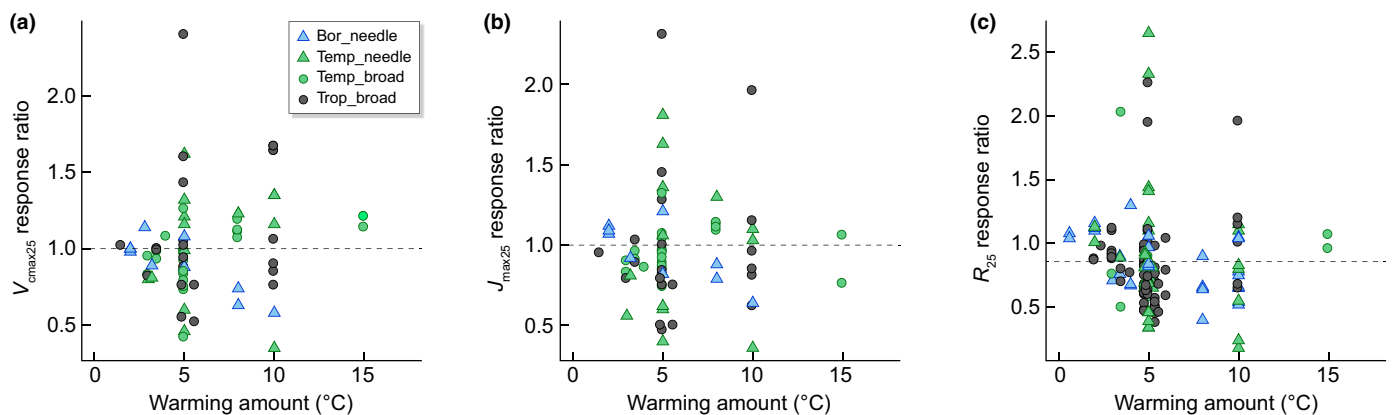
Fig. 4 The response ratio of (a) maximum carboxylation rate at 25°C (V_{cmax25}), (b) maximum electron transport rates at 25°C (J_{cmax25}), and (c) mitochondrial respiration at 25°C (R_{25}) as a function of the amount of warming. A response ratio > 1 indicates an increased value in warming compared with control conditions, whereas a response ratio < 1 indicates a decreased value in warming compared with control conditions. There was no significant relationship with warming amount (Table 2, dashed line) but the intercept of R_{25} was significantly negative (-0.858 ± 0.001; $P < 0.0001$), reflecting an overall 14% reduction of R_{25} with warming amount across biomes (Bor, boreal in skyblue; Temp, temperate in green; Trop, tropical in black) and leaf form (triangles are needleleaf and circles are broadleaf evergreen species).

of $J : V_{25}$ and A_{net25} with increasing mean temperature of the warmest quarter (Table 2; Fig. 5a,b), demonstrating that the overall photosynthetic response to warming was more negative in the tropics compared with cooler climates (despite the slightly increased response to warming of V_{cmax25} and N_a with higher summer growth temperatures; Fig. 5c,d; Table 2). For every 10°C increase in mean temperature of the warmest quarter, the RR of A_{net25} decreased by 5.3% (Fig. 5a). Moreover, the rates of V_{cmax25} or J_{max25} in tropical species are often lower compared with the equivalent measure in temperate or boreal species (Fig. 1). These lower rates combined with the smaller RR observed in $J : V_{25}$ and A_{net25} in the tropics can contribute to seemingly small or no thermal acclimation response of photosynthesis or photosynthetic capacity in tropical species (Scafaro *et al.*, 2017; Crous *et al.*, 2018; Fauset *et al.*, 2019; Carter *et al.*, 2020; Dusenge *et al.*, 2021). The mechanisms behind this limited thermal acclimation in the tropics need to be further explored, including limits to acclimation capacity and the potentially stronger role of stomatal conductance limitations to photosynthesis at higher temperatures (Carter *et al.*, 2021; Slot *et al.*, 2021). Slot & Winter (2016) indicated a possible VPD effect at higher temperatures, which may influence photosynthesis by stomatal conductance. Controlled experiments explicitly separating temperature and VPD could be valuable for improved mechanistic understanding (Slot & Winter, 2016; Grossiord *et al.*, 2020).

Regardless of how V_{cmax} or J_{max} respond to warming, one consistent response in the literature is the decrease in $J_{max} : V_{cmax}$ ratio at higher growth temperatures. This response is observed in almost all studies that have investigated the shift in temperature responses of V_{cmax} and J_{max} (Yamori *et al.*, 2005; Hikosaka *et al.*, 2006; Kattge & Knorr, 2007; Sage & Kubien, 2007; Kositsup *et al.*, 2009; Lin *et al.*, 2012; Crous *et al.*, 2013; Slot & Winter, 2017a; Dusenge *et al.*, 2019; Kumarathunge *et al.*, 2019; Bermudez *et al.*, 2020; Slot *et al.*, 2021). However, the magnitude of the decline in the $J_{max} : V_{cmax}$ ratio often does not change in response to the amount of experimental warming (Way & Sage, 2008; Crous *et al.*, 2018; Dusenge *et al.*, 2020; Slot *et al.*, 2021), which was also found in the ESWE dataset (Table 2). A reduced $J_{max} : V_{cmax}$ ratio, often observed with higher growth temperatures may result from relatively less N investment in RuBP regeneration, or relatively more investment in RuBP carboxylation, or both processes at higher temperatures (Onoda *et al.*, 2005; Hikosaka *et al.*, 2006). However, at temperatures above 35°C, photosynthesis can be limited by a decrease in V_{cmax} due to the heat lability of Rubisco activase (Salvucci & Crafts-Brandner, 2004; Busch & Sage, 2017). Scafaro *et al.* (2017) reported a decline of Rubisco content with higher growth temperatures reducing V_{cmax} and A_{net} in tropical species. A similar result was found in two *Eucalyptus* species, *E. tereticornis* and *E. grandis* (Crous *et al.*, 2018), for which reduced photosynthetic capacity was related to lower leaf nitrogen and lower leaf Rubisco content in tropical compared with temperate provenances of these two evergreen species. Our finding of higher $J : V_{25}$ RR with warming in cooler climates may reflect that warming stimulates carboxylation-limited processes more than RuBP regeneration and electron transport for which plants are
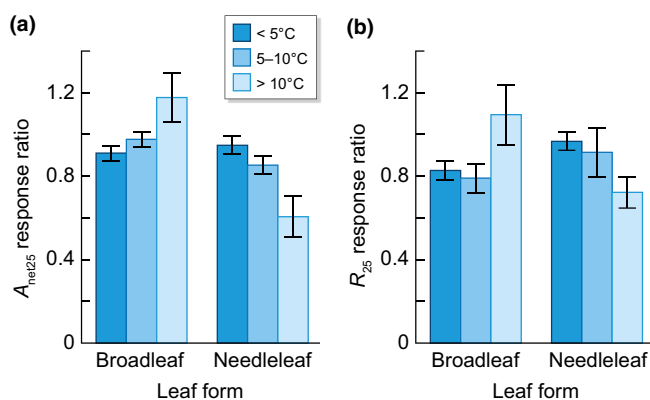
Fig. 5 Partial residuals with 95% confidence intervals (grey area) of various response ratios (RR) as a function of mean temperature of the warmest quarter from the VISREG R package to represent the effect of biome for (a) net photosynthesis at 25°C (A_{net25}) (slope of RR_A_{net25} = exp(−0.0055x), (b) the ratio of maximum carboxylation rate at 25°C (V_{cmax}) to maximum electron transport rate measured at 25°C (J_{max}) ($J_{max} : V_{cmax}$ ratio measured at 25°C: slope of RR_$J : V_{25}$ = exp(−0.0057x), (c) maximum carboxylation rate at 25°C (slope of RR_V_{cmax25} = exp(0.0099x)), and (d) area-based nitrogen (N_a) (slope of RR_N_a = exp(0.006x). Colours indicate biome (Bor, boreal in skyblue; Temp, temperate in green; Trop, tropical in black). Leaf form is represented with triangles for needleleaf and circles for broadleaf species. A response ratio > 1 indicates an increased value in warming compared with control conditions (positive response), whereas a response ratio < 1 indicates a decreased value in warming compared with control conditions (negative response). The dashed line separates positive from negative responses to warming.
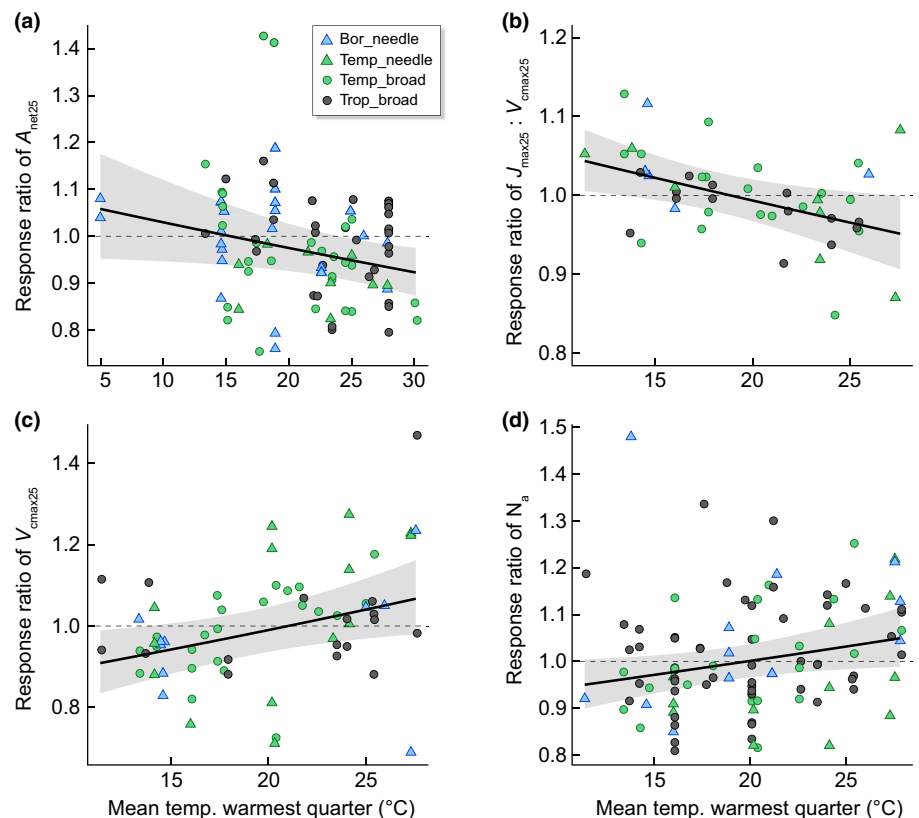
likely to operate below their T_{optA}. By contrast, in warmer environments and biomes, both rapidly increasing photorespiration and declining stomatal conductance act to increase carboxylation limitations of photosynthesis, shifting N investments towards V_{cmax} to maintain a balance between the two processes.

While we found no significant changes in responses to warming amount for V_{cmax25}, J_{max25} and A_{net25} (Table 2), there was a significant interaction between warming amount and leaf form in the RR of A_{net25} (and R_{25}; Table 2). Needleleaf evergreen species clearly declined A_{net25} in response to warming, from a 5% reduction in the 5°C up to a 15% and 40% reduction with 5–10°C and > 10°C warming, respectively. Broadleaf species mostly maintained their response of A_{net25} and R_{25} to warming with a slight increase in response to stronger warming, > 10°C (Fig. 6). A_{growth} had a 30% lower RR in needleleaf species compared with broadleaf evergreen species (Table 2), consistent with a slight negative relationship of A_{growth} as a function of warming in needleleaf evergreen species reported in Dusenge *et al.* (2019). This interaction highlights the sensitivity of needleleaf evergreen species to climate warming despite growing in cooler climates (Reich *et al.*, 2015).

Species growing at warmer growth temperatures may benefit less from warming than species growing in cooler temperatures (Way & Oren, 2010; Ghannoum & Way, 2011). The response of A_{net25} to warming clearly declined with higher growth/summer temperatures (Figs 5a, S5a). Therefore, increased growth temperatures may have negative effects on photosynthesis (−8% in A_{growth}, Fig. 7), possibly related to reduced leaf nitrogen content at higher growth temperatures (Figs 1, S2). Negative effects of warming on photosynthesis can be indirectly linked to several studies observing reduced growth rates in tropical species (Way & Oren, 2010; Drake *et al.*, 2015). There is a need for more research conducted at higher control growth temperatures to investigate the warming responses upwards of 30°C, as many ecosystems currently experience these growth temperatures at some point in the year or will experience these conditions in the future. This includes the likely detrimental effects of warming on the balance of photosynthesis and respiration when growth temperatures are already high, as well as whole-plant growth processes.

IV. Acclimation of leaf respiration to warming

1. The temperature response of leaf respiration

Leaf respiration is essential for growth and survival by supporting the energetic and maintenance requirements of the cell, as well as providing C-skeletons for biosynthesis (Penning de Vries, 1975). The temperature response of leaf respiration is described by an exponential function over a large range of temperatures (Hofstra & Hesketh, 1969; Atkin & Tjoelker, 2003; Heskel *et al.*, 2016), indicating that leaf respiration is highly sensitive to temperature (Fig. 2c). At temperatures higher than 45°C, usually between 48°C and 60°C, leaf respiration reaches its maximum (O'Sullivan *et al.*, 2013; Heskel *et al.*, 2014; Weerasinghe *et al.*, 2014) followed by a steep decline. This temperature maximum for respiration exists because, above this threshold, cell disruption or lysis of mitochondria has occurred and leaves stop respiring, signalling the point of cell death. This respiration temperature maximum varies somewhat by species, and depends on environmental factors such as growth temperatures, canopy position and species-specific traits (O'Sullivan *et al.*, 2017; Zhu *et al.*, 2018).

The exponential part of the temperature response curve of respiration is used to determine the temperature sensitivity (i.e. the slope), usually across a temperature range below 45°C. While some exponential functions can fit the short-term temperature response of respiration (Atkin *et al.*, 2005b), the Q_{10} function is most commonly used, with parameters reflecting the basal reference temperature at a given temperature and an exponential slope. The slope parameter, Q_{10}, reflects the proportional increase in respiration with a 10°C increase in temperature:

$$R_T = R_{25} \cdot Q_{10}^{(T-25)/10} \qquad \text{Eqn 4}$$

In Eqn 4, basal respiration rate is given as R_{25}, but other temperatures are possible as long as they are within the measurement range to avoid extrapolation.

The Q_{10} has been shown to be temperature dependent (Tjoelker *et al.*, 2001; Atkin *et al.*, 2005a; Heskel *et al.*, 2016) declining with warmer temperatures (Bruhn *et al.*, 2002; Covey-Crump *et al.*, 2002; Atkin & Tjoelker, 2003; Heskel *et al.*, 2016). Therefore, the temperature sensitivity of respiration is not well represented by one value, especially in cooler biomes (Heskel *et al.*, 2016). Heskel *et al.* (2016) proposed a general second order polynomial function for all biomes and PFTs to describe the temperature response of respiration:

$$\log_e R = a + 0.1012\,T - 0.0005\,T^2 \qquad \text{Eqn 5}$$

where T represents a given growth temperature and a varies by biome or PFT (Heskel *et al.*, 2016), with a global value of $a = -2.23$. In contrast to the exponential Q_{10} function (Eqn 4),

Fig. 6 Bar plots showing the interaction between warming amount and leaf form for the mean and standard error for (a) the response ratio of net photosynthesis at 25°C (A_{net25}) and (b) the response ratio leaf respiration at 25°C (R_{25}) in broadleaf and needleleaf evergreen species for three different categories of warming (< 5°C, 5–10°C, > 10°C). The interaction shows a more negative response to warming in needleleaf species with higher warming amount whereas broadleaf species had a fairly constant response and even a slight increase in R_{25} with >10°C warming.

Fig. 7 Mean (solid points) and 95% confidence interval (bars) across all evergreen species for the response ratio to warming in each of 10 variables: maximum carboxylation rate at 25°C (V_{cmax25}), maximum electron transport rate at 25°C (J_{max25}), the ratio of $V_{cmax} : J_{max}$ at 25°C ($J : V_{25}$), net photosynthesis at 25°C (A_{net25}) and net photosynthesis at prevailing growth temperatures (A_{growth}), the temperature optimum of photosynthesis (T_{optA}), mitochondrial respiration at 25°C (R_{25}), and dark respiration at growth temperatures (R_{growth}), the temperature sensitivity of respiration (Q_{10}) and area-based nitrogen content (N_a). A response ratio > 1 indicates an increased value in warming compared with control conditions, whereas a response ratio < 1 indicates a decreased value in warming compared with control conditions (black dashed line). Overall, the response ratios of A_{growth} (−8%), R_{25} (−14%) and Q_{10} (−5%) responded negatively to warming, while T_{optA} (15%) and R_{growth} (18%) were increased with warming. Sample sizes for each variable are indicated on the right.

the polynomial function allows for a peaked relationship, along with a temperature-dependent slope parameter (i.e. $Q_{10} = -0.0005 \times T + 0.1012$) which is more appropriate for applications over large temperature ranges. However, both Q_{10} and R_{25} adjust to changing growth temperatures (thermal acclimation) and their responses to warming are evaluated in the next sections.

### 2. Acclimation of the temperature sensitivity of respiration, Q_{10}

The temperature response curve of respiration, described by the Q_{10} and R_{25} parameters in Eqn 4, changes in response to higher growth temperatures (e.g. acclimation of respiration; Fig. 2f). Atkin & Tjoelker (2003) described two types of respiratory acclimation. Type I acclimation is observed when the Q_{10} (slope parameter) has changed. This enables the plant to dynamically respond to changes in surrounding growth temperatures. A reduced slope or temperature sensitivity results in lower respiration rates at higher temperatures as the upwards exponential increase is reduced compared with when acclimation did not occur (compare pink triangle with pink circle in Fig. 2f). Type II acclimation occurs when there is a change predominantly in R_{25} (basal rate), often being reduced when exposed to higher growth temperatures compared with cooler temperatures, especially in new leaves developed under the new, warmer conditions. The change in R_{25} is likely to be due to changes in enzyme capacity (Atkin & Tjoelker, 2003). Both types of acclimation result in reduced respiration rates at warmer temperatures compared with nonacclimated leaves.

The RR of Q_{10} not only generally declined with experimental warming (−5%; Fig. 7) but also exhibited a significant negative

relationship with warming amount ($P = 0.0028$, $R^2 = 0.30$; Fig. 8). This suggests that type I acclimation is important when evergreen species adjust to new growth temperatures. There was not much change in Q_{10} with warming up to 5°C, but Q_{10} declined up to *c.* 12% with warming above 5°C. Although Q_{10} is reduced with warming, which results in lower respiration rates than would have occurred without acclimation, it is unclear which underlying respiratory processes drive this reduction. The temperature sensitivity of respiration is influenced by a range of internal factors, including the balance between enzyme activity, substrate availability and adenylate control over mitochondrial activity (i.e. the ratio of ATP : ADP and the concentration of ADP *per se*, Hoefnagel *et al.*, 1998), each of which can change with seasonal variation, irradiance and nutrient availability (Zaragoza-Castells *et al.*, 2007; Crous *et al.*, 2011). For an in-depth review on the variation of Q_{10}, including the respiratory mechanism behind this variation, see (Atkin *et al.*, 2005a,b). While a decline in Q_{10} has been observed before across latitudes (Tjoelker *et al.*, 2001), here we showed how Q_{10} decreased with higher growth temperatures across a large range of warming (Fig. 8c).

3. Acclimation responses of leaf respiration rates to warming are universal

Thermal acclimation of respiration generally refers to processes associated with maintenance respiration, and helps to minimise carbon loss at higher temperatures while optimising ATP supply and carbon skeletons (Slot & Kitajima, 2015). As with photosynthesis, respiration measured at a common temperature determines the degree of thermal acclimation between different warming
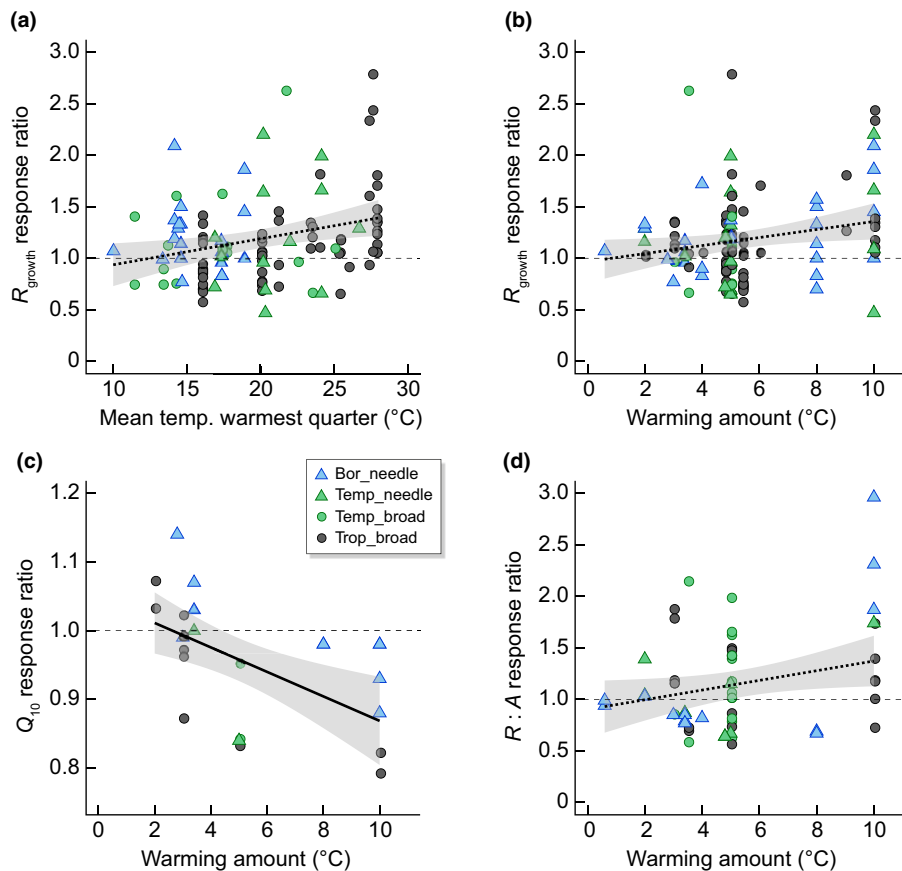
Fig. 8 Linear regression relationships with 95% confidence intervals (grey area) between (a) dark respiration at growth temperatures (R_{growth}) and the mean temperature of the warmest quarter (RR_R_{growth} = 0.0252x + 0.68, R^2 = 0.05, P = 0.0083), (b) the response ratio of R_{growth} and the amount of warming (RR_R_{growth} = 0.039x + 0.967, R^2 = 0.03, P = 0.03), (c) the response ratio of Q_{10} (where the slope parameter, Q_{10}, reflects the proportional increase in respiration with a 10°C increase in temperature) and the amount of warming (RR_Q_{10} = 0.0178x + 1.047; R^2 = 0.30; P = 0.0028), and (d) the response ratio of $R : A$ at growth temperatures and the amount of warming (RR_RA = 0.047x + 0.902; R^2 = 0.06; P = 0.04). The dotted lines indicate a significant but weak relationship with R^2 < 0.1. A response ratio > 1 indicates an increased value in warming compared with control conditions, whereas a response ratio < 1 indicates a decreased value in warming compared with control conditions (black dashed line separates positive from negative responses to warming). Colours indicate biome (Bor, boreal in skyblue; Temp, temperate in green; Trop, tropical in black). Leaf form is represented with different symbols with triangles for needleleaf and circles for broadleaf species.

treatments or biomes. Respiration rates have been shown to adjust to new temperatures within a few days (Billings *et al.*, 1971; Bolstad *et al.*, 2003; Lee *et al.*, 2005; Slot *et al.*, 2014) although more complete thermal adjustments can be achieved over time by changes in protein density and amounts of mitochondria (Armstrong *et al.*, 2006). Complete acclimation or homeostasis of respiration is achieved when rates of respiration in warm-acclimated trees are the same at the higher growth temperature as rates in nonacclimated control trees at the original growth temperature. Homeostatic acclimation can be more easily achieved at moderate temperature changes, whereas larger temperature changes may not always result in complete acclimation (Campbell *et al.*, 2007).

In the ESWE dataset, we observed reduced R_{25} rates with higher mean temperatures of the warmest quarter (Fig. S2e; Table 1). Regarding the responses of respiration to warming, R_{25} decreased by 14% across evergreen tree species in the ESWE dataset (Figs 4c, 7). The magnitude of R_{25} reduction was independent of the amount of warming (Fig. 4; Table 2), but there was an interaction with leaf form in which needleleaf species showed a reduced RR with higher warming amounts (> 10°C), whereas broadleaf species did not. Needleleaf species reduced R_{25} from a *c.* 6% on average up to 5–10°C warming to a 28% reduction with warming > 10°C (Fig. 6b; Table 2). A similar RR of R_{25} across biomes (Table 2) implied a similar, universal degree of respiration acclimation for evergreen plants across the biogeographical domain. In a review across 103 species subjected to

experimental warming, Slot & Kitajima (2015) suggested similar thermal acclimation of leaf respiration across species, which has been found in studies with boreal (Teskey & Will, 1999; Tjoelker *et al.*, 1999) and nonevergreen species (Campbell *et al.*, 2007), and is also apparent in the ESWE dataset. Vanderwel *et al.* (2015) demonstrated similar acclimation responses in respiration when examining seasonal adjustment (acclimation-over-time) compared with climate gradients (acclimation-over space) based on a global analysis. Both Aspinwall *et al.* (2016) and Reich *et al.* (2016) found common underlying physiological mechanisms in respiratory acclimation responses to experimental warming and seasonal temperature changes. Therefore, a growing body of evidence suggests that respiration acclimates in a general, predictable manner to a change in growth temperature across a wide range of species and biomes (Heskel *et al.*, 2016), resulting in the possibility of global predictions of R based on growth temperatures (Eqn 5).

The response of respiration at prevailing growth temperatures, R_{growth} increased by 18% with warming across the entire ESWE dataset (Fig. 7). The response of R_{growth} to warming increased both with mean temperature of the warmest quarter (R^2 = 0.05; Table 2; Fig. 8a) and warming amount (R^2 = 0.03, P = 0.03; Fig. 8b) as well as with experimental growth temperatures (Fig. S5b), although all significant relationships had low R^2 < 0.1. This increase in growth respiration to higher temperatures is consistent with expectations based on a universal respiration response to warmer growth temperatures. A similar response was observed in a global analysis in

which respiration rates at prevailing growth temperatures were higher in the tropics than the Arctic (Atkin *et al.*, 2015). Leaf form tended to affect the RR of R_{growth} to warming; needleleaf species increased $25 \pm 9\%$, while broadleaf evergreen species increased R_{growth} with $15 \pm 5\%$ in response to warming ($P = 0.06$; Table 2).

While the processes of photosynthesis and leaf respiration have traditionally been studied separately, it has been long known that these processes are interlinked (Hoefnagel *et al.*, 1998). In a meta-analysis across several PFTs such as C_3 herbaceous, C_4 species, deciduous and woody evergreen trees, Dusenge *et al.* (2019) found that the ratio of respiration over photosynthesis rates, $R : A$, at prevailing growth temperatures was constant across a wide range of temperatures, suggesting that the processes of respiration and photosynthesis are coordinated. Our analyses found an increase in $R : A$ with growth temperature and the amount of warming (Fig. 8d; $P = 0.04$; $R^2 = 0.06$) across 10 degrees of warming, consistent with the responses of increased R_{growth} but not A_{growth} with warmer temperatures (Table 2). It is likely that plants thermally acclimate photosynthesis and respiration in a coordinated fashion (Dusenge *et al.*, 2019) although we note the scatter, which may result from variation in factors underpinning A_{growth}, such as stomatal conductance. Respiration, being a more temperature sensitive process, can rapidly adjust to changing growth temperatures and does so in a predictable manner (Heskel *et al.*, 2016) both in response to seasonal and experimental warming and regardless of the amount of warming (Table 2). By contrast, photosynthesis can adjust to warmer growth temperatures (Fig. 1b), but the degree of photosynthetic acclimation is more constrained with warmer temperatures (Fig. 5a; Table 2), despite increased T_{optA} (Fig. 3a). Therefore, the adjustment of photosynthesis rates to warming is limited and factors other than growth temperatures may set additional limits on the acclimation capacity of photosynthesis.

V. Limits to the thermal acclimation capacity

While natural selection could optimise processes of carbon uptake and carbon loss, there are limits to plant thermal acclimation capabilities. What these limits are and what factors determine them is currently unclear. From our analyses, it is clear that photosynthesis can partially adjust by shifting the temperature optimum by 0.34°C per °C warming (Fig. 3b), but the warming response of net photosynthesis (A_{net25}) also declined with higher growth temperatures (Figs 5a, S5). In a field study in which *Eucalyptus globulus* was moved 700 km north outside its native range and additionally exposed to 3°C warming, the species demonstrated a limited ability to acclimate to high summer temperatures, but was still able to adjust to winter temperatures (Crous *et al.*, 2013). This evidence and others suggest that there is an upper limit of thermal tolerance for photosynthesis, which may be influenced by a species' physiological plasticity as well as its distribution range. While changes in growth temperatures play a major role in thermal acclimation of photosynthesis (Kumarathunge *et al.*, 2019), the RR of A_{net25} and R_{25} declined more in needleleaf species compared with broadleaf evergreen species (Fig. 6), which may be a reflection of gymnosperm evolutionary history contrasting with angiosperms

in the ESWE dataset. There is some evidence that the overall acclimation capacity in photosynthesis can be limited by genetic adaptation and evolutionary history (Read & Busby, 1990; Jump & Peñuelas, 2005), as indicated by studies on contrasting taxonomic groups with a diverse evolutionary history (i.e. PFT) (Cunningham & Read, 2002; Yamori *et al.*, 2014; Reich *et al.*, 2015).

While the climate at the seed of origin has been suggested to determine population responses to climate change, species generally respond to a broad range of temperatures, perhaps the temperature range experienced along a species' native distribution. Plant species with large geographic range sizes have been indicated to cope better with climate warming than species with smaller range sizes (Thuiller *et al.*, 2005; Aitken *et al.*, 2008; Pacifici *et al.*, 2015; Gonzalez-Orozco *et al.*, 2016). This is presumably because species with broad climatic distribution are adapted to a broader range of growth temperatures and environmental tolerances (Hamrick *et al.*, 1992; Leimu *et al.*, 2006; Morin & Thuiller, 2009; Slatyer *et al.*, 2013). Gene flow among populations can also contribute to a species' thermal acclimation as genetic adaptations to warmer temperatures can be passed on from warmer to cooler populations, which cannot occur for populations at the warmest edge of a species' native distribution (Savolainen *et al.*, 2007; Sexton *et al.*, 2011).

A shift towards higher temperatures will induce large changes in most biological processes and these changes are likely to emerge at the ecosystem level by changes in species composition and shifts in distribution ranges. This has already been observed along tropical elevations (Duque *et al.*, 2015; Fadrique *et al.*, 2021) as well as in boreal climates (Boisvert-Marsh *et al.*, 2014; Lesica & Crone, 2017; Villén-Peréz *et al.*, 2020). Andean tropical forest plot inventories have revealed directional shifts in tree community composition over time towards greater relative abundances of species from lower, warmer elevations (Fadrique *et al.*, 2021), often driven by enhanced mortality of higher elevation species (Duque *et al.*, 2015). Moreover, biological processes such as competition among plants may further reduce the ultimate geographic range at which plants can occur (Ghalambor *et al.*, 2006; Penuelas *et al.*, 2013). For example, temperate species may be competitively excluded from tropical forests due to outshading of seedlings and slower growth rates compared with tropical species (Cunningham & Read, 2003). Other processes such as seed dispersal and germination can also contribute to competitive exclusion. Therefore, the realised geographic range of a species is often smaller compared to which geographic range is fundamentally possible based on physiological tolerances alone (Cunningham & Read, 2003; Ghalambor *et al.*, 2006).

VI. Can spatial gradients and seasonal changes help to predict warming responses?

Current knowledge on tree physiological responses to increased temperature is primarily based on controlled warming experiments (Way & Oren, 2010; Yamori *et al.*, 2014; Slot & Kitajima, 2015; Dusenge *et al.*, 2019) and analyses of environmental dependencies using observational data (Ali *et al.*, 2015; Atkin *et al.*, 2015;

Kumarathunge *et al.*, 2019; Smith *et al.*, 2019). While controlled experiments may have limited applicability in the field, they can provide more detailed insights into mechanisms that would not easily be derived using a field-based approach. More ecologically relevant, field-based observations come with inevitable uncertainties regarding the causality and origin due to co-varying environmental factors such as light and nutrients in addition to genetic variability among different populations of a given species.

Studies along natural temperature gradients, either latitudinal or elevational, may offer a useful compromise between these two approaches to study warming responses (Malhi *et al.*, 2010). Gradient studies still require that other co-varying environmental variables are carefully considered. For example, the influence of temperature (and associated shifts in VPD, Amthor *et al.*, 2010) on plant physiological traits and processes along wet tropical elevation gradients can be assessed if also potential co-variation in nutrient availability is considered (Fyllas *et al.*, 2017; Mujawamariya *et al.*, 2021). Similarly, latitudinal gradients can be used to assess thermal acclimation if measurement campaigns account for variation in photoperiod and phenology (Tjoelker *et al.*, 1999; Dillaway & Kruger, 2010; Benomar *et al.*, 2018).

Most physiological studies using latitudinal or elevation gradients have used trees that grow naturally along the gradient (Tjoelker *et al.*, 2009; Wertin *et al.*, 2010; Girardin *et al.*, 2014; Fyllas *et al.*, 2017), which does not allow for separation between thermal acclimation and genetic adaptation. These studies are valuable for assessing the longer term (more than centuries) responses of tree community composition and population dynamics at a given location. They are perhaps less useful for assessing the impacts of rapid ongoing global warming on the physiology and growth of long-lived and slow-migrating organisms such as trees over the coming decades. For this, additional approaches are needed. Translocation experiments with the same genetic material planted at different sites along natural temperature gradients have been conducted to assess physiological thermal acclimation of both boreal (Dillaway & Kruger, 2010; Benomar *et al.*, 2018) and tropical (Mujawamariya *et al.*, 2021) trees. However, translocation experiments are mostly done on a few and/or small trees, sometimes growing in pots, compromising the ability to evaluate responses on mature trees over a longer term. By contrast, an elevation gradient approach with both multispecies plantations and established trees at different sites offers a promising approach to predict warming responses based on spatial temperature gradients (Mujawamariya *et al.*, 2021).

Observations of seasonal changes in tree physiological processes may also offer insight into thermal acclimation. Numerous studies have explored seasonal or interannual shifts in leaf photosynthesis and respiration in relation to changes in temperature (Crous *et al.*, 2011; Aspinwall *et al.*, 2016; Lamba *et al.*, 2018). In some cases, these seasonal responses agree well with long-term warming responses, especially during the warmer part of the year (Vanderwel *et al.*, 2015; Aspinwall *et al.*, 2016). However, seasonal responses, even in the warmer part of the year, generally do not extend the mean growth temperatures that a tree may experience compared with long-term climate warming. Whereas long-term climate warming has a consistent warming response, seasonal responses are usually limited in time and vary in strength over the years. Therefore, seasonal studies offer limited insight regarding responses to climate warming. Moreover, phenology and other co-varying environmental factors such as soil moisture or photoperiod can further confound seasonal physiological data (Bauerle *et al.*, 2012; Lamba *et al.*, 2018). We argue that seasonal responses are a different layer within the response to climate warming. Therefore, spatial gradients, whether elevation or latitudinal gradients, are more useful to predict climate change responses.

VII. Including acclimation capacity of photosynthesis and respiration in land surface models

Most land surface models (LSMs) have not considered physiological acclimation (discussed in Sections III and IV, above). They either rely on a single, global photosynthesis/respiration temperature response function (Leuning, 2002; Kowalczyk *et al.*, 2006), or assume differences in the response functions of different PFTs (Clark *et al.*, 2011; Smith & Dukes, 2017). As a consequence of assuming a fixed instantaneous temperature response, the simulated climate-carbon feedback from such models remains a key uncertainty (Ziehn *et al.*, 2011), particularly as the climate warms (Booth *et al.*, 2012). Several studies have recognised the importance of accounting for acclimation in their representation of carbon fluxes (Smith & Dukes, 2013; Huntingford *et al.*, 2017; Mercado *et al.*, 2018). Furthermore, LSMs have separately considered acclimation in both respiration (Huntingford *et al.*, 2017) and photosynthetic physiology (Mercado *et al.*, 2018), but not both as a full acclimation scenario.

Given that respiration readily acclimates to warmer temperatures in a universal and predictable way, it is imperative that the thermal acclimation of respiration is considered in models. The temperature sensitivity of respiration can be predicted using growth temperatures (i.e. $Q_{10} = -0.0005 \times T + 0.1012$, Heskel *et al.*, 2016), while the relationship between the RR of Q_{10} and warming amount (Fig. 8c) can help to modify the temperature response of respiration to long-term warming, rather than assuming a Q_{10} of 2. Modelling assessments of short-term and long-term acclimation effects on gross primary productivity and canopy respiration have effects ranging between 9% and 20% (Atkin *et al.*, 2008; Huntingford *et al.*, 2017; Mercado *et al.*, 2018) with acclimation effects on these processes largest for tropical evergreen forests. This suggests that, in spite of uncertainties in the trajectory of carbon cycle processes with warming, short-term and long-term aspects of physiological acclimation are important to quantify and include in LSMs.

Predicting the acclimation of photosynthesis to temperature seems less straightforward compared with the consistent response of respiration to a change in growth temperature. When thermal acclimation has been represented in LSMs (Lombardozzi *et al.*, 2015; Smith *et al.*, 2016; Mercado *et al.*, 2018), there remain several knowledge gaps. First, there is uncertainty about the magnitude of species' temperature acclimation of photosynthesis and respiration. For respiration, we found an overall acclimation of R_{25} of −14% with no significant differences between biomes or warming amount (Table 2; Fig. 7). For photosynthesis, our

analyses in evergreen species have shown that (1) the T_{optA} shift per °C warming is predictable regardless of the amount of warming (Fig. 3b) and (2) the thermal acclimation response of photosynthesis is reduced with warmer growth temperatures (Figs 5a, S5), a relationship useful to represent in models. There were also effects of higher mean temperatures of the warmest quarter on the responses of $V_{cmaxt25}$ and $J:V_{25}$ to warming (Fig. 5). By contrast, the response of photosynthetic capacity at a common temperature ($V_{cmaxt25}$ and J_{max25}) was not affected by warming amount, because a similar amount of observations responded either with an increased or decreased response to warming across the ESWE dataset (Fig. 4; Table 2).

When models have included acclimation mechanisms, implementation is assumed to continue indefinitely with future warming. However, it is likely that there is a limit to the acclimation potential of plants with the temperature optimum unlikely to shift much beyond this limit (Crous *et al.*, 2013; Hogan *et al.*, 2021). More research is needed to investigate where potential limits to the shift in T_{optA} may lie. Regarding the timing of thermal acclimation, it is clear that the timing of acclimation of respiration is more rapid (i.e. days to 1 wk; Bolstad *et al.*, 2003; Lee *et al.*, 2005) than the timing of acclimation of photosynthesis. A timescale of *c.* 1 month (Smith & Dukes, 2017) to 8–10 wk for photosynthesis (Hogan *et al.*, 2021) has been suggested. We need to better understand the timescale over which acclimation occurs, the mechanisms that control this timescale and how this varies amongst PFTs.

Some models such as CABLE (Kowalczyk *et al.*, 2006) currently assume a fixed $J:V_{25}$ ratio, linking J_{max} to the parameterisation of V_{cmax}. However, evidence from our review, consistent with previous studies (Kattge & Knorr, 2007; Kumarathunge *et al.*, 2019), has shown that the $J:V_{25}$ ratio declines with increasing temperature (Fig. 1), and its response to warming was reduced from boreal to tropical latitudes (Fig. 5). This implies that models that fix this ratio should consider linking the response to temperature (e.g. growing season temperature) or by leaf N changes with temperature (Fig. 1). Both $J:V_{25}$ and nitrogen decreased with warmer temperatures (Figs 1, 5a), and this relationship could be used to predict V_{cmax} and J_{max} rates across a range of growth temperatures.

VIII. Conclusions

The literature on evergreen species responses to warming has expanded considerably in the last 10 yr, particularly for tropical evergreen species. We found reduced acclimation of photosynthesis to warming from boreal to tropical biomes (Table 2; Fig. 5), but this response was not affected by the amount of warming (Fig. 4). While R_{25} reduced with mean summer growth temperatures (Table 1), there was a universal response of respiration to warmer temperatures (Table 2; Figs 4, 7). Looking forward, there needs to be a better understanding of the role of stomatal responses in controlling the thermal acclimation response of photosynthesis, and a strengthening of the links among the thermal acclimation of leaf N, A_{net} and R_d, including physiological acclimation and plasticity for improved predictions with warming. These

acclimation responses should also be linked to longer term processes such as adaptation, growth responses and carbon stocks (Sullivan *et al.*, 2020) for parameterising large-scale LSMs. Model experiments involving acclimation of both photosynthetic components and respiration are important to explore and elucidate key responses that influence large-scale terrestrial carbon fluxes. As an extension from stronger climate forcing and global warming, extreme heat events are likely to occur more frequently (Meehl & Tebaldi, 2004). Heatwaves may negatively impact the persistence of species, habitat suitability and the diversity and function of ecosystems (Allen *et al.*, 2015; Buckley & Huey, 2016). More studies simulating extreme temperature events and their impacts are needed to determine species' upper heat tolerances and understand the mechanisms involved in adjustments at all scales, including variation among functional plant types and interactions with water availability. We argue that thermal acclimation of photosynthesis and respiration across biomes can be included with the help of the relationships and analyses from this review to enhance the understanding of how the carbon cycle at large scales will be affected by climate warming.

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Data availability

All data used in this manuscript are available online and/or have been published before (see Appendix A2). The dataset used for this study is available from the corresponding author upon reasonable request for future collaborations.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Boxplots and relationship between biome, mean annual temperature and mean temperature of the warmest quarter in the ESWE dataset.

Fig. S2 Partial residuals with 95% confidence intervals of the ANCOVA as a function of mean temperature of the warmest quarter (meanTWQ) to represent the effect of biome.

Fig. S3 Linear regression relationships with 95% confidence intervals between several variables against experimental control growth temperatures across biomes.

Fig. S4 Partial residuals with 95% confidence intervals from the ANCOVA as a function of mean annual temperature (mat) to represent the effect of biome.

Fig. S5 Linear relationships with 95% confidence intervals against experimental control growth temperature for the response ratio (RR) of net photosynthesis at 25°C, A_{net25}, and respiration rates a prevailing growth temperatures, R_{growth}.

Table S1 Species list per biome and plant functional type, including latitude and longitude, the reference where the data originated and how controlled the study was.

Table S2 ANCOVA results with mean annual temperature as a covariate for both absolute control values and the response ratios.

Table S3 Table with sample sizes for each variable in each category (warming amount, biome and leaf form).

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Appendix A1

Data summary and statistical analyses of the 'Evergreen species in a warming environment' (ESWE) dataset

The ESWE dataset focused on both field and controlled environment studies with a control and warming treatment (Appendix A2). There were 268 lines from field studies and 927 lines from glasshouse studies out of 1195 lines in the ESWE dataset across all variables. Common garden studies without warming treatment were not included. Generally, a mean and standard error (or standard deviation) of control and warming treatments were collected for each species, along with information on biome, latitude and longitude, growth temperatures of control and warmed treatments, sample size and the amount of warming applied. When studies tracked ambient data, an average temperature across the duration of the sampling was taken to represent the control growth temperature. Data were collected from tables or digitised from graphs using DATATHIEF III (v.1.5, www.datathief. org). Latitude and longitude were added based on the coordinates mentioned in the study or the study location if using a locally grown species (Supporting Information Table S1). Mean annual temperature, the maximum temperature of the warmest month and the mean temperature of the warmest quarter based on latitude were extracted from the BIOClime database (Hijmans *et al.*, 2005). There were clear relationships between biome and mean annual temperature, as well as mean temperature of the warmest quarter (Fig. S1).

Variables collected were measured in both control and warming treatment(s) at growth temperatures and/or at a common temperature. The variables include: photosynthesis at 25°C (A_{net25}), photosynthesis at growth temperature (A_{growth}), maximum carboxylation rates and maximum electron transport rates measured at 25°C (V_{cmax25} and J_{max25}), the $J_{max} : V_{cmax}$ ratio at that

temperature ($J : V_{25}$) and mitochondrial dark respiration at a common temperature (R_{25}), as well as dark respiration at growth temperatures (R_{growth}). The temperature optimum of photosynthesis (T_{optA}) and area-based nitrogen content (N_a) were also recorded and, when available, the temperature sensitivity of the respiration temperature response, Q_{10}. As not all variables were recorded in each study, sample sizes and species involved varied depending on the variable investigated (Table S3). The warming amount across the ESWE dataset spanned from 0.6°C to 16°C warming, which we divided into three categories: < 5°C, 5–10°C and ≥ 10°C. For V_{cmax25}, J_{max25} and $J : V_{25}$, there were no warming studies that went beyond 10°C warming in the boreal biome.

Statistical analyses were conducted in R v.3.6.1 (R Core Team, 2020). All variables were tested for a normal distribution and transformed when necessary. To evaluate how the absolute values in control conditions varied across biomes and to determine intrinsic trends across biomes and functional groups (Section II on biogeographic patterns), we used an analysis of covariance (ANCOVA) approach with leaf form as categorical factor and mean temperature of the warmest quarter as a covariate to address the collinearity between biome and leaf form. Tukey's post hoc tests (using *glht* from the MULTCOMP package; Hothorn *et al.*, 2008) were used to determine differences between leaf form groups and warming amount categories. We chose mean temperature of the warmest quarter as our covariate to best reflect the conditions in which most experiments are measured (i.e. during the growing season). Using mean annual temperature as a covariate instead of mean temperature of the warmest quarter gave similar results (Table S2; Fig. S4). All results from this statistical analyses on control/ambient conditions are summarised in Table 1.

Similarly, a second ANCOVA was used to evaluate the response ratios to warming of several variables, summarised in Table 2 (Sections III and IV) with warming category and leaf form as categorical factors, and mean temperature of the warmest quarter as covariate to reflect trends across biomes. Data from different species were considered independent and no weighting factor for study/experiment was included due to similar variances among experiments and the small amount of studies used (Koricheva & Gurevitch, 2014). The response ratio of a given variable in warmed divided by ambient treatments assessed the degree of acclimation and was log-transformed to meet linearity assumptions for ANCOVA. A response ratio > 1 indicated a positive warming response, while a response ratio < 1 referred to a negative response to warming. Regarding T_{optA}, we used the absolute (in °C) as well as the relative (in °C per °C warming) temperature shifts to evaluate responses to warming instead of a response ratio.

A third approach was linear regression analyses using warming amount or bioclimatic temperature indices (e.g. mean annual temperatures, mean temperature of the warmest quarter) as a continuous factor to test for the basic functional relationships that underlay all evergreens. While the statistics were done on the logarithmic of the response ratio to satisfy linearity assumptions, graphics are displayed using the response ratio for easier interpretability or using back-transformed partial residuals from the VISREG package (Breheny & Burchett, 2017).

Appendix A2

Studies used in the analyses

Aspinwall MJ, Drake JE, Campany C, Varhammar A, Ghannoum O, Tissue DT, Reich PB, Tjoelker MG. 2016. Convergent acclimation of leaf photosynthesis and respiration to prevailing ambient temperatures under current and warmer climates in *Eucalyptus tereticornis*. *New Phytologist* 212: 354–367.

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