Received: 28 March 2020 | Accepted: 30 June 2020

DOI: 10.1111/1365-2435.13643

RESEARCH ARTICLE

Functional Ecology

Low predictability of energy balance traits and leaf temperature metrics in desert, montane and alpine plant communities

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Funding information
Natural Environment Research Council, Grant/Award Number: NE/M019160/1; Norges Forskningsråd, Grant/Award Number: KLIMAFORSK 250233; National Science Foundation, Grant/Award Number: DBI-1262713; Los Alamos National Laboratory, Grant/Award Number: Director's Fellowship

Handling Editor: Carlos Perez Carmona

Abstract

1. Leaf energy balance may influence plant performance and community composition. While biophysical theory can link leaf energy balance to many traits and environment variables, predicting leaf temperature and key driver traits with incomplete parameterizations remains challenging. Predicting thermal offsets (δ, $T_{leaf} - T_{air}$ difference) or thermal coupling strengths (β, T_{leaf} vs. T_{air} slope) is challenging.
2. We ask: (a) whether environmental gradients predict variation in energy balance traits (absorptance, leaf angle, stomatal distribution, maximum stomatal conductance, leaf area, leaf height); (b) whether commonly measured leaf functional traits (dry matter content, mass per area, nitrogen fraction, $\delta^{13}C$, height above ground) predict energy balance traits; and (c) how traits and environmental variables predict δ and β among species.
3. We address these questions with diurnal measurements of 41 species co-occurring along a 1,100 m elevation gradient spanning desert to alpine biomes. We show that (a) energy balance traits are only weakly associated with environmental gradients and (b) are not well predicted by common functional traits. We also show that (c) δ and β can be partially approximated using interactions among site environment and traits, with a much larger role for environment than traits. The heterogeneity in leaf temperature metrics and energy balance traits challenges larger-scale predictive models of plant performance under environmental change.

KEYWORDS

elevation gradient, energy balance, leaf functional trait, leaf temperature, subalpine, thermal ecology

1 | INTRODUCTION

Leaf temperature (T_{leaf}) plays a key role in plant performance (Gates, 1980; Jones, 2014; Monteith & Unsworth, 2007). There has been long-term interest in accurately predicting variation in T_{leaf}, as well as in identifying the drivers of variation in T_{leaf} (either environmental or trait variables; e.g. Blonder & Michaletz, 2018; Gates, 1968; Leuzinger & Körner, 2007; Linacre, 1972). Predicting T_{leaf} across environmental gradients is critical for accurately modelling plant stress (e.g. in croplands, or in studies of drought and heat waves; Jackson, Idso, Reginato, & Pinter, 1981), as well as for modelling photosynthetic rates (Farquhar & Von Caemmerer, 1982) and transpiration rates (Drake et al., 2018). Ultimately, if environmental filtering occurs (i.e. selection based on T_{leaf}-dependent performance), variation in T_{leaf} could influence the traits of species and the structure of communities across environmental gradients (Doughty & Goulden, 2008; Doughty et al., 2018; Jackson, Idso, & Otterman, 1975).

T_{leaf} can be coupled to the air temperature (T_{air}; Grace, 1988), but often diverges. This divergence can be summarized in terms of two temperature metrics: first, a 'thermal offset':

$$\delta = T_{leaf} - T_{air}, \tag{1}$$

which describes the magnitude of the difference between leaf and air temperature; and second, a 'thermal coupling strength':

$$\beta = \partial T_{leaf}/\partial T_{air}, \tag{2}$$

which describes the slope of the relationship between T_{leaf} and T_{air} as both vary over time. Many empirical studies have shown that these temperature metrics vary widely in nature (Dong, Prentice, Harrison, Song, & Zhang, 2017; Gates, Hiesey, Milner, & Nobs, 1964; Linacre, 1967; Michaletz et al., 2016; Upchurch & Mahan, 1988; Yu et al., 2015). For example, thermal offsets may exceed ±15°C in deserts, tropical forests or the alpine, while thermal coupling strengths may vary from <1 (limited homeostasis) to >1 (megathermy) across biomes (Blonder & Michaletz, 2018; Michaletz et al., 2016).

Energy balance theory provides a process-based framework for understanding the drivers of thermal offsets (δ) and thermal coupling strengths (Gates, 1980; Jones, 2014). The energy budget of a leaf can be written following Monteith and Unsworth (2007) in terms of a large number of parameters. Several are constants (σ, Stefan-Boltzmann constant; ρ, mass density of air; γ, psychrometer constant; c_p, specific heat capacity of air). Others relate to leaf traits (ε, emissivity; α_s, absorptance; r_H, convective resistance; g_S, stomatal conductance; n, stomatal distribution), and others relate to the environment (T_{air}; h, relative humidity; e_S, vapour pressure; R_l, net longwave radiation, R_s, net shortwave radiation). The convective resistance parameter in turn depends on leaf width, wind speed and overall canopy exposure of the leaf, which may in turn be driven by other traits relating to branching architecture and canopy structure (Schuepp, 1993). Similarly, some of these traits (e.g. stomatal conductance) may in turn depend on other environmental variables, e.g. soil water availability (Gollan et al., 1986).

The thermal coupling strength can be rewritten in terms of the derivatives (with respect to time) of T_{leaf} and T_{air}. This formulation is useful because the transient temporal dynamics of T_{leaf} can also be approximated as Michaletz et al. (2015) in terms of a leaf's 'thermal time constant'. This formulation is useful, as it in turn depends on a range of other traits: φ (dimensionless) is the ratio of projected-to-total leaf area, LMA is the leaf mass per area, LDMC is the leaf dry matter content, $c_{p,d}$ is the specific heat capacity of dry leaf matter, $c_{p,w}$ is the specific heat capacity of water and η is a heat transfer coefficient.

Prior studies have primarily focused on directly testing energy balance theory predictions, summarizing variation in leaf temperature metrics or examining variation in individual parameters of this theory. It is well established that parameterized energy balance theory can successfully predict leaf temperatures (Field, Chiariello, & Williams, 1982; Leuning et al., 1989). Many authors have documented spatial and temporal variation in leaf temperatures, e.g. Gates (1980); Doughty and Goulden (2008) among many others, and these have been compiled into large datasets (Michaletz et al., 2016). Others have documented how trait-related energy balance parameters vary across environmental gradients (Ehleringer, 1988; Körner, Allison, & Hilscher, 1983; McDowell, White, & Pockman, 2008; Wright et al., 2017).

There is an opportunity to better integrate these biophysical, highly focused approaches with a comparative approach drawn from functional ecology (McGill, Enquist, Weiher, & Westoby, 2006), which would be more able to address knowledge gaps around trait integration, community-scale responses and drivers of these responses. We seek to determine whether easy-to-measure traits are good proxies for much harder-to-measure traits that are in turn much more tightly related to plant performance, how this relationship might vary across environmental conditions, and whether any of these variables improve our ability to empirically predict these δ and β metrics. We therefore address three interlinked questions.

First, we ask whether environmental gradients predict variation in energy balance traits. This question is motivated by the observation that many common functional traits vary strongly along environmental gradients (possibly due to environmental filtering and links to performance; Bruelheide et al., 2018). Given the links between leaf temperature and performance, we hypothesized that energy balance traits would be filtered across environments.

Second, we ask whether commonly measured functional traits (LDMC, LMA, nitrogen fraction, $\delta^{13}C$, height) can predict (i.e. are correlated with) energy balance traits (absorptance, leaf angle, stomatal distribution, stomatal conductance, leaf width, canopy exposure). We hypothesized such a linkage, as recent studies have demonstrated linkages between energy balance traits and functional traits, potentially supporting coordination along the well-known fast–slow continuum of leaf and plant economics (Reich, 2014). For example, stomatal conductance model parameters have been linked to LMA (Wu et al., 2020) and other stoichiometric traits (Hasper et al., 2017;

Kröber, Plath, Heklau, & Bruelheide, 2015), while stomatal ratio has been linked to growth form (Muir, 2018). Strong relationships have been identified between leaf size and angle and photosynthetic rates (Falster & Westoby, 2003), and various relationships have been found between leaf economic traits and leaf albedo (Bartlett, Ollinger, Hollinger, Wicklein, & Richardson, 2011; Ollinger et al., 2008). Additionally, this question is motivated by the potential utility of using simple and widely collected traits as proxies for energy balance traits that require more time and effort to collect (McGill et al., 2006).

Third, we integrate these results to ask whether common functional traits, energy balance traits and/or site-level environment time series are sufficient to predict leaf thermal offsets (δ) and thermal coupling strengths (β). This question allows us to determine whether traits or environment or interactions among them are most important predictors, with prior studies suggesting that environmental variation is the primary driver of leaf temperature variation (Leuzinger & Körner, 2007). This question is motivated by the observation that it would be difficult to directly measure the complete set of these trait and environment variables over time, then directly parameterize energy balance equations: doing so would require intensive measurement efforts at a single time point. The alternative approach that we explored here is to approximate δ and β via low-order series expansion, which is equivalent to carrying out a regression model. We hypothesized that inclusion of a large number of traits and environment variables in a model would yield high predictability of δ and β.

To address these questions, we measured functional traits, energy balance traits, site environment and leaf temperature metrics for a large number of dominant species at sites spanning desert to alpine biomes, over diurnal periods. Answering these questions may improve our empirical ability to predict leaf temperature metrics across environmental gradients.

2 | MATERIALS AND METHODS

2.1 | Site selection

In June and July 2016, we set up seven vegetation plots across six sites spanning an elevation gradient in the Washington Gulch and East River drainages of southwestern Colorado (USA). Sites were chosen to cover all major biomes occurring along this elevation gradient, i.e. from scrubland at the lowest elevation to screefield at the highest elevation. Details of site locations and vegetation are provided in Table 1 and shown as a map in Figure S1. At these sites, elevation is strongly correlated ($|\rho| > 0.95$) with mean maximum temperature of June, July and August (PRISM data; Daly, Taylor, & Gibson, 1997), mean precipitation of June, July and August (PRISM data) and aridity index (CGIAR *Global-Aridity* data; Zomer, Trabucco, Bossio, & Verchot, 2008; Figure S2), with the lowest sites being hottest and driest. Each plot was chosen to include representative vegetation of the site. Plots included herbs, forbs and/or shrubs, but no trees, with bare ground common at the lowest and highest elevations. Plots were 4 m^2 in area, situated on flat or slightly south-facing terrain in open areas and demarcated using stakes and aluminum squares.

2.2 | Thermal imagery

At each site, we chose a single day during the summer growing season for diurnal measurements of T_{leaf} (except at the high-diversity Pfeiler site, which was visited twice at locations separated by ~5 m to capture different species; dates provided in Table 1). Weather conditions ranged from sunny to overcast within and across days and did not include significant rain. Before sunrise, we positioned an infrared camera (A615, FLIR, coupled to a 13 mm lens with 45° field of view) above the plot. The camera was oriented with the sensor and lens facing down to capture orthographic imagery. The camera was attached to a ball-head camera mount on a wooden beam, which was suspended at ~2 m height between two aluminum ladders (Figure S3). To limit radiative heating, the camera was placed in a ventilated radiation shield built from reflective Mylar plastic. A Linux computer (Odroid, C2) was used to control the camera (Figure S4). Code is available (Blonder, 2020a) and is described in Supporting Information Text S2. The camera was configured for 16-bit radiometric output at 640 × 480 pixel resolution, yielding images with spatial resolution of approximately 3–4 pixels/cm. Conversion of photon fluxes to temperatures was achieved assuming that the emissivity of vegetation was 0.97 (Supporting Information Text S1).

TABLE 1 Summary of sites and leaf sampling

Site	Latitude (°)	Longitude (°)	Elevation (m)	Vegetation type	Date of measurement	# of species (# of leaves) measured
Almont	38.655077	−106.862304	2,453	High desert/scrubland	15 July 2016	4 (19)
CBT	38.881809	−106.980003	2,703	Riparian meadow	20 June 2016	10 (61)
Road	38.897010	−106.978678	2,818	Dry meadow	24 June 2016	7 (42)
Pfeiler-1	38.961132	−107.031231	3,180	Moist meadow	28 June 2016	6 (38)
Pfeiler-2	38.961132	−107.031231	3,180	Moist meadow	8 July 2016	7 (40)
Painter Boy	38.969596	−107.040755	3,351	Subalpine meadow	3 July 2016	7 (39)
Baldy	38.978435	−107.041704	3,540	Alpine screefield	29 July 2016	6 (28)

Thermal imagery was captured at 5-s intervals, with a non-uniformity correction every 25 frames. Data were collected from local sunrise to local sunset. In a few isolated cases, there were 10–30-min gaps in the data caused by needing to temporarily power down the system to switch batteries (most sites), removal of the system during lightning at the Road site, or wind gusts at the Baldy site. After each incident, the camera was re-aligned to its previous field of view. Variation in camera perspective was corrected using image stabilization and transformation methods (see Supporting Information Text S1).

We also made simultaneous ground-truth temperature measurements in each thermal image frame for calibration purposes. We measured the temperature of a 2 cm^2 piece of black duct tape (with high emissivity, i.e. a good blackbody proxy) at 5-min intervals. These temperature measurements were made using a 0.13 mm diameter Type K thermocouple (Omega, 5SRTC-TT-K-24-36) placed under the tape, and connected to a digital thermometer (Omega, HH147U). The tape was placed next to a star-shaped piece of cardboard covered in aluminum foil. This foil has low emissivity relative to leaf tissue, and thus appears with low temperature in thermal imagery. As such, the foil enabled identification of the tape square in each image frame.

2.3 | Site environment

We also obtained site-level free-atmosphere environmental data from paired weather stations near each site. Data included air temperature, photosynthetic photon flux density (a proxy for light/ net solar radiation), wind speed, and relative humidity, and were recorded at 10-min intervals. All weather stations reported air temperature, but some stations were missing observations for other sensors. Details and distances to weather stations are reported in Table S1. Because of the spatial decoupling, transient effects from passing clouds are only partially captured by the weather stations.

We were unable to distinguish site differences from date differences because each site was only sampled once, and on a different day than other sites. The impact of this conflation is likely minimal as the site environment varied extensively within the day at each site, enabling regression of leaf temperature metrics against a wide range of site environment values. The use of site environment data from nearby weather stations may have led to some scale mismatches in data, e.g. if open-clearing wind speeds reported by the station did not correspond to wind speeds observed at ground-level for individual leaves, or if weather station light level did not match leaf-level shading induced by canopy structure.

2.4 | Site composition

Immediately before or after thermal data collection during diffusely illuminated conditions, we obtained a high-resolution photograph of each site. These images were taken in order to be able to co-register thermal and visible data for later identification of objects (e.g. leaves) within each set of thermal imagery. A DSLR camera (6D, Canon, with 17–40 mm f/4L lens set to 17 mm focal length) was placed on the same ladder/beam apparatus used for the thermal camera, and used to obtain an orthographic image of each site. A metre stick was placed in each of these images for scale calibration. Images had a spatial resolution of approximately 30–40 pixels/cm.

2.5 | Trait measurements

On the day following collection of thermal imagery, we revisited each site and selected a subset of species that were common at each site based on a visual assessment of cover, which is reliable for dominant species (Kennedy & Addison, 1987; Sykes, Horrill, & Mountford, 1983). We typically measured three leaves per individual of three individuals per species, for 4–10 species per site. Individuals were chosen at random; leaves were selected at random from those visible in the upper canopy. Sample sizes are given in Table 1. Species were identified via voucher specimens (Rocky Mountain Biological Laboratory herbarium) and via comparison to data from nearby long-term plots. To uniquely identify each leaf, we obtained another high-resolution photograph of the site via the same ladder + DSLR method described above, also using a narrow stick pointing to the leaf of interest. After field collection, each leaf was stored with a moist paper towel in a plastic bag in a cooler for no more than 3–4 hr prior to analysis.

2.6 | Energy balance traits

During mid-morning conditions under similar vapour pressure deficits and light conditions, we measured leaf stomatal conductance (mmol m^{-2} s^{-1}) using a steady-state porometer (LI-COR, LI-1600M). The measured values are meant to provide a one-time proxy for maximum stomatal conductance rather than a time series record. We ensured that all leaf surfaces were completely dry prior to measurement. For leaves that filled the porometer chamber area, measurements were obtained on the abaxial side of each leaf. For leaves that did not fill the chamber area, we measured the actual leaf area inside the chamber and performed an area correction of instrument-reported values (see below) using the one- and two-sided areas for hypostomatous and amphistomatous leaves respectively. One- and two-sided area correction is necessary in order to obtain the most accurate estimate of conductance per unit area (e.g. without correction, readings for amphistomatous leaves would be twice as high as the actual value since both sides of the leaf are exposed to the chamber air and sensor). Since the LI-1600M outputs a total leaf conductance comprising stomatal and boundary layer conductance in series, estimates of stomatal conductance require subtraction of the boundary layer conductance. To

accomplish both area correction and boundary layer subtraction, we used Eq. 4.3 from the user manual, which gives the true conductance C (mmol m^{-2} s^{-1}) as:

$$C = \frac{1}{\left(\frac{1}{C_r}\right)\left(\frac{A_c}{A}\right) - R_b\left(\frac{8.314 \times 10^{-4}(T)}{P}\right)},$$

where C_r (mmol m^{-2} s^{-1}) is the instrument-reported total leaf conductance, A_c (cm^2) is the leaf area in the chamber, A (4 cm^2) is the leaf area entered into the instrument, R_b (0.15 s/cm) is the boundary layer resistance given in the user manual for a typical broadleaf subjected to the fan-driven wind environment of the instrument's cuvette, T (293 K) is the cuvette temperature and P (kPa) is the atmospheric pressure calculated as a function of site elevation (assuming a sea-level pressure of 101.325 kPa, temperature of 288.15 K, lapse rate of 0.0065 K/m and a molar mass of air of 0.0289644 kg/mol). The instrument was calibrated 2 years prior to our measurements.

We also estimated the canopy exposure of the leaf. We scored each leaf has having a low, medium or high value (<2, <10 or >10 cm protrusion beyond the approximate upper canopy layer of the site). We calculated leaf width (cm) as the maximum breadth of the leaf. In the case of compound or highly lobed leaves, we measured the width of a leaflet or leaflet lobe when leaflets were highly dissected. These two variables together provided a partial proxy for the leaf boundary layer.

We also measured the leaf angle from horizontal (degrees) with a protractor. We used the midvein orientation to determine leaf orientation.

We measured leaf absorptance (dimensionless) using a field spectroradiometer (ASD, FieldSpec HandHeld 2). The instrument was calibrated against white and black references before usage. Spectral reflectance (R) was measured from 325 to 1,075 nm over three replicates per leaf. We then estimated transmittance (T) at each wavelength from 400 to 2,500 nm via inversion of the PROSPECT-5B radiative transfer model (Feret et al., 2008; Jacquemoud & Baret, 1990; Wu et al., 2018) after optimization to correspond with the reflectance data from 400 to 1,075 nm. We used the PROSPECT-5B default values for all six structural and biochemical parameters. Estimates of T from PROSPECT inversion have been shown to strongly agree with values measured using an integrating sphere (Shiklomanov, Dietze, Viskari, Townsend, & Serbin, 2016; Wu et al., 2018). We then calculated spectral absorptance as the mean value of $1 - T - R$, across the spectral band 400–2,500 nm. We then identified unrealistic absorptance spectra using a hierarchical clustering analysis, calculating dissimilarities among spectra using Manhattan distance, then removing all spectra in a single cluster corresponding to files with unrealistic near infrared absorptance. We retained 715/757 spectra. We then averaged absorptance values across all wavelengths and then across three spectral replicates to obtain a final leaf-level estimate.

We next measured stomatal distribution (dimensionless) via a stomatal peel (clear nail polish) of the abaxial and adaxial side of the leaf. We imaged each peel using a brightfield microscope (Leica, DM750) at 40× magnification. We scored a leaf as hypostomatous if only the abaxial side showed guard cells, and amphistomatous if the abaxial and adaxial side showed guard cells.

2.6.1 | Functional traits

For the same sampling scheme and leaves as described above, we also measured several functional traits. We measured the height of the leaf above the ground with a metre stick (cm). We used the location of petiole attachment to the stem as the point of measurement.

We calculated leaf mass per area (dry mass divided by fresh area; g/m^2) and leaf dry matter content (dry mass divided by fresh mass; dimensionless). We first measured fresh leaf area (cm^2) with a flatbed scanner (Canon, LiDE 220) at 300 pixels per inch resolution, and fresh leaf mass (g) using a digital balance, then dry mass (g) after drying the leaf sample at 60°C for at least 72 hr. Petioles were removed before analysis. For compound leaves, all leaflets and the rachis were included in the measurement.

We then measured leaf nitrogen content (%) as a proxy of photosynthetic capacity, and δ^{13}C as a proxy of water use efficiency, both from dried leaf tissue. We flash froze dried leaf samples in liquid nitrogen and ground them to fine powder with a mortar and pestle. We sent samples for elemental analysis at the University of California at Davis' Stable Isotope Facility. Measurements were made using an elemental analyzer (Sercon, PDZ Europa ANCA-GSL) interfaced to an isotope ratio mass spectrometer (Sercon, PDZ Europa 20-20). Values of δ^{13}C are expressed relative to international standard VPDB (Vienna PeeDee Belemnite).

2.7 | Thermal image analysis

We used the thermal image datasets to construct temperature time series for each leaf identified in the trait measurements. Details of this process are explained in Supporting Information Text S1. Code is available (Blonder, 2020b) and comes with a full usage guide in Supporting Information Text S2.

2.8 | Statistical analysis

Question 1—To assess coordination of leaf energy balance traits along environmental gradients, we built a linear mixed model using elevation as a fixed effect, and with site as a random intercept. High collinearity between elevation, temperature and precipitation in these montane valleys (Figure S2) precluded use of multiple climate variables for the analysis. Predictor and response variables were scaled and centred prior to analysis. We estimated the effect strength as the coefficient estimate for the elevation predictor (in *SD*/*SD*).

Question 2—To assess variation in energy balance traits relative to common functional traits, we conducted a principal components analysis. A matrix was created treating each leaf as a sample, with

columns for each trait. Stomatal distribution was treated as a continuous variable (with integer codes) to include it in the analysis. All axes were scaled and centered before analysis. We then reported the loadings for the leading axes as a metric of correlation among traits. To formally determine whether common functional traits predict energy balance traits, we also used the above matrix in a multiple linear regression to predict each energy balance trait using all common functional traits. The performance of each model was summarized as its root mean square error.

Question 3—To determine the drivers of leaf temperature metrics, we built linear mixed models in which β and δ were treated as the dependent variable. The model of δ used the time series data for $T_{leaf} - T_{air}$ at its original resolution. The model of β used data aggregated by mean value within 30-min intervals over the duration of the measurements, in order to estimate β as the slope of a $T_{leaf} - T_{air}$ regression at leaf level. Fixed effect predictors for each model included site environment variables (air temperature, wind speed, light and relative humidity) averaged within each temporal bin, and all energy balance and functional trait variables. Interactions between the environment and the trait variables were included. Random effects for each model included nested intercepts for species and site. Individual-level random intercepts were not included as some traits were measured only at species level, and thus had no individual-scale variance. Each response variable and fixed effect predictor was scaled and centred prior to analysis. Response variables were further sign-sqrt transformed as $x \mapsto \frac{x}{|x|}\sqrt{|x|}$ to improve normality of model residuals. We inferred a significant fixed effect if the 95% confidence interval excluded zero, and estimated the strength of the effect as the coefficient estimate (*SD*/*SD*). We estimated the variance explained by the random and fixed effects using a pseudo-R^2 (Nakagawa & Schielzeth, 2013). We then repeated the analysis for trait-only, environment-only and trait + environment (i.e. no interaction term) models, and reported the AIC and pseudo-R^2 for each model.

All statistical analyses were conducted in R (version 3.5.1). Data were pre-processed using the LUBRIDATE, DPLYR and DATA.TABLE packages. Models were analysed using the LME4, SJPLOT and MUMIN packages.

3 | RESULTS

We obtained trait measurements for 267 leaves of 41 species across seven sites spanning 1,060 m of elevation (Figure S1). The dataset includes 1,532,364 T_{leaf} measurements of the same leaves. Photographs of each site are shown in Figure 1. Thermal videos for each site are provided in Supporting Information File S3.

3.1 | Question 1: Environment predictors of energy balance traits

Some traits varied with elevation, our integrative proxy for site environment (Figure 2). There were significant relationships between elevation and several traits (with standardized effects in *SD*/*SD* with absolute magnitudes ≥ 0.2 and confidence intervals not including zero). For common functional traits, these relationships included leaf dry matter content (−0.49), leaf mass per area (−0.39), $\delta^{13}C$ (+0.48) and nitrogen fraction (+0.49). There were no strong effects for energy balance traits, though there were some weaker but significant effects for absorptance (−0.18), leaf angle (−0.18), stomatal distribution (−0.13) and leaf width (0.15).

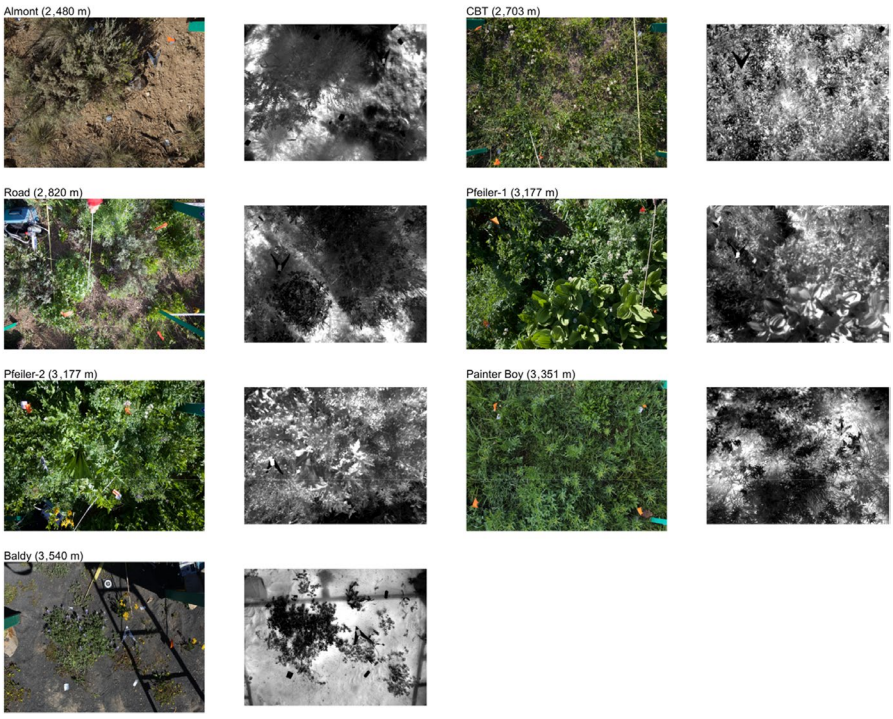

FIGURE 1 Example images of plots, arranged by site elevation. Left panels show visible images; right, selected thermal images (time of day in example visible and thermal images may differ). Thermal videos for each plot are available in Supporting Information

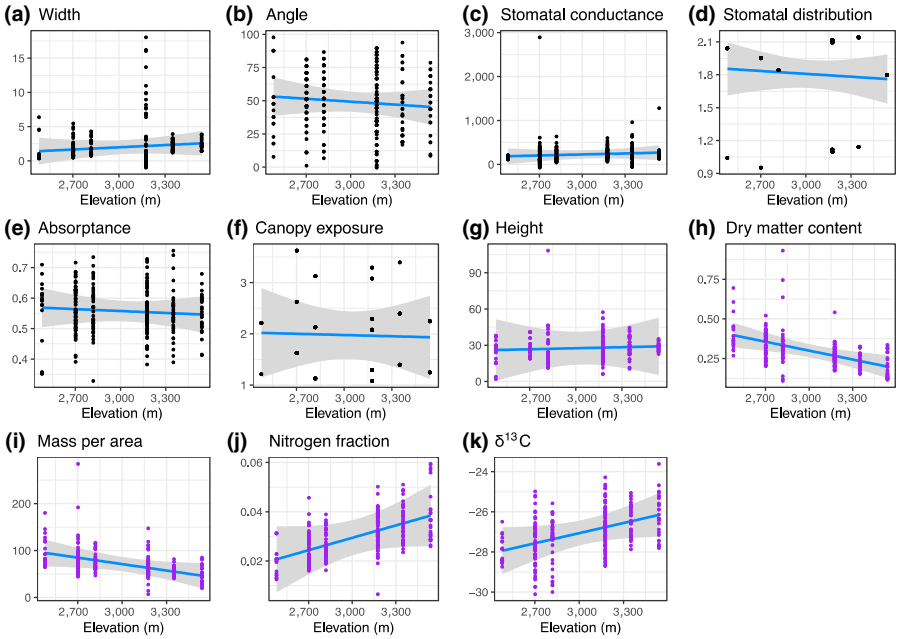

FIGURE 2 Trait–elevation relationships. Panels indicate partial effects plots (no random effects) of the elevation fixed effect in a linear mixed model with site nested random intercept. Energy balance traits are shown in black; common functional traits in purple. Dots indicate individual leaves for all sites and species. Units for traits are given in Section 2

3.2 | Question 2: Relationship between energy balance and common functional traits

The energy balance and common functional traits showed limited covariation across species, reflecting a diversity of possible ecological strategies (Figure 3). In a principal component analysis, the first component explained 29.6% of the variation, and the second component explained 14.4% of the variation. Eight components were required to explain 90% of the variation.

The first axis had strongest loadings (absolute values ≥ 0.2) for leaf width (+0.20), stomatal distribution (−0.26), absorptance (−0.31), height (+0.38), dry matter content (−0.33), mass per area (−0.33), nitrogen fraction (+0.47) and $\delta^{13}C$ (+0.39). The second axis had strongest loadings for leaf width (+0.20), stomatal conductance (−0.33), canopy exposure (+0.61), height (+0.37), leaf dry matter content (+0.27), leaf mass per area (+0.40) and $\delta^{13}C$ (+0.32).

The common functional traits had limited ability to predict the energy balance traits. In multiple linear regressions, models for each energy balance trait had low R^2 values: between a minimum of 0.04 (for stomatal conductance, $p = 0.08$) and a maximum of 0.20 (for canopy exposure, $p < 10^{-9}$; Figure S5).

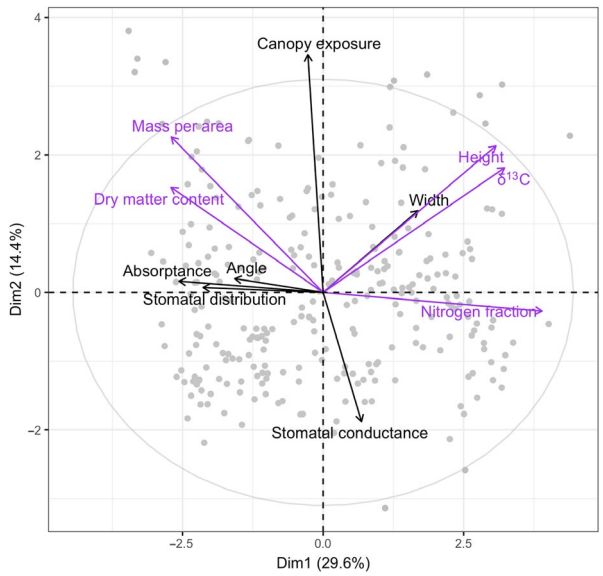

FIGURE 3 Principal component analysis of traits. Axes are for the first two principal components. Energy balance traits are shown in black; common functional traits in purple. Grey dots indicate individual leaves for all sites and species

3.3 | Question 3: Trait and environment drivers of leaf temperature metrics

Across all leaves and time points, mean T_{leaf} values within sites varied from a minimum of 14.6°C at Painter Boy to a maximum of 32.7°C at Almont (Table 2; Figure S6). Because sites at each elevation were measured on days with different weather conditions, the large differences within sites are more relevant than between sites. Standard deviations of T_{leaf} across time within sites varied from a minimum of 5.1 K at Painter Boy to a maximum of 12.1 K at Almont, reflecting strong temporal variation in T_{leaf} among leaves. There also was extensive spatial variation in T_{leaf} among leaves at a single time point. The mean standard deviation of T_{leaf} across all times within sites was 3.5 K. Across all sites and leaves, approximately 6.7% of T_{leaf} values were greater than 40°C and 2.2% were greater than 45°C.

The leaf thermal coupling strength, β, showed high levels of variation (Table 2; Figure 4a). Overall, leaves exhibited limited homeostasis ($\beta < 1$) at all sites except for Almont, where leaves exhibited megathermy ($\beta > 1$; Table 2). Mean values of β varied from +0.34 K/K at Pfeiler-2 to +1.12 K/K at Almont. Standard deviations

TABLE 2 Summaries of temperature metrics at each site. Sites are ordered by increasing elevation (see Table 1). Site data are sunrise to sunset gap-filled means from the day of measurement, as estimated from nearby weather stations. Light values are not reported due to variation in sensor technology between sites (instead, rescaled within-site data are used in analyses)

Site	T_{leaf} (mean; °C)	T_{leaf} (*SD*; K)	δ (mean; K)	δ (*SD*; K)	β (mean; dimensionless)	β (*SD*; dimensionless)	T_{air} (°C)	Wind (m/s)	Relative humidity (%)
Almont	32.71	12.15	6.23	6.35	1.12	1.08	21.6	2.9	20.8
CBT	35.4	7.56	4.02	4.93	0.46	1.87	26.0	3.1	28.4
Road	24.82	8.76	−0.07	6.16	0.57	0.8	16.9	4.2	52.5
Pfeiler-1	24.34	7.58	−0.81	5.66	0.36	0.79	18.6	1.1	39.1
Pfeiler-2	25.25	6.47	0.44	4.27	0.34	0.62	18.5	1.1	33.0
Painter Boy	14.61	5.15	−5.23	3.63	0.35	0.59	13.5	1.2	61.9
Baldy	26.37	8.01	5.13	7.57	0.62	4.18	18.5	4.0	23.7

of β varied from 0.61 K/K at Pfeiler-2 to 4.2 K/K at Baldy. The mean standard deviation of β across all times within sites was 0.63 K/K. At species scale, we also observed wide ranges of variation in β. This variation was most apparent at midday, when presumably radiation loading would be high and transpiration would differentiate among species' behaviour (Figure 5). At some sites, all species showed high values (e.g. *Chrysothamnus viscidiflorus* with $\beta > 1$ at the Almont site) or intermediate values (e.g. most species with $\beta \approx 1/2$ at the Road site). At other sites, there was considerable divergence among species (e.g. values ranging from $\beta < -1/2$ to $\beta > 1/2$ at the CBT and Baldy sites). Thus, β can show strong heterogeneity among species.

The leaf thermal offset, δ, also varied widely (Table 2; Figure 4b). Mean values of δ varied from −5.2 K at Painter Boy to +6.2 K at Almont. Standard deviations of δ varied from 3.6 K at Painter Boy to 7.6 K at Baldy. The mean standard deviation of δ across all times within sites was 3.1 K. We also observed similarly wide ranges of variation in δ at species scale. At some sites, all species showed similar behavior (e.g. values near −5 K for all species at Painter Boy). At other sites, species showed strongly divergent responses (e.g. values from +5 K to +25 K at Baldy, or +2 K to +15 K at CBT; Figure 5). Thus, δ can also show strong heterogeneity among species.

The model for β had low explanatory power (Figure 6a). The total variation explained by the model was 11.0% for fixed effects and 17.5% for random effects (total 28.6%). Among the fixed effects, there were only a small number of significant effects (with confidence intervals not including zero, and with absolute magnitudes >0.2). These included canopy exposure × air temperature (+0.24), leaf height × relative humidity (−0.32) and leaf height × air temperature (−0.59). In a model selection analysis, the environment-only model was better supported than the trait × environment model (ΔAIC = +80), the trait + environment model (ΔAIC = +67) or a trait-only model (ΔAIC = +90). However, the fixed-effect R^2 for the trait × environment model was higher than in the trait + environment model (+0.02), the environment-only model (0.02) or the trait-only model (0.01).

The model for δ had higher explanatory power (Figure 6b). The total variation explained by the model was 25.0% for fixed effects and 37.7% for random effects (total 62.7%). Among the fixed effects, the strongest significant effects (with confidence intervals not including zero, and with absolute magnitudes >0.2) were stomatal distribution (+0.24), nitrogen fraction × air temperature (+0.21) and light (+0.33). In a model selection analysis, the model trait × environment model was better supported than the trait + environment model (ΔAIC = +148,293), the environment-only model (ΔAIC = +178,802) or a trait-only model (ΔAIC = +551,441). The fixed-effect R^2 for the trait × environment model was higher than in the trait + environment model (=0.22), the environment-only model (0.20) or the trait-only model (0.03).

4 | DISCUSSION

Our empirical data for leaf temperature metrics and energy balance traits spanned a wide environmental gradient and multiple co-occurring species. The overall finding from these measurements was low predictability of the leaf temperature metrics and energy balance traits, rejecting most of the study's hypotheses. There was high variation in species' energy balance traits, with limited correlation with common functional traits. There also were weak relationships between energy balance traits and the environment. Leaf temperature metrics varied widely across species, but traits and time series of climate variables had some limited ability to predict these patterns. Heterogeneity in energy balance traits and leaf temperature metrics appears to be common, such that diverse responses of leaf traits and temperature metrics to changing environments are possible, and predictability remains low.

4.1 | Question 1: Environment predictors of energy balance traits

These results demonstrated weak trait–environment relationships for energy balance traits, contrary to the hypothesis of strong unidimensional environmental filtering. This finding indicates that there

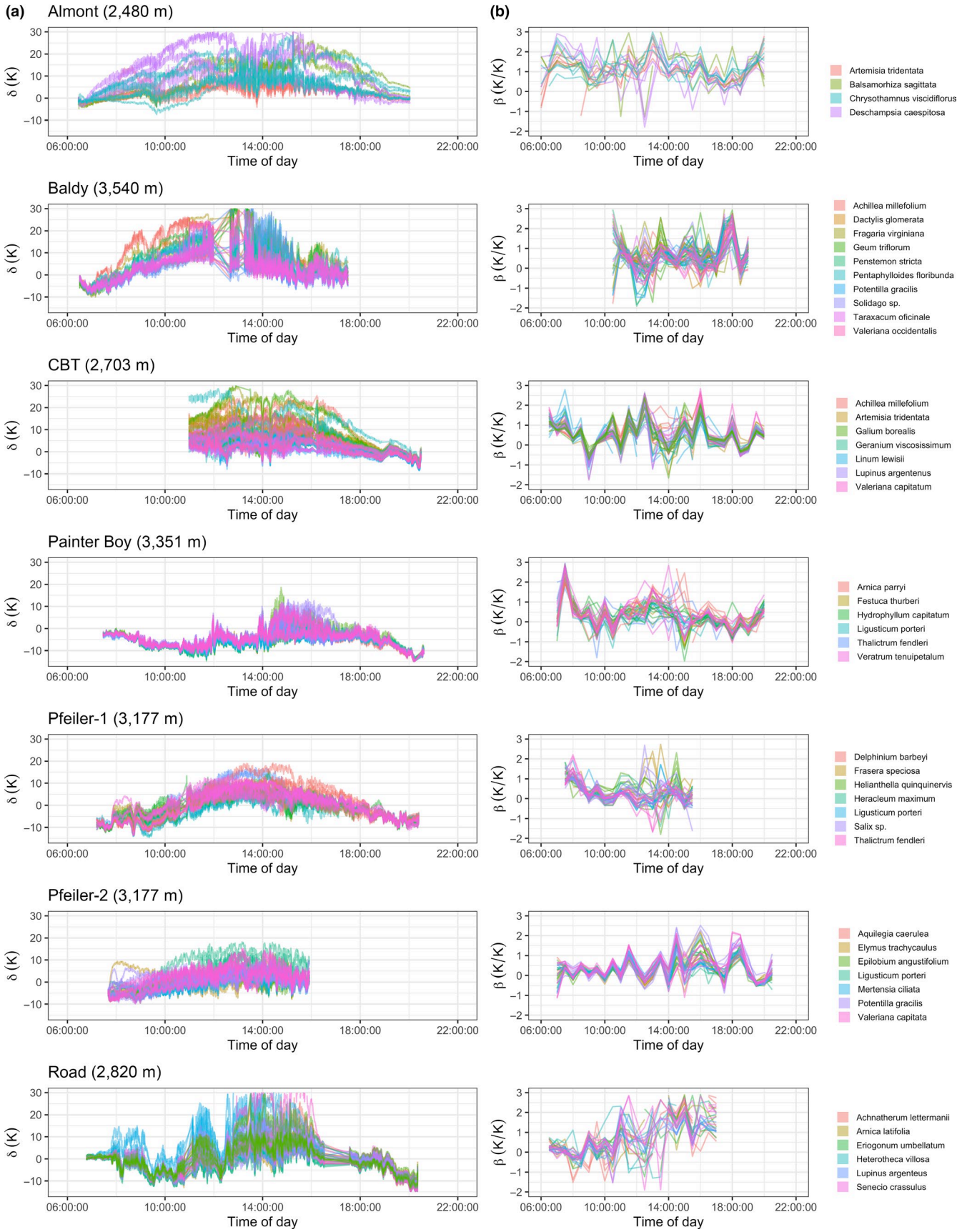

FIGURE 4 Time series of (a) $\beta = \partial T_{\text{leaf}}/\partial T_{\text{air}}$ (thermal coupling strength) and (b) $\delta = T_{\text{leaf}} - T_{\text{air}}$ (thermal offset). Lines correspond to different leaves, coloured by species. Error bars are omitted for visual clarity

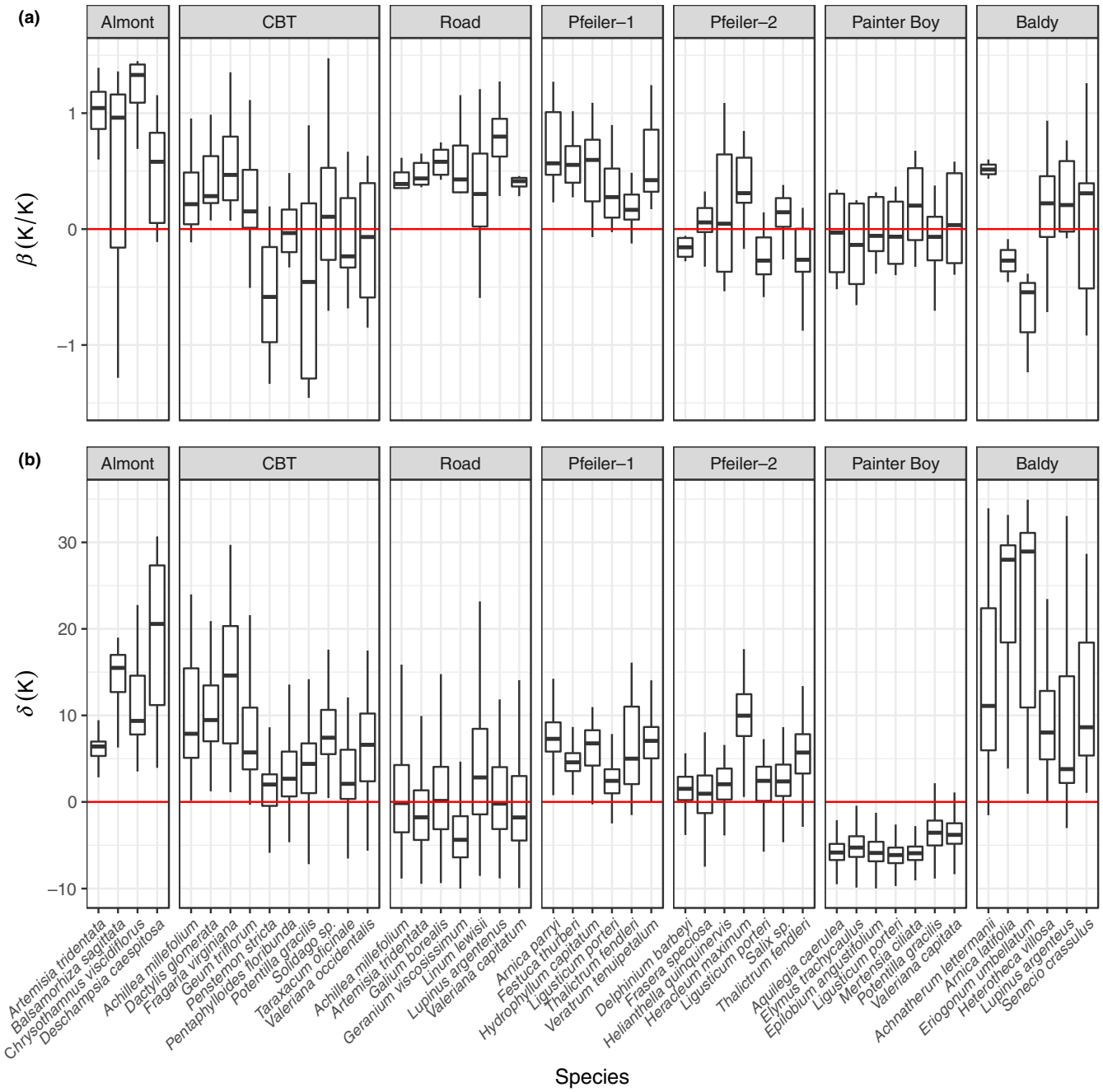

FIGURE 5 Summaries of midday (12 p.m.–1 p.m.) values of (a) β and (b) δ for each species and site. Boxplots omit outliers for visual clarity

is limited impact on community assembly via species sorting for these traits. This finding is surprising, as prior studies have demonstrated variation in energy balance traits with environment, e.g. with albedo in tropical forests (Doughty et al., 2018) and along elevation gradients (Ehleringer, 1988), for leaf size (related to leaf width) along global precipitation gradients (Parkhurst & Loucks, 1972; Peppe et al., 2011; Wright et al., 2017), for leaf angle and stomatal distribution with latitude, elevation and availability of light and moisture (Ehleringer, 1988; Hopkins, Schmitt, & Stinchcombe, 2008; Körner et al., 1983; Smith, Bell, & Shepherd, 1998) and for stomatal conductance (Körner et al., 1983; McDowell et al., 2008). While this study spanned a broad range of landscape types (high desert, montane meadow, subalpine meadow, alpine scree), the range of environmental variation and lack of data for tree growth forms may have not captured the types of trait–environment relationships that have been previously reported. Regardless, for short-statured plants over these regional scales, species sorting does not occur based on energy balance traits that were measured. In contrast, trait–environment relationships for several common functional traits were stronger, suggesting that leaf functional traits may play a more central role in species sorting—or alternatively that other energy balance related traits not measured here (e.g., related to canopy structure) could also be important (Körner, 2003; Leuzinger & Körner, 2007; Salisbury & Spomer, 1964).

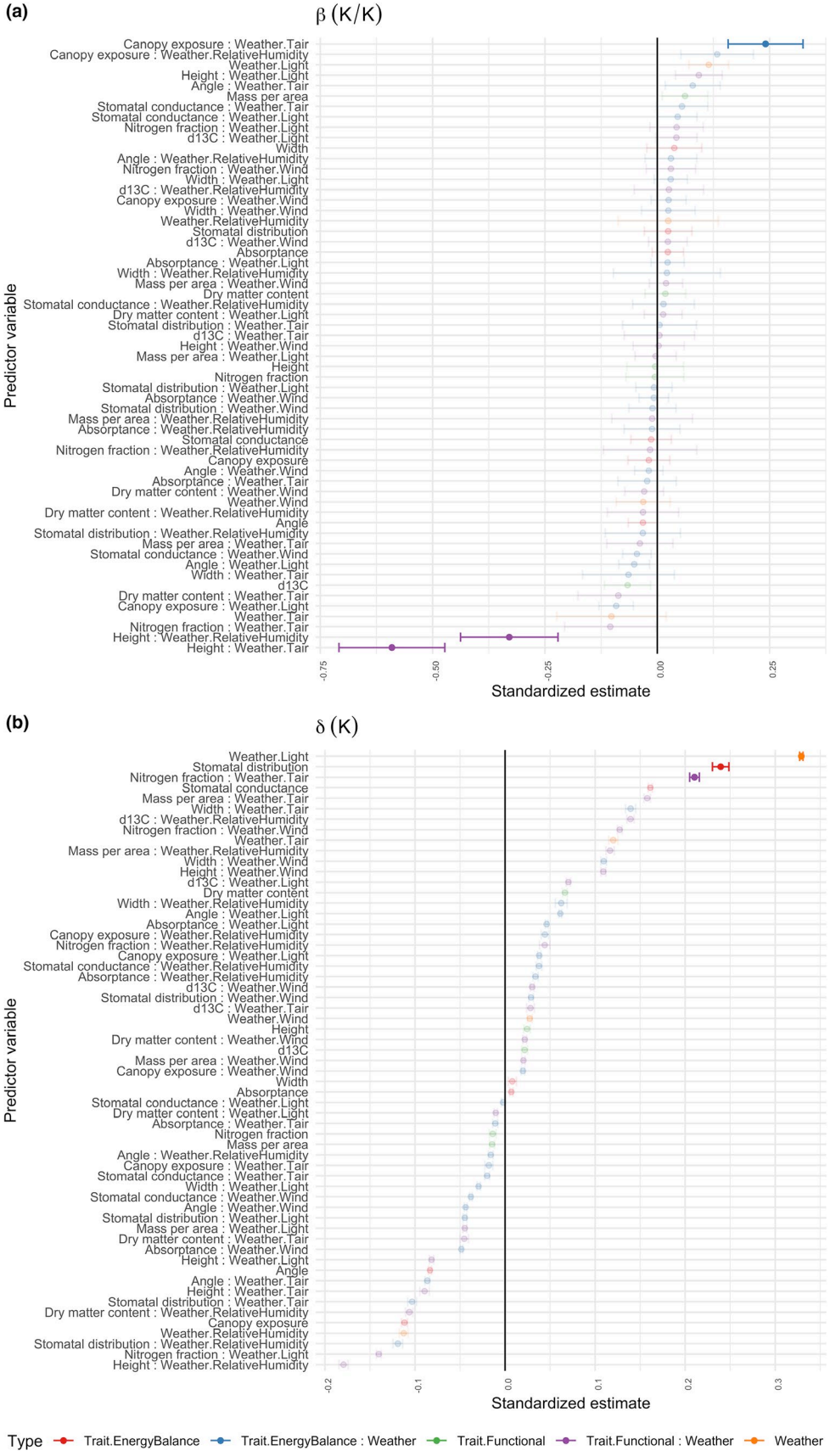

FIGURE 6 Summary of linear mixed models for (a) β and (b) δ. Predictor variables are grouped by type. Dots indicate standardized parameter estimates (effect strengths) and error bars indicate 95% confidence intervals. Significant predictors (with confidence intervals not overlapping zero, and absolute magnitudes ≥ 0.2) are shown in darker colours

Instead, these results show that within a single site, species may co-occur with a wide range of energy balance trait values. This is consistent with multiple strategies yielding viable levels of performance (i.e. the 'alternative design' perspective; Marks & Lechowicz, 2006; Pistón et al., 2019). Directly measuring performance would have required additional population growth data not available at these sites (Salguero-Gómez et al., 2015). Alternatively, the energy balance traits measured in this study may not be the ones key to performance. For example, canopy structure indirectly affects boundary layer conductance. As such it does not appear in energy balance equations and was not measured in our study—but could play a major role in energy balance. Quantifying canopy structure in quantitative rather than qualitative ways remains challenging, especially for small-statured plants (Poorter, Bongers, Sterck, & Wöll, 2003).

4.2 | Question 2: Relationship between energy balance and common functional traits

These results indicate that leaf energy balance traits are not strongly correlated with more commonly measured leaf functional traits, contrary to our hypothesis of strong predictability. The species in this study thus independently vary their energy balance traits and their other traits, without strong trade-offs being necessary. This result contrasts with some of the linkages hypothesized or observed between energy balance and functional traits in prior studies (Falster & Westoby, 2003; Ollinger et al., 2008; Wu et al., 2020) and has several possible explanations.

First, it is possible that the strength of correlations is scale-dependent, with predictability only emerging across wider (e.g. global) trait gradients than present in this study. Our study covered a relatively small fraction of plant phenotypic diversity (primarily herbaceous and woody plants, no trees). Studies at broader scales might find stronger patterns. Second, it is possible that many trait combinations can achieve similar levels of performance for a similar selective gradient. The possibility of multiple solutions to a similar selective gradient is consistent with the high dimensionality of the energy balance equations, which clearly show that species may vary multiple energy balance traits and functional traits to achieve the same leaf temperatures (e.g. cooling via either leaf angle modification or reduced leaf area, and more rapid transient cooling responses with lower leaf mass per area; Michaletz et al., 2015). Third, it is possible that multiple selective gradients may occur, leading to the persistence of multiple viable trait combinations. That is, selection for species with 'fast' economic strategies may not necessarily imply selection for strong thermoregulatory ability. This seems reasonable given the diversity of microenvironments present within sites.

Regardless, the main implication of this finding is that commonly measured functional traits are not sufficient to achieve high statistical predictability of energy balance traits, limiting our ability to infer energy balance without the extensive work that has characterized prior studies (Monteith & Unsworth, 2007).

4.3 | Question 3: Trait and environment drivers of leaf temperature metrics

Our results demonstrated high heterogeneity in leaf temperature metrics, consistent with the hypothesis of species-specific differences. We found that β ranged from less than 1 to far higher than 1 across species and across sites. Many prior studies have suggested a general homeostasis of leaf temperature with values of β that converge globally to an approximate value of 3/4, though with some variation around this mean (Michaletz et al., 2016). However, the generality of this pattern has recently been questioned (Still, Sibley, Page, Meinzer, & Sevanto, 2019). Our results, using thermal videography not subject to the methodological issues identified by Still et al. (2019), also show that mean values of β exhibit a wide range of values, with an overall mean close to (but lower than) 3/4. Values of $\beta > 1$ were also possible, contrary to findings in some prior temperate studies (Pincebourde & Woods, 2012) and consistent with other tropical studies (Pau, Detto, Kim, & Still, 2018).

Broadly, our results show that β and δ also vary widely across contexts, such that neither cannot be treated as a stable species- or site-specific property. Individuals may obtain diverging values of both temperature metrics due both to trait variation and environmental forcing, as detailed below. Cryptic microclimate variation (Kaspari, 2019; Pincebourde & Casas, 2019) beyond the scope of our measurements could drive variation in leaf-level environmental forcing that also would yield high variation in β and δ. These results build on work showing variation in leaf temperature across species (Michaletz et al., 2016) and spatial scales (Pincebourde & Suppo, 2016), and at high temporal frequencies (Aubrecht et al., 2016; Doughty & Goulden, 2008; Leuzinger & Körner, 2007; Singsaas & Sharkey, 1998). More strongly, our results now show that such heterogeneity can be experienced over very small spatial scales. The ranges of temperature metric variation experienced with a site can be of the same approximate magnitude as experienced between sites, consistent with prior landscape-scale studies (Scherrer & Körner, 2010).

The performance implications of this variation remain uncertain. The transiently high values of δ are potentially high enough to cause thermal damage, but this conclusion seems at odds with the regularity with which these extremes are reached. While rates of cellular injuries and necrosis increase exponentially with temperature (Hare, 1961), short exposure periods to these high temperatures may not pose a major stress to these species. Similarly, the highly variable values of β suggest extensive variation in how plants are thermally coupled to the environment. Theory indicates that variation in β can be critical to plant performance in thermally stressful environments (Blonder & Michaletz, 2018). There may be adaptive variation over diurnal timescales, e.g. through plant modification of stomatal conductance or of canopy structure and leaf orientation. While such variation is known to occur for δ, e.g. through leaf angle modulation (Ehleringer & Forseth, 1989b), its linkages to β remain less clear.

Our results indicated that both β and δ were only partially predictable through regression approaches involving traits and site environment, contrary to the hypothesis that regression would yield high predictability. Fixed effects explained no more than 30% of the variation in either response variable, indicating that our regression models did not fully capture the processes inherent to the full energy balance theory. β was more difficult to predict than δ.

In the case of δ, the most parsimonious (lowest AIC) models included interactions among both traits and environment variables, while in the case of β, the most parsimonious models included only environment variables. In both cases, the models with the highest explanatory power included interactions among both traits and environment variables (though this is not unexpected given the increase in predictor numbers). However in both cases, the largest contributions to the explained variation came from environment, rather than from trait variables. Both models identified consistent direct roles for the site environment: light for β, and light plus relative humidity for δ. Thus, the measured environmental variables seem more important for predicting leaf temperature metrics than the measured energy balance traits or commonly measured functional traits.

The main way in which both functional traits and energy balance traits affected leaf temperature metrics was via interactions with the site environment: primarily via canopy exposure and height for β, and via stomatal traits and leaf stoichiometry for δ. Thus the overall canopy structure and water use strategy of these species appears more critical to understanding their thermal ecology than any other traits we measured (Körner, 2003). This perspective is consistent with the atmospheric decoupling of short-statured plants that has previously been reported, and with findings that when canopy effects are smaller such as in the canopy-top of tall trees (Leuzinger & Körner, 2007), leaf traits become more important in determining leaf temperatures. Our results provide a complementary perspective to this prior study, which focused on broadleaf and conifer trees, which are growth forms not present in our data.

There are several reasons why the regression approach did not yield higher predictive power for leaf temperature metrics. First, this study was not able to measure all of the relevant aspects of site environment affecting individual leaves, e.g. longwave radiation, which we assumed implicitly to be correlated with our light proxy, or leaf-level wind speed, which we assumed was related to site-level from weather station data). Second, we only measured traits at a single time point, when some of these traits may also vary over time. Over the diurnal timescales studied here, stomatal conductance could have varied extensively (e.g. decreasing at midday, likely with parallel decreases in photosynthetic rates; Billings, Clebsch, & Mooney, 1966; Lambers, Chapin, & Pons, 2006), as could have leaf angle (Ehleringer & Forseth, 1989a). Over longer time-scales (beyond the scope of this study), acclimatory responses in other traits (through production of new leaves or stems) could also occur. Inclusion of such variation was beyond the logistic scope of this study but could be important in quantifying the direct contribution of traits to variation in leaf temperature metrics.

5 | CONCLUSIONS

Given the potential influence of leaf temperature on gas exchange, our results indicate significant uncertainty in models of leaf performance that either do not include high-frequency leaf-level environmental variation as drivers or that do not have access to such data—both likely scenarios. For now, predicting leaf temperature metrics via empirical regression approaches remains highly challenging. A key challenge going forward will be understanding how this heterogeneity and unpredictability in leaf temperature metrics scales up to or influences time-integrated or space-integrated resource fluxes, e.g. Doughty and Goulden (2008).

ACKNOWLEDGEMENTS

B.B. was supported by a UK Natural Environment Research Council independent research fellowship (NE/M019160/1) and by a travel grant from the Norwegian Research Council (KLIMAFORSK 250233). S.T.M. was supported by a Los Alamos National Laboratory Director's Fellowship. S.E. was supported by an NSF REU site award (DBI-1262713) to the Rocky Mountain Biological Laboratory. Leaf elemental analyses were supported by a Los Alamos National Laboratories LDRD award. Research permits were obtained from the United States Forest Service, the Rocky Mountain Biological Laboratory and the Crested Butte Land Trust. Brian Enquist provided access to several field sites. Amanda Henderson assisted with logistics. Lorah Patterson assisted with species identification. David Inouye loaned a field vehicle. Roxana Safipour helped transport equipment. Will Pockman loaned a leaf porometer. Vanessa Buzzard coordinated leaf processing for elemental analysis. Jin Wu provided code and advice for PROSPECT model inversion.

AUTHORS' CONTRIBUTIONS

Authors have been ordered alphabetically by last name. B.B. and S.T.M. co-developed the idea for the study; B.B. built the equipment and wrote computer code for the thermal analyses; B.B., S.E., R.E.K. and S.T.M. collected field data; S.E. and R.E.K. analysed the thermal imagery; B.B. and S.T.M. wrote the manuscript with inputs from S.E. and R.E.K.

DATA AVAILABILITY STATEMENT

All supporting data files are available on Dryad Digital Repository: https://doi.org/10.6078/D1NQ59 (Blonder, Escobar, Kapas, & Michaletz, 2020). Code for thermal data logging is available on Github and Zenodo: https://doi.org/10.5281/zenodo.3951688 (Blonder, 2020a). Code for thermal data analysis is available on Github and Zenodo: https://doi.org/10.5281/zenodo.3951689 (Blonder, 2020b). All other Supporting Information is available electronically with this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Blonder B, Escobar S, Kapás RE, Michaletz ST. Low predictability of energy balance traits and leaf temperature metrics in desert, montane and alpine plant communities. *Funct Ecol*. 2020;00:1–16. https://doi.org/10.1111/1365-2435.13643