

## **New Phytologist Supporting Information**

Article title: Evaluating the kinetic basis of plant growth from organs to ecosystems

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The following Supporting Information is available for this article:

**Fig. S1** A typical temperature response curve for a biological rate.

**Fig. S2** Modified Arrhenius plots of Sharpe-Schoolfield model fits (with  $E_h$  as a free parameter) to photosynthesis temperature response data.

**Fig. S3** Modified Arrhenius plots of Sharpe-Schoolfield model fits (with  $E_h$  as a fixed parameter) to photosynthesis temperature response data.

**Fig. S4** Tree growth rates across a broad air temperature gradient.

**Fig. S5** Distributions of intraspecific optimal temperatures for photosynthesis, estimated from Eqn (2) with  $E_h$  as a free parameter.

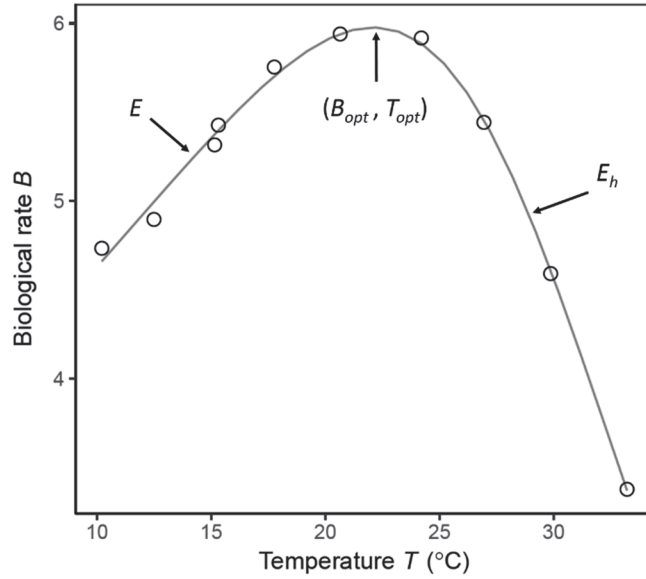
**Fig. S6** Distributions of intraspecific optimal temperatures for photosynthesis, estimated from Eqn (2) with  $E_h$  as a fixed parameter.

**Table S1** List of taxa, number of curves per taxon, and primary sources for photosynthesis temperature response data used in analyses.

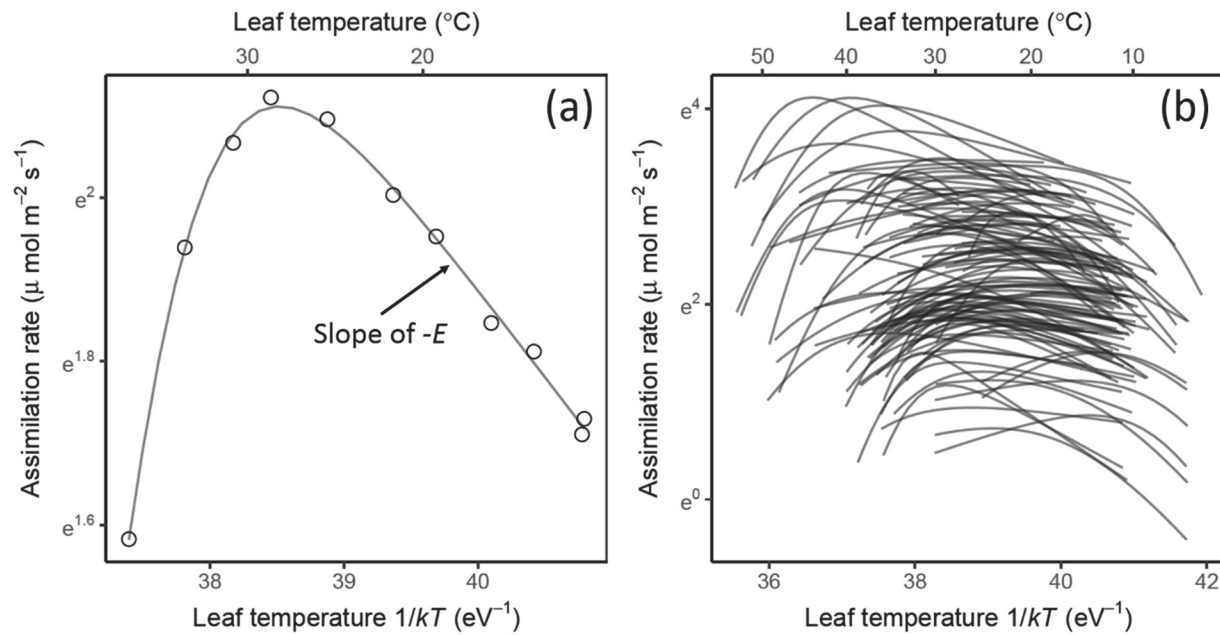
**Table S2** List of growth variables, temperature variables, sample sizes, and primary sources for growth analyses.

**Methods S1** Description of data and methods used for analyses.

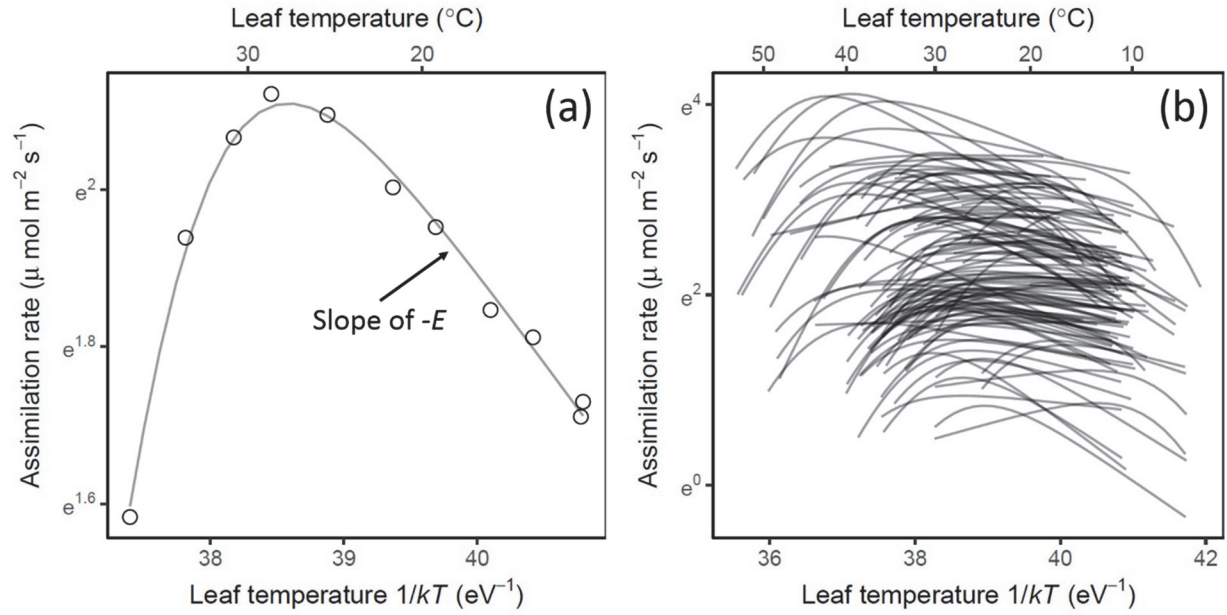
**Notes S1** R code for fitting the Sharpe-Schoolfield model (TPCfitting\_stm.R).



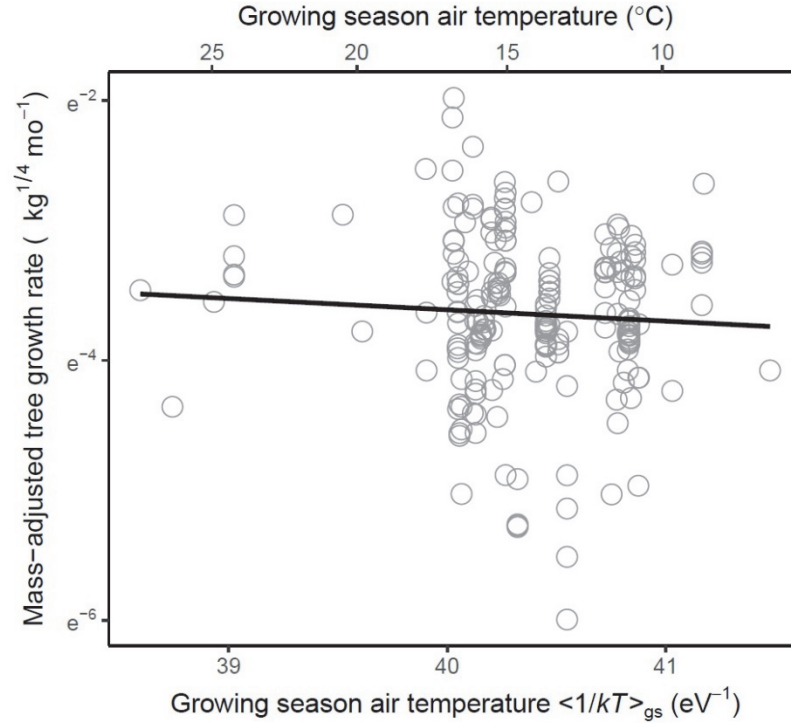
**Fig. S1** A typical temperature response curve for a biological rate. In general, biological rates  $B$  increase with temperature  $T$  to a maximum value  $B_{opt}$  at an optimal temperature  $T_{opt}$ , and then decrease with temperature above this optimum. The effective activation energy  $E$  and the enzyme inactivation parameter  $E_h$  (both nonlinear in this space) influence the increasing and decreasing portions of the curve, respectively, as formalized in Eqn (2). Data points are net photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) of *Juniperus monosperma* (Michaletz *et al.*, 2016b), and solid line is a fitted Sharpe-Schoolfield model (Eqn (2)).



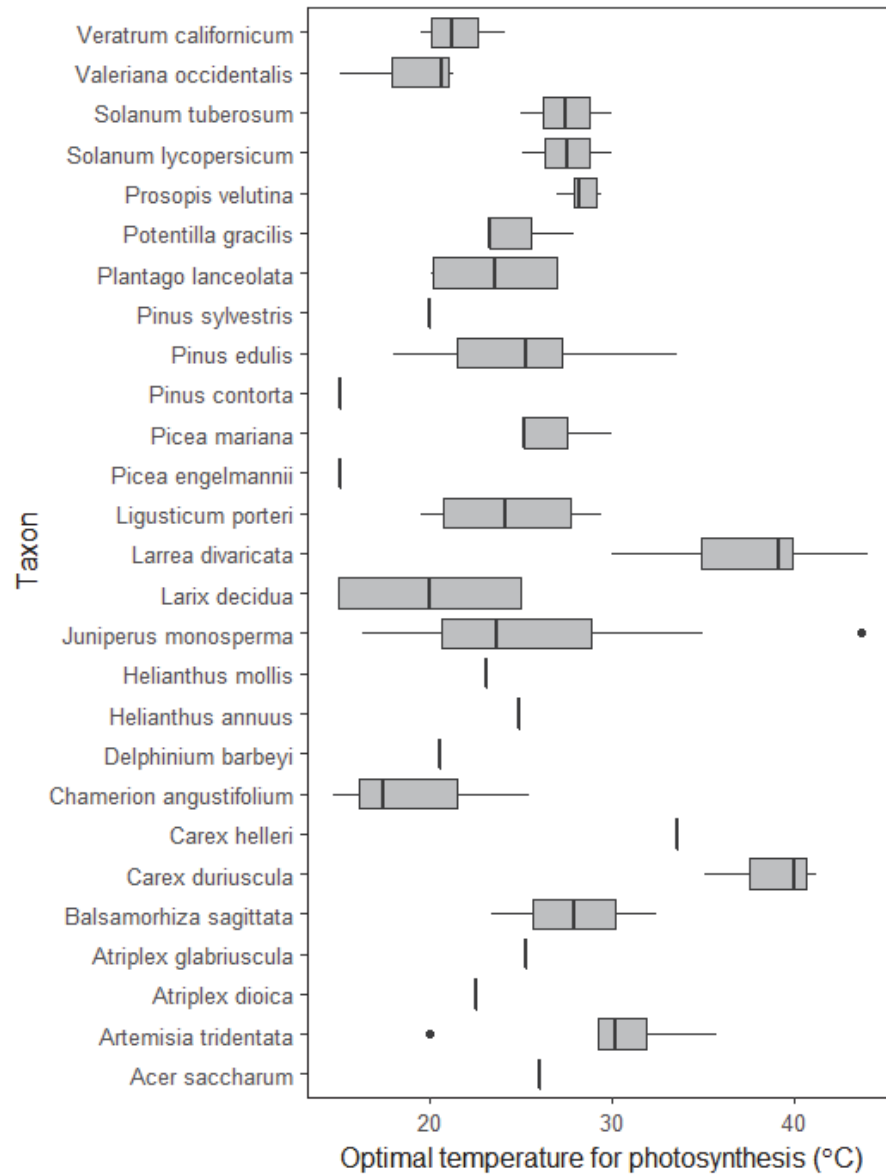
**Fig. S2** Modified Arrhenius plots of Sharpe-Schoolfield model (Eqn (2)) fits (with  $E_h$  as a free parameter) to photosynthesis temperature response data for (a) an individual *Juniperus monosperma* leaf cluster ( $E = 0.22$  eV, quasi  $r^2 = 0.996$ ) and (b) 119 leaves from 32 species ( $E = 0.03$  to  $3.06$  eV, quasi  $r^2 = 0.672$  to  $1.000$ ). Relationships are presented as modified Arrhenius plots that linearize assimilation rates relative to leaf temperature  $1/kT$ , yielding a linear slope of  $-E$  on the decreasing portion of the curve. Data used in analyses are described in Table S1.



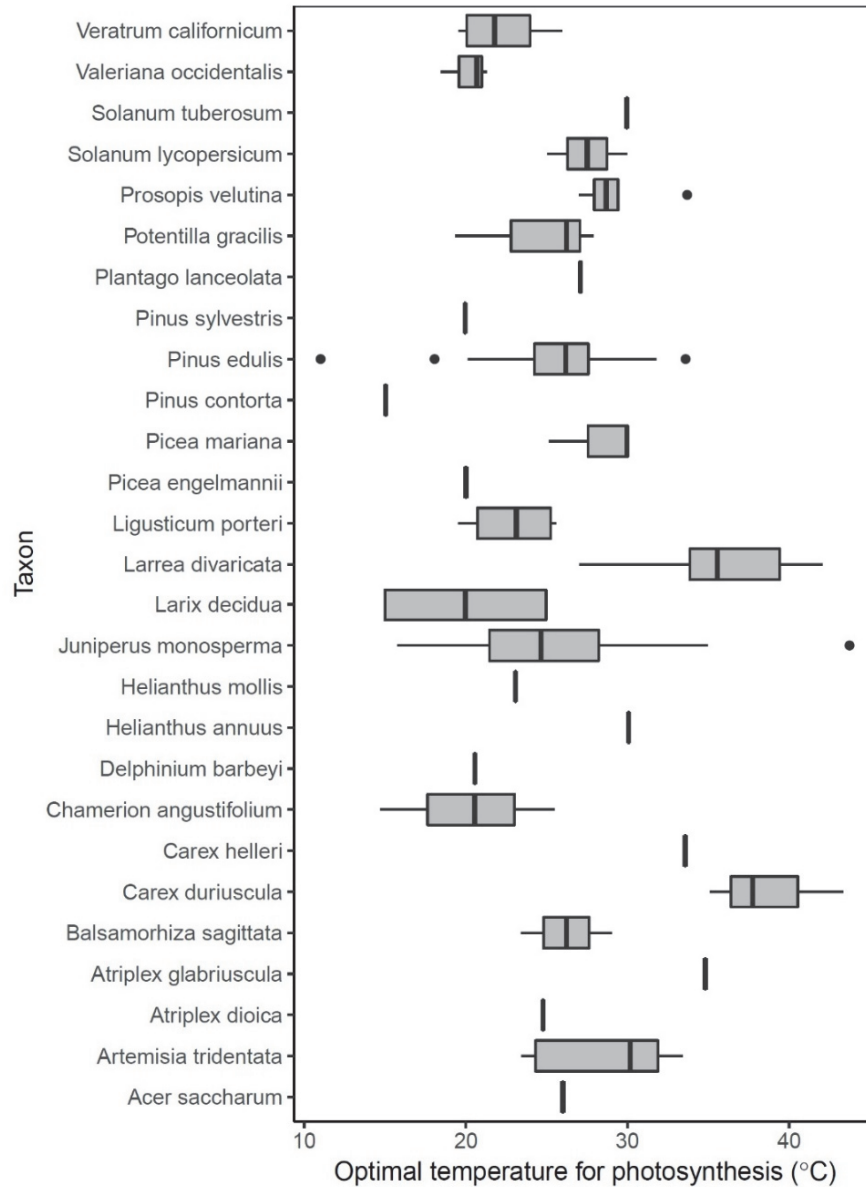
**Fig. S3** Modified Arrhenius plots of Sharpe-Schoolfield model (Eqn (2)) fits (with  $E_h$  as a fixed parameter) to photosynthesis temperature response data for (a) an individual *Juniperus monosperma* leaf cluster ( $E = 0.24$  eV, quasi  $r^2 = 0.993$ ) and (b) 119 leaves from 32 species ( $E = 1.98 \times 10^{-8}$  to  $2.07$  eV, quasi  $r^2 = 0.146$  to  $0.999$ ). Relationships are presented as modified Arrhenius plots that linearize assimilation rates relative to leaf temperature  $1/kT$ , yielding a linear slope of  $-E$  on the decreasing portion of the curve. Data used in analyses are described in Table S1.



**Fig. S4** Tree growth rates across a broad air temperature gradient ( $N = 210$ ). Data from Fig. 2b replotted with within-site measurements treated as independent samples rather than site means. The same general results are observed here and in Fig. 2b. Tree growth rate was invariant with air temperature ( $P = 0.373$ ,  $r^2 = 0.004$ ). The fitted  $E = 0.09$  has 95% CI = -0.11 to 0.28 that exclude hypothesized values of 0.32 eV (Allen *et al.*, 2005) and 0.65 eV for respiration (Gillooly *et al.*, 2001). This is a modified Arrhenius plot that linearizes the relationship between growth and temperature to yield a slope  $-E$  that is equal in magnitude but opposite in direction to the activation energy  $E$  (Eqns (1) and (S1)). Temperature is quantified as  $1/kT$  ( $\text{eV}^{-1}$ ), where  $k$  ( $8.617 \times 10^{-5} \text{ eV K}^{-1}$ ) is Boltzmann's constant and  $T$  (K) is air temperature. Tree growth rates are expressed as mass-adjusted rates,  $BM^{-3/4} = B_1 e^{-E/kT}$ . This relationship is obtained via rearrangement of  $B = B_1 M^{3/4} e^{-E/kT}$ , which is in turn obtained by unpacking the normalization constant  $B_0$  in Eqn (1) to reveal the influence of biomass  $M$ , where  $B_1$  is a biomass-independent normalization constant. Data from Enquist *et al.* (2007).



**Fig. S5** Distributions of intraspecific optimal temperatures for photosynthesis, estimated from Eqn (2) with  $E_h$  as a free parameter. Optimal temperatures for photosynthesis vary substantially within and among species, reflecting acclimation and local adaptation of photosynthetic traits to site-averaged leaf operating temperatures. The mean optimal temperature across all samples is 25.66 °C. Thick black lines correspond to medians, lower and upper hinges correspond to first and third quartiles, respectively, lower and upper whiskers correspond to smallest and largest values that do not exceed 1.5 times the interquartile range of the hinges, respectively, and points correspond to outliers beyond the end of the whiskers.



**Fig. S6** Distributions of intraspecific optimal temperatures for photosynthesis, estimated from Eqn (2) with  $E_h$  as a fixed parameter. Optimal temperatures for photosynthesis vary substantially within and among species, reflecting acclimation and local adaptation of photosynthetic traits to site-averaged leaf operating temperatures. The mean optimal temperature across all samples is 26.21 °C. Thick black lines correspond to medians, lower and upper hinges correspond to first and third quartiles, respectively, lower and upper whiskers correspond to smallest and largest values that do not exceed 1.5 times the interquartile range of the hinges, respectively, and points correspond to outliers beyond the end of the whiskers.



**Table S1** List of taxa, number of curves per taxon, and primary sources for photosynthesis temperature response data used in analyses

<b>Taxon</b>	<b>Number of curves</b>	<b>Primary source</b>
<i>Acer saccharum</i>	1	Gunderson <i>et al.</i> (2000)
<i>Artemisia tridentata</i>	5	Michaletz <i>et al.</i> (2016b)
<i>Atriplex dioica</i>	1	Sage <i>et al.</i> (2011)
<i>Atriplex glabriuscula</i>	1	Osmond <i>et al.</i> (1980)
<i>Balsamorhiza sagittata</i>	2	Michaletz <i>et al.</i> (2015)
<i>Carex duriuscula</i>	3	Monson <i>et al.</i> (1983)
<i>Carex helleri</i>	1	Sage <i>et al.</i> (2011)
<i>Chamerion angustifolium</i>	3	Michaletz <i>et al.</i> (2016b)
<i>Delphinium barbeyi</i>	1	Michaletz <i>et al.</i> (2016b)
<i>Helianthus annuus</i>	1	Paul <i>et al.</i> (1990)
<i>Helianthus mollis</i>	1	Zhou <i>et al.</i> (2007)
<i>Juniperus monosperma</i>	31	Michaletz <i>et al.</i> (2016b)
<i>Larix decidua</i>	4	Tranquillini <i>et al.</i> (1986)
<i>Larrea divaricata</i>	7	Mooney <i>et al.</i> (1978)
<i>Ligusticum porteri</i>	4	Michaletz <i>et al.</i> (2016b)
<i>Picea engelmannii</i>	1	Huxman <i>et al.</i> (2003)
<i>Picea mariana</i>	3	Way & Sage (2008a) (2008b)
<i>Pinus contorta</i>	1	Huxman <i>et al.</i> (2003)
<i>Pinus edulis</i>	21	Michaletz <i>et al.</i> (2016b)
<i>Pinus sylvestris</i>	1	Wang <i>et al.</i> (1996)
<i>Plantago lanceolata</i>	4	Atkin <i>et al.</i> (2006)
<i>Potentilla gracilis</i>	3	Michaletz <i>et al.</i> (2016b)
<i>Prosopis velutina</i>	6	Barron-Gafford <i>et al.</i> (2012)
<i>Solanum lycopersicum</i>	2	Yamori <i>et al.</i> (2010)
<i>Solanum tuberosum</i>	2	Yamori <i>et al.</i> (2010)
<i>Valeriana occidentalis</i>	3	Michaletz <i>et al.</i> (2016b)
<i>Veratrum californicum</i>	6	Michaletz <i>et al.</i> (2016b)

**Table S2** List of growth variables, temperature variables, sample sizes, and primary sources for growth analyses

Level of organization	Growth variable	Temperature variable	Sample size	Primary source
Organ	Root meristem cell doubling rate ( $\text{h}^{-1}$ )	Cell temperature ( $^{\circ}\text{C}$ )	60	Körner (2003a)
Individual	Mass-adjusted individual tree growth rate ( $\text{kg}^{1/4} \text{ mo}^{-1}$ )	Growing season air temperature ( $^{\circ}\text{C}$ )	210	Enquist <i>et al.</i> (2007)
Ecosystem	Adjusted net primary production ( $\text{kg m}^{-2} \text{ mo}^{-1}$ )	Growing season air temperature ( $^{\circ}\text{C}$ )	138	Michaletz <i>et al.</i> (2014; 2016a)

**Methods S1** Description of data and methods used for analyses.

***Photosynthesis temperature response data and Sharpe-Schoolfield fitting procedures***

Photosynthesis temperature response curves were obtained from Michaletz *et al.* (2016b). All curves were unimodal (e.g. see Fig. S1) and comprise data measured in Colorado and New Mexico, as well as compiled from the literature. Further details on measurement methodologies are available in the primary sources. A total of 184 curves from 32 species were available. Taxa, number of curves per taxa, and primary sources are summarized in Table S1. These temperature response data were used to estimate activation energies  $E$  for net photosynthesis.

Various approaches can be used to estimate activation energies  $E$  from unimodal temperature response data. For example, the Boltzmann-Arrhenius model (Eqn (1)) can be fit separately to the increasing and decreasing portions of the curve, yielding separate estimates of  $E$  for each portion (Knies & Kingsolver, 2010; Dell *et al.*, 2011). However, such estimates can be strongly biased by the temperature ranges used to define the increasing and decreasing portions of the curve (Knies & Kingsolver, 2010; Pawar *et al.*, 2016). Thus, in this paper, activation energies  $E$  for net photosynthesis were estimated using Sharpe-Schoolfield model fits (Sharpe & DeMichele, 1977; Schoolfield *et al.*, 1981). This approach can help reduce bias and variation in estimates of  $E$  as compared with the Boltzmann-Arrhenius approach described above (Pawar *et al.*, 2016). Following recent methodology, Eqn (2) was fit to curves for which photosynthesis was measured at a minimum of five temperatures spanning a range of at least 5 °C (Dell *et al.*, 2011; Pawar *et al.*, 2016), yielding a total of 119 fitted curves from 27 species (Figs S2, S3). Fitting was accomplished using Levenberg-Marquardt nonlinear regression with Gaussian random starting values, followed by AICc model selection from 100 fits for each curve. Model fitting was conducted in the statistical software R using a modified version of code provided by Tony Dell, Samraat Pawar, and Sofia Sal (see Notes S1).

Eqn (2) has been suggested to be over-parameterized for some photosynthesis datasets that are relatively limited in the number of observations or range of temperatures (Harley *et al.*, 1992; Dreyer *et al.*, 2001; Medlyn *et al.*, 2002). Thus, I also conducted a second set of Sharpe-Schoolfield model fits using a fixed value of  $E_h = 200 \text{ kJ mol}^{-1} = 2.073 \text{ eV}$ . This value has been used in many previous studies (Farquhar *et al.*, 1980; Medlyn *et al.*, 2002; Slot & Winter, 2017; Stinziano *et al.*, In press), and originates from data for  $J_{max}$  in *Hordeum vulgare* (Nolan & Smillie, 1976). However, estimates of  $E_h$  for  $J_{max}$  are available for other taxa (Dreyer *et al.*, 2001; Leuning, 2002; Warren & Dreyer, 2006; Galmés *et al.*, 2015), and these estimates show that of  $E_h$  varies more than 8-fold across taxa (Dreyer *et al.*, 2001). It is thus unclear how appropriate it is to apply a single fixed value of  $E_h$  for  $J_{max}$  from a single species to net photosynthesis data for diverse taxa (as in Table S1). Additionally, the data used here were all unimodal with a relatively large number of observations and range of temperatures (e.g. Figs S1-S3). It may be for these reasons that the Sharpe-Schoolfield model provided vastly better fits to data (Table S1) when  $E_h$  was taken as a free parameter (quasi  $r^2 = 0.672$  to 1.000) rather than a fixed parameter (quasi  $r^2 = 0.146$  to 0.999).

Perhaps a better alternative to a fixed  $E_h$  is to use a free  $E_h$  and reject fitted curves based on standard errors of estimates for each parameter (cf. Pawar *et al.*, 2016). Nonetheless, evaluation of Sharpe-Schoolfield fitting procedures is beyond the scope of this paper, and the above two approaches are presented in order to highlight the sensitivity of  $E$  to Sharpe-Schoolfield fitting procedures.

### ***Plant growth data and Boltzmann-Arrhenius fitting procedures***

Plant growth data were compiled and analyzed for three levels of biological organization: organs, individuals, and ecosystems. Root organ growth data (Fig. 2a) were obtained from Figure 3 of Körner (2003b), which is a compilation of data from approximately 50 primary sources. Data are division rates of root meristem cells. For land plants, root meristem cells provide one of the most accurate and resolved measures of *in situ* growth rates, for three reasons. First, rates of cell division are tightly coupled to rates of cell differentiation, when most

biomass growth occurs (Körner, 2003a; Körner, 2012). Second, root operative temperatures are in thermal equilibrium with soil, so they are relatively straightforward to control and quantify (unlike aboveground organs; Michaletz *et al.*, 2015; Michaletz *et al.*, 2016b). Third, cell size is essentially constant, which eliminates confounding effects of biomass. Data were extracted from Figure 3 using the software DataThief III v1.7. Data were given as cell doubling times (h), which were calculated as the statistical means across all cells within a meristematic region. The inverse of cell doubling times was used to calculate the cell growth rates ( $\text{h}^{-1}$ ) that were used in Fig. 2a.

Individual growth data (Fig. 2b) were obtained from Enquist *et al.* (2007). Data comprise mass-adjusted tree growth rates that control for variation in tree size and growing season length ( $\text{mo yr}^{-1}$ ), which is needed to properly evaluate temperature effects on plant metabolic kinetics (Michaletz *et al.*, In press). Growth rates correspond to total (above- plus belowground) biomass growth. Mass-adjusted rates  $BM^{-3/4}$  ( $\text{kg}^{1/4} \text{mo}^{-1}$ ) are given by  $BM^{-3/4} = B_1 e^{-E/kT}$  (Brown & Sibly, 2012; White *et al.*, 2012), where  $B$  ( $\text{kg mo}^{-1}$ ) is the seasonal growth rate (Michaletz *et al.*, In press),  $M$  (kg) is the total tree biomass, and the 3/4 scaling exponent is based on extensive empirical and theoretical support (Brown & Sibly, 2012). Since multiple growth rate data were available for some sites in this dataset, they were taken as the mean  $\pm 1$  standard error in Fig. 2b (although the same general results were obtained when these were treated as independent samples; Fig. S4). Air temperature data are based on monthly average air temperatures during the growing season (including day and night). Growing season air temperature is the monthly average air temperature during the growing season months (including day and night). Data were calculated from site latitude and longitude and a gridded global climate dataset (New *et al.*, 2002). This data set interpolates weather station data, so these temperatures correspond to weather station standards and not plant operative temperatures. Growing season months were estimated from air temperature, precipitation, and potential evapotranspiration data as described in Kerkhoff *et al.* (2005).

Ecosystem production data (Fig. 2c) were obtained from Michaletz *et al.* (2016a), which is a subset of data compiled by Michaletz *et al.* (2014). Data are monthly net primary production (NPP;  $\text{kg m}^{-2} \text{ mo}^{-1}$ ) rates calculated over the growing season ( $\text{mo yr}^{-1}$ ). Fig. 2c is a partial regression plot that shows the correct relationship (slope and variance) between net primary production and temperature while controlling for the influence of biomass, age, and precipitation. In this analysis, samples from the same latitude and longitude that share temperature and precipitation data all have unique data for age and/or stand biomass, and are thus treated as independent samples. Air temperature data are based on monthly average air temperatures during the growing season (including day and night). Growing season air temperature is the monthly average air temperature during the growing season months (including day and night). Data were calculated from site latitude and longitude and a gridded global climate dataset (New *et al.*, 2002). This data set interpolates weather station data, so these temperatures correspond to standard weather station measurements and not plant operative temperatures. Growing season months were estimated from air temperature, precipitation, and potential evapotranspiration data as described in Michaletz *et al.* (2014).

Since organ, individual, and ecosystem-level growth data correspond to temperatures below those optimal for plant metabolism (Figs S5, S6; Dell *et al.*, 2011; Slot & Winter, 2017), activation energies  $E$  were estimated using Boltzmann-Arrhenius model fits. Specifically, Eqn (1) was  $\log_e$ -transformed to give the growth rate  $B$  as

$$\ln(B) = \ln(B_0) - E \frac{1}{kT} \quad (\text{S1})$$

where  $B_0$  is a normalization constant that implicitly includes effects of other variables not considered here,  $k$  is the Boltzmann constant ( $8.617 \times 10^{-5} \text{ eV K}^{-1}$ ), and  $E$  (eV) is an effective activation energy that characterizes the temperature-dependence of the rate under consideration. Note that here, the units of  $B$  and  $B_0$  will vary depending on the growth rate under consideration ( $\text{h}^{-1}$  for cells,  $\text{kg}^{1/4} \text{ mo}^{-1}$  for individuals, and  $\text{kg m}^{-2} \text{ mo}^{-1}$  for ecosystems). These  $\log_e$ -scaled growth data were then regressed over temperature  $1/kT$ , to produce modified Arrhenius plots (Fig. 2) with a slope  $-E$  that is equal in magnitude but opposite in direction to the activation energy  $E$ .

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