

Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient

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Abstract

Aim: Tropical elevation gradients are natural laboratories to assess how changing climate can influence tropical forests. However, there is a need for theory and integrated data collection to scale from traits to ecosystems. We assess predictions of a novel trait-based scaling theory, including whether observed shifts in forest traits across a broad tropical temperature gradient are consistent with local phenotypic optima and adaptive compensation for temperature.

Location: An elevation gradient spanning 3,300 m and consisting of thousands of tropical tree trait measures taken from 16 1-ha tropical forest plots in southern Perú, where gross and net primary productivity (GPP and NPP) were measured.

Time period: April to November 2013.

Major taxa studied: Plants; tropical trees.

Methods: We developed theory to scale from traits to communities and ecosystems and tested several predictions. We assessed the covariation between climate, traits, biomass and GPP and NPP. We measured multiple traits linked to variation in tree growth and assessed their frequency distributions within and across the elevation gradient. We paired these trait measures across individuals within 16 forests with simultaneous measures of ecosystem net and gross primary productivity.

Results: Consistent with theory, variation in forest NPP and GPP primarily scaled with forest biomass, but the secondary effect of temperature on productivity was much less than expected. This weak temperature dependence appears to reflect directional shifts in several mean community traits that underlie tree growth with decreases in site temperature.

Main conclusions: The observed shift in traits of trees that dominate in more cold environments is consistent with an 'adaptive/acclimatory' compensation for the kinetic effects of temperature on leaf photosynthesis and tree growth. Forest trait distributions across the gradient showed overly peaked and skewed distributions, consistent with the importance of local filtering of optimal growth traits and recent shifts in species composition and dominance attributable to warming from climate change. Trait-based scaling theory provides a basis to predict how shifts in climate have and will influence the trait composition and ecosystem functioning of tropical forests.

KEYWORDS

Amazon, Andes, ecosystem function, elevation gradient, metabolic scaling theory, scaling, stoichiometry, trait-based ecology

1 | INTRODUCTION

Tropical forests are among the most productive ecosystems on the Earth and account for about one-third of global net primary productivity (NPP; Field, 1998). However, we still know relatively little about what controls variation in tropical forest NPP because they are relatively undersampled compared with their importance (Malhi, Doughty, & Galbraith, 2011). Globally, terrestrial primary productivity varies geographically and is influenced by physiological and environmental processes operating over a wide range of scales (Roy, Saugier, & Mooney, 2001; Schlesinger, 1991). As species respond individually to variation in climate, there is increasing need to disentangle how productivity and other biogeochemical processes are influenced by shifts in both climate and species-specific plant traits (Chapin, 2003; Diaz et al., 2004; Kerkhoff, Enquist, Elser, & Fagan, 2005; Lavorel & Garnier, 2002).

A promising approach to linking plant functioning and ecosystem processes comes from trait-based scaling theory (Box 1). It assumes that for a given environment, for any trait closely associated with variation in plant growth or demography, there is a mean trait value and an optimal trait value that maximizes growth rate given the constraints of the environment (Enquist et al., 2015; Norberg et al., 2001; Savage, Webb, & Norberg, 2007). Recently, Feeley (2012) and Feeley et al. (2011) argued that the species composition of tropical forests is shifting because of increases in temperature associated with climate change. They found directional (upward) shifts in the elevation ranges of multiple tree genera. However, the rate of tree migration was lower than the observed rate of temperature increase. Thus, if organismal traits are matched to the local environment (Ackerly, 2003), the functional composition of tropical forests may be increasingly out of equilibrium with the local climate. Indeed, climate change is expected to induce marked vegetation disequilibrium and impact ecosystem functioning as the trait or

functional composition of vegetation is disrupted and increasingly lags behind (Davis & Shaw, 2001; Svenning & Sandel, 2013).

Although trait-based ecology has provided a useful foundation for ecology and global change biology (Díaz et al., 2007; Quétiér, Lavorel, Thuiller, & Davies, 2007), much of the work has largely been correlative. What is needed is the development of quantitative theory that can generate predictions (Enquist et al., 2015; Fyllas et al., 2014; Houlihan, Mckinney, Anderson, & McGill, 2017; Suding et al., 2008; Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010). Furthermore, theory based on first principles will be better able to scale from traits to ecosystems and predict shifts in community traits and diversity across space and time (Enquist, 2010; Marquet et al., 2014; McGill, Enquist, Weiher, & Westoby, 2006).

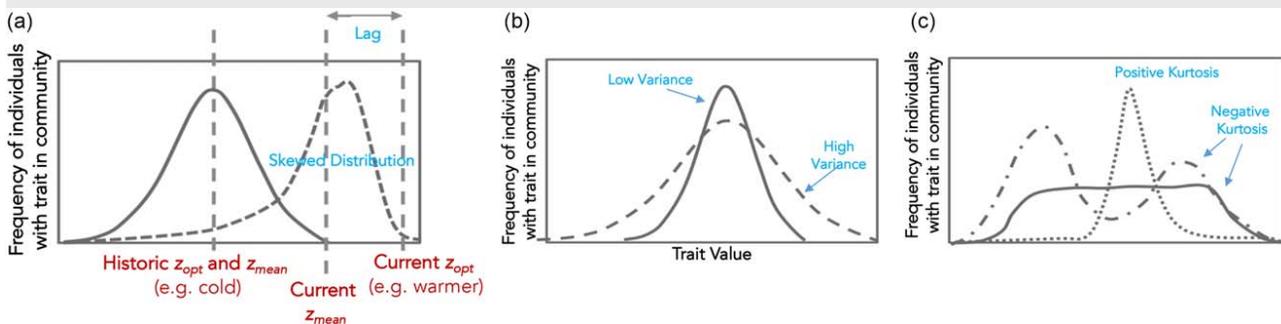
Here we test several key predictions of trait-based scaling theory (see Figure 1; Table 1) in a series of highly diverse tropical forest communities along an elevation gradient in the Andes. Together, these tests allow us to assess whether changes in the dominance and diversity of forest traits and variation in ecosystem productivity are consistent with local phenotypic optima and adaptive compensation for temperature. The gradient offers a natural laboratory for assessing the environmental controls on functional traits, forest composition and ecosystem processes (Asner et al., 2017; Malhi et al., 2010). We assess several predictions across tropical forests that span a 3,300 m elevation range and a c. 16.2 °C gradient in mean annual temperature and where recent increases in temperature attributable to climate change have caused upward shifts in the distribution of tree species. Across this gradient, we sampled a suite of functional traits, forest structure and ecosystem measures based on multiple field measurements (Malhi et al., 2017). We show how variation in forest biomass and the abundance of several stoichiometric traits and other traits linked to variation in organismal relative growth rate can then be used to predict variation in forest ecosystem productivity.

BOX 1

Overview of a dynamical trait-based scaling theory. For any trait closely associated with variation in growth or demography and for a given environment there is a mean trait value, z_{mean} , and an optimal trait value, z_{opt} , that maximizes growth rate, f , given the constraints of the environment (see (Enquist et al., 2015; Norberg et al., 2001; Savage et al., 2007). The given biomass, C , of a trait value linked to growth, f , will vary depending on the environment. Thus, the trait distribution is a function of environment, $C(z)$.

The theory gives rise to the following predictions:

1. Reflecting selection and ecological filtering for optimal phenotypes, local community trait distributions will tend toward a unimodal distribution (a and b), strong local sorting and dominance of specific traits will lead to more peaked distributions (positive kurtosis) (c).
2. In a shifting climate (a), community trait distributions will shift reflecting a shift in the optimal trait value, but the mean (z_{mean}) will lag behind z_{opt} . In the case where the mean community trait decreases as temperature also decreases, we would expect that with warming due to climate change, trait distributions will be characterized by negative skewness (as in a) as the community shifts to the new optimal trait value. In contrast, if the mean community trait is observed to increase across a temperature gradient then warming would lead to communities characterized by positive skewness. Thus, the skewness of the trait distribution can reflect shifting optima and past change (a).
3. Communities with greater trait variance (b) will be better able to respond to and more quickly track climate change.
4. The current biomass distribution of a trait may be a legacy of environmental history and ecological interactions within the forest community. Different degrees of local ecological interactions will be reflected in different degrees of spread in distributions (c). However, if there is strong filtering and competitive dominance of individuals with traits closer to z_{opt} , we would predict communities to be characterized by peaked distributions or positive kurtosis. As we discuss in the main text, we can take the distribution of traits that underlie variation in growth rate to then scale up and predict ecosystem net primary productivity and forest mortality.



2 | TRAIT-BASED SCALING THEORY: FROM TRAITS TO ECOSYSTEMS

We assess six predictions from trait-based scaling theory (see Table 1; Enquist et al., 2015; Norberg et al., 2001; Savage et al., 2007). This theory builds on earlier work, including metabolic scaling theory (MST). These predictions are outlined in Table 1 and detailed in the Supporting Information. We also assess how some of these predictions are further modified by two differing hypotheses regarding the temperature dependencies of traits (Box 1).

Whole-plant functioning is affected by numerous traits reflecting differences in allocation to the quantity and quality of tissue (Enquist et al., 2007; Evans, 1972; Garnier, 1991; Lambers, Freijsen, Poorter, Hirose, & Van Der Werf, 1990). For example, the stoichiometric composition, that is the relative concentrations of various macro- and micronutrients in plant tissues, influences whole-canopy rates of production and biomass turnover (Ågren, 1988, 2004; Chapin, Vitousek, &

Van Cleve, 1986). Furthermore, variation in plant metabolism (i.e., respiration rates, gross photosynthesis) is influenced by the combined effects of two variables, body size, m (West, Brown, & Enquist, 1997), and the absolute temperature, T in kelvin (K; Gillooly, Brown, West, Savage, & Charnov, 2001). Metabolic scaling theory (see Supporting Information) shows how variation in plant growth can be linked to variation in plant size, and the specific traits that underlie the normalization, b_0 , of growth rate (Enquist, West, Charnov, & Brown, 1999, 2007; Kerkhoff et al., 2005). Variation in the relative growth rate, $\mu = dm/(m dt)$, is linked to body mass, m , and temperature, T , as follows:

$$\mu \propto b_0 e^{-E/kT} m^{-1/4} \quad (1)$$

Here, the effect of temperature is given by the Van't Hoff/Boltzmann factor, $e^{-E/kT}$, and describes the exponential kinetic dependence of metabolic rate on temperature, T . Here, E is the activation energy (measured in eV) and is a measure of the sensitivity of

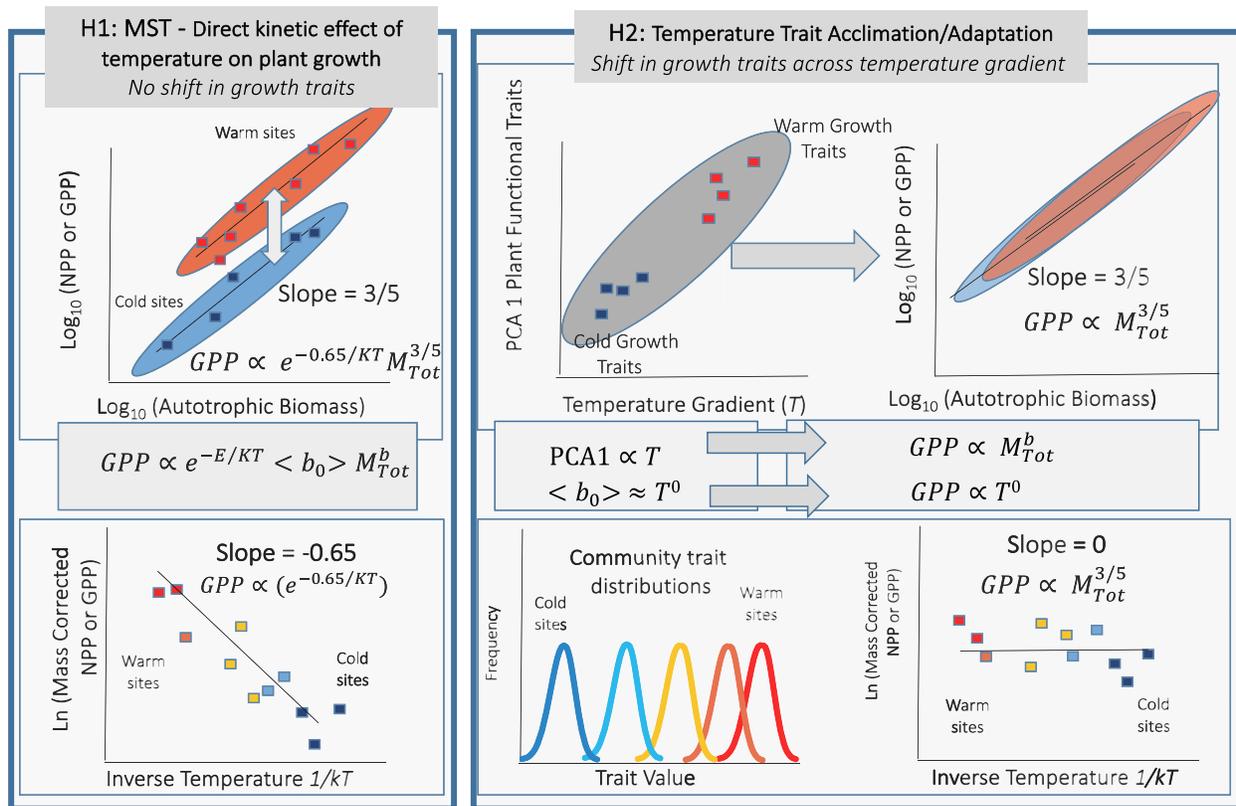


FIGURE 1 Graphical overview of several predictions of trait-based scaling theory that stem from two interrelated hypotheses. Hypothesis 1 (H1) states that variation in ecosystem fluxes (NPP and GPP) is attributable to variation in autotrophic biomass and environmental temperature. Ecosystem productivity will scale with biomass raised to the 3/5 power. The effect of temperature will be reflected in an exponential temperature response characterized by a Boltzmann relationship with rates increasing with temperature as E c. 0.65 eV, with higher rates of mass-corrected productivity in warmer sites. This would be reflected in an exponential response of the growth rate normalization b_0 to temperature (see Supporting Information Equation S8). In contrast, hypothesis 2 (H2) states that covariation in traits that underly plant growth can compensate for the kinetic effects of temperature on plant growth and ecosystem productivity. As a result, the growth rate normalization b_0 will be independent of temperature (see Equation 3). The temperature response of ecosystem productivity will deviate from $E = 0.65$ eV and will result in a shallower if not flat temperature response curve

metabolism to changes in temperature and k is Boltzmann's constant, $k = 8.62 \times 10^5$ eV K^{-1} (Gillooly et al., 2001; see Supporting Information for more detail and Appendix S1 for a detailed listing of

all variables with associated units). The $-1/4$ exponent reflects the importance of plant size, m , via the allometric effects of how growth rates change within increases in plant size.

TABLE 1 Summary of six predictions made by trait-based scaling theory

- I. **Directional shifts in traits associated with growth and metabolism** (see b_0 ; Equation 1; Supporting Information Equation S15) across environmental gradients. A shift in traits will be attributable to a shift in the optimal phenotype across temperature gradients. If there is a strong convergence in trait values around optimal trait values then trait distributions will be unimodal and characterized by positive kurtosis (Box ; Enquist et al., 2015).
- II. **Temperature as a driver.** If temperature is a major driver of community composition then shifts in community trait distributions will be reflected by increases in leaf P:N and PNUE (Kerkhoff et al., 2005) and LMA (Michaletz et al., 2016).
- III. **Measures of community trait skewness can reveal whether there are ongoing or recent directional shifts in community composition attributable to a change in an environmental driver.** For example, shifting communities attributable to increased warming from climate change would be reflected by skewed trait distributions with either positive or negative skew depending on how mean community trait values change along environmental gradients (see Box ; Norberg et al., 2001).
- IV. **Variation in NPP will scale as stand biomass raised to the 3/5 power.** NPP and GPP will scale allometrically with biomass; biomass will be the best predictor, followed by traits (if there is a sufficient shift in traits); see H1 in Figure 1 (West et al., 2009; Enquist et al., 2009).
- V. **Variation in GPP and NPP will be influenced primarily by stand biomass and temperature** (Enquist et al., 2003) and characterized by a Q_{10} of c. 2.5. However, if community-level growth traits (see Equation 3) covary with temperature, reflecting temperature acclimation and/or adaptation, then the temperature sensitivity of NPP and GPP will be muted (Figure 1).
- VI. **Temperature acclimation and adaptation, if strong, will be reflected in an exponential shift in community weighted N:P and PNUE, resulting in a weak linkage with temperature on NPP and GPP.** Thus, the expected strength of the role of temperature in the scaling of NPP will be significantly less than an E of c. 0.65 eV. Perfect temperature acclimation and/or adaptation will result in no significant influence of temperature (see H2 in Figure 1; Kerkhoff et al., 2005).

Note. These predictions are then modified via either hypothesis 1 or hypothesis 2 (H1 or H2, respectively), as detailed in Figure 1.

Previous research has indicated that if the temperature sensitivities for respiration and photosynthesis are similar then the value of E , although not well established, is expected to approximate 0.65 eV (Allen, Gillooly, & Brown, 2005; Gillooly et al., 2001; Kerkhoff et al., 2005). An E of c. 0.65 eV is equivalent to a Q_{10} of c. 2.5, so that physiological rates increase c. 2.5 times for a 10 °C increase in temperature. Over a 15 °C temperature gradient, a temperature sensitivity of $E = 0.65$ eV will result in an approximately 3.6-fold proportional change in biological rates. If, however, the temperature responses of respiration and photosynthesis differ, the value of E has been proposed to be closer to 0.32 (Allen et al., 2005). Thus, the value of E is expected to fall between 0.65 and 0.32, which have been hypothesized to correspond to respiration and photosynthesis, respectively.

Elaborations of MST have shown that b_0 can be linked to several key traits, including nutrient composition (Allen & Gillooly, 2009; Elser, Fagan, Kerkhoff, & Enquist, 2010; Gillooly, Charnov, West, Savage, & Brown, 2002; Kerkhoff et al., 2005). Elser et al. (2010) hypothesize that variation in growth rate can be modified by the traits that underlie b_0 . Specifically, $b_0 \propto \phi \left(\frac{X}{C}\right)$, where C is the mass of carbon, and X is the mass of a nutrient, such as nitrogen (N) or phosphorous (P). The value of ϕ is the efficiency of using X to generate C (e.g., photosynthetic nutrient use efficiency, PNUE). Equation 1 shows that variation in relative growth rate, μ , will be influenced by plant size, m , temperature, T , tissue nutrient stoichiometry, X/C , and the nutrient use efficiency, ϕ . The model implicitly assumes that no other resources are limiting (water availability, etc.) and that X/C , ϕ , and m do not covary with temperature. Equation 1 states that μ will decrease to the $-1/4$ power with increases in plant size, but that the growth rate will increase exponentially with increases in temperature.

Next, we extend MST to include a stoichiometrically based allometric tree growth model to scale from the distribution of traits associated with plant relative growth rate to the gross primary productivity (GPP) and NPP (see Supporting Information). This work builds on that of Enquist et al. (2015) and focuses on the importance of two forest community distributions, namely the distribution of traits and the distribution of tree sizes. The importance of the community trait distribution is reflected in the community weighted mean (CWM) value of $\langle b_0 \rangle$ and the importance of the distribution of tree sizes reflected in the total stand biomass, M_{Tot} , and its associated scaling exponent, α . Taking Equation 1, we can next sum the relative growth rates, μ , of all individuals to then derive an equation for the scaling of the total stand metabolism, B_{Tot} , and productivity, NPP, with the total stand biomass, as follows:

$$NPP \propto GPP \propto B_{Tot} \propto \langle b_0 \rangle \left[\frac{5}{3} M_{Tot} \right]^\alpha \quad (2)$$

where $\langle b_0 \rangle$ is the abundance weighted mean of the metabolic growth coefficient that depends on a set of traits (see Supporting Information Equation S11). Metabolic scaling theory predicts that for forests in approximate demographic steady state, α is 3/5 or 0.60 (Enquist, West, & Brown, 2009).

In the Supporting Information, we derive how traits influence plant growth via their influence on the growth rate normalization, b_0 , that

includes the different hypothesized temperature dependencies of plant growth, as follows:

$$b_0 = \langle h \cdot \phi_L^A \cdot \left(\frac{m_L}{a_L}\right)^{-1} \cdot \beta_L \cdot \left(\frac{P}{N}\right) \rangle e^{-E/kT} \quad (3)$$

Here, h is the carbon use efficiency (the quotient of GPP and NPP), ϕ_L^A is the photosynthetic nutrient use efficiency or PNUE on a per unit leaf area basis (in grams of carbon per metre squared of leaf per gram of nutrient per unit time), $\frac{m_L}{a_L}$ is the quotient of leaf mass, m_L , and leaf area, a_L , or the leaf mass per unit area (LMA), and β_L is the leaf mass fraction reflecting variation in allocation to leaf biomass (leaf mass divided by total plant biomass). A full derivation is given in the Supporting Information.

3 | MATERIALS AND METHODS

3.1 | Census and abundance data

This study included 16 1-ha permanent plots along an elevation gradient in the departments of Cusco and Madre de Dios in southeastern Perú. The plots range in temperature from 25.2 °C at the lowest elevation plot to 9.0 °C at the highest elevation plot (see Supporting Information Table S1). Plots also vary significantly in solar radiation, precipitation and soil moisture, as well as above-ground standing biomass (Malhi et al., 2017). All plots are located in areas that have relatively homogeneous soil substrates and stand structure and show minimal evidence of human disturbance (Araujo Murakami et al., 2014; Girardin et al., 2014).

Of these plots, we selected 10 plots that spanned the elevation gradient and where detailed measures of plant traits and physiology could be measured accurately (Supporting Information Table S1). Six of the plots are montane plots in the Kosñipata Valley, spanning an elevation range from 1,500 to 3,500 m a.s.l., two are submontane plots located in the Pantiacolla front range of the Andes (range 600–900 m a.s.l.) and two plots are found in the Amazon lowlands in Tambopata National Park (range 200–225 m a.s.l.). The lowland plots were established in the early 1980s, and the montane ones between 2003 and 2013. All of these plots belong to a group of permanent 1-ha plots operated by the Andes Biodiversity Ecosystems Research Group (ABERG; <http://www.andesconservation.org>) and that are part of the ForestPlots (<https://www.forestplots.net/>) and Global Ecosystems Monitoring (GEM; <http://gem.tropicalforests.ox.ac.uk/projects/aberg>) networks.

Plots have been measured annually for carbon allocation and cycling, following the standard GEM Network protocol (Marthews et al., 2014). As such, gross and net primary productivity estimates (Girardin et al., 2010; Malhi et al., 2017) and comprehensive descriptions of the carbon cycle (Malhi et al., 2017) exist for all of these plots (Girardin et al., 2013; Huasco et al., 2014; Malhi et al., 2014, 2017). Within each plot, all stems ≥ 10 cm diameter at breast height were tagged, sized and identified to species level in the 2013 tree census, and then recorded in the ForestPlots database. These individuals were examined and potentially renamed by taxonomic experts at the Carnegie Institute

(<http://spectranomics.ciw.edu/species>). A full description of the taxonomic standardization methodology is given by Blonder et al. (2017). Additional details of the plot methodology are provided in the Supporting Information.

3.2 | Trait sampling

From April to November 2013, we measured plant traits as part of the CHAMBASA (CHallenging Attempt to Measure Biotic Attributes along the Slopes of the Andes) project. Based on census data for 2013 or the most recent year before 2013, we sampled tree species that contributed to 80% of total plot basal area (see Supporting Information). For each sampled species in each plot, five individual trees in upland sites and three individual trees in lowland sites were chosen for sampling. Using single-rope tree-climbing techniques, we sampled one fully sunlit canopy branch and a fully shaded branch where possible, each at least 1 cm diameter, from each tree. From each branch, we measured five leaves from each species. Overall, we ended up analysing 3,013 individual leaves for leaf traits. Data are available in Shenkin et al. (2017) and additional methodological detail is given in the Supporting Information. These leaves were sampled from 1,025 branches from 620 trees, comprising 180 tree species from the 10 plots.

We focused on the following seven leaf traits that underlie the allometric normalization of the scaling of plant growth, b_0 : leaf mass per unit area (LMA); leaf phosphorus concentration (%P); total leaf nitrogen concentration (%N); light-saturated leaf photosynthetic rate under saturating light (in micromoles of carbon dioxide per metre squared per second); total leaf carbon concentration (%C); and from these traits we calculated the photosynthetic nitrogen use efficiency (PNUE) and the leaf P:N ratio (see Supporting Information for additional information on methods). All measures of leaf stoichiometry and LMA were conducted at the University of Arizona.

3.3 | Estimating trait distributions

To test the predictions of trait-based scaling theory, we calculated two measures of community weighted trait values. The first method focused on the most abundant or dominant species in each plot (Supporting Information). We used the traits measured from species that contributed to 80% of basal area within each plot. The second method, outlined by Enquist et al. (2015), bootstrapped the trait data so as to incorporate the full spectrum of trait variation within and across species. We used this method to estimate better the moments of each forest plot trait distribution (mean, variance, skewness and kurtosis) and calculate 95% confidence intervals (CIs) for each moment. This method uses parametric bootstrapping (Efron & Tibshirani, 1993) to approximate better how intraspecific variation influences the community trait distribution (see Supporting Information).

3.4 | Statistical analyses

All analyses were performed in the R programming environment (R Core Team, 2013). A description of the functions and packages used are detailed in the Supporting Information.

We assessed the importance of CWM trait values as measured by the mean of the community trait distributions of LMA, and leaf P, N, C, photosynthesis, and the calculated values of P:N and PNUE. We calculated the CWM trait value by averaging the mean species trait values that are each multiplied by the species measure of dominance (e.g., cover, biomass, abundance; Garnier et al., 2004; Grime, 1998). For these analyses, we used the notation subscript a to specify mean values calculated by this first method (so $\langle P:N \rangle_a$ corresponds to the CWM P:N value from these most abundant species). Second, we assigned trait values to all individuals within each forest plot and calculated a whole-community trait average, as well as the higher moments of the trait distribution, using our trait parametric bootstrapping procedure (see Supporting Information). For this second method, we used the notation subscript c to specify the community mean values estimated by the resampling procedure (so $\langle P:N \rangle_c$ corresponds to our estimate of community trait mean P:N value from all individuals from within the entire community, including trait estimates for all of the rare species in the community).

4 | RESULTS

Multivariate analyses using either the mean dominant and community traits, $\langle \text{trait} \rangle_a$, or the mean community bootstrapped traits, $\langle \text{trait} \rangle_c$, showed that the best abiotic predictor of variation in the shift of trait composition was mean annual temperature (see Supporting Information Tables S2 and S3; Figures S1 and S2). Consistent with predictions of hypothesis 2 (H2; Table 1; Figure 1) and recent work by Asner et al. (2017), there is a coordinated multivariate shift in the CWM of several temperature-related traits. For the mean dominant community traits, $\langle \text{trait} \rangle_a$, the first principal component, PCA1_a , explained 42.9% of trait variation, and the second component 21.04%. Trait loadings along PCA1 reflect the 'cold-warm' continuum of leaf economics. Community weighted trait values of LMA, PNUE, or ϕ_L^A , and P:N show the most positive loadings, whereas leaf N and C show the most negative loadings (Supporting Information Figure S2; Tables S2 and S3). Of all of the environmental variables, the best predictor of variation in plot PCA1_a trait loadings was mean annual temperature (t -value = -3.193 ; $p = .013$; $r^2 = .56$; see Supporting Information Figure S2b,c).

By itself, solar radiation (in gigajoules per metre squared per year) was not a significant predictor of multivariate community trait shifts (t -value = -0.604 ; $p = .604$; $r^2 = .06$; see Supporting Information Figure S1). However, a model containing both temperature and solar radiation was a slightly better model, explaining shifts in PCA1_a based on the corrected Akaike information criterion (AICc; adjusted $R^2 = .80$, $p = .017$). Other variables [precipitation (in millimetres per year), soil moisture (as a percentage), aspect (in degrees) and slope (in degrees)] were not significant. Similar results were also found for the community bootstrapped CWM $_c$ (Supporting Information Figure S1). However, variations in PCA2_c scores were negatively correlated with soil moisture. The CWM values of leaf phosphorus, $\langle \%P \rangle_c$, and photosynthetic rate or $\langle \text{photo} \rangle_c$ had the most negative and positive loadings, respectively, on PCA2_c (Supporting Information Table S3), indicating that variation in soil moisture might also be an important, although secondary, driver of those CWM trait values.

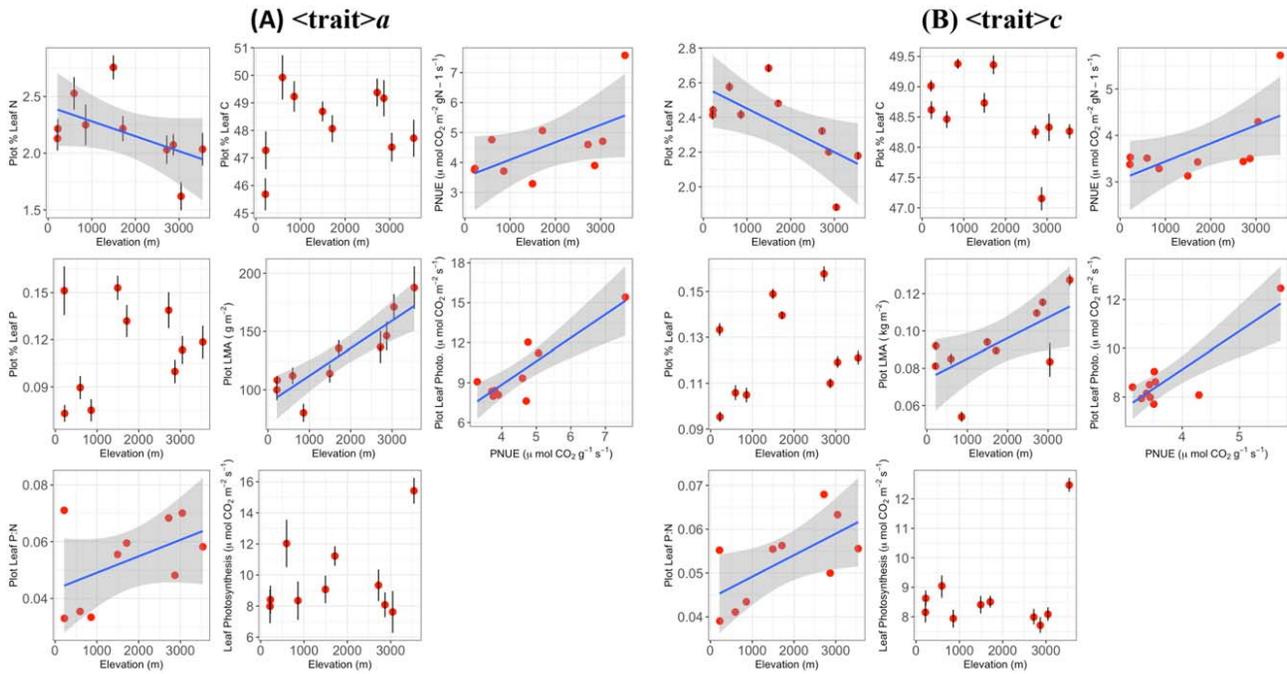


FIGURE 2 Variation in community weighted trait values for the (a) most abundant species within each forest plot; and (b) for all species within the forest plot. Across the gradient, we see significant shifts in the community weighted mean for the dominant species, $\langle \text{trait} \rangle_a$, and estimates of the entire community trait mean, $\langle \text{trait} \rangle_c$, of leaf P:N, leaf photosynthesis and photosynthetic nitrogen efficiency or PNUE. These shifts in leaf P:N are reflected in increased leaf PNUE, suggesting that P-mediated increases in N productivity may directly offset the temperature dependence of net primary productivity

Bivariate correlations show that many of the traits of the most abundant tree species per community, a , as well as the whole-community trait distribution, c , covary with temperature (Figures 2 and 3; Supporting Information Figures S1 and S2). Consistent with predictions from H2 (Figure 1), mean community traits that underlie the growth equation $\langle \text{P:N} \rangle$, $\langle \text{LMA} \rangle$ and $\langle \text{PNUE} \rangle$, all shift along the elevational gradient (Table 2; Supporting Information Tables S4 and S5). The shifts in PNUE and photosynthesis are strongly correlated with each other (Figure 1a,b; $r^2 = .764$; $p = .001$), indicating that shifts in leaf P:N with increased elevation (decreases in temperature) are also associated with greater photosynthetic efficiency that together appear to result in similar values of leaf-level photosynthesis. We observe decreases in N with temperature, but that P content is independent of temperature. Thus, compared with warmer forests at lower elevations, colder forests tend to be composed of leaves with higher values of LMA, greater amounts of P relative to N, higher PNUE (as measured by ϕ_L^A or grams of carbon dioxide per metre square of leaf per gram of nutrient per unit time) and increased photosynthetic rates per unit nitrogen, but approximately constant rates of photosynthesis (in grams of carbon dioxide per metre square of leaf per gram of nutrient per unit time). We also observed significant negative shifts in $\langle \%N \rangle_c$ ($r^2 = .47$, $p = .028$). Leaf $\langle \%C \rangle_c$ also tended to decrease across the elevational gradient, but it was marginally significant ($r^2 = .33$, $p = .08$).

Consistent with theory (see Table 1 VI), our analyses indicate that the community mean trait values $\langle \text{P:N} \rangle_c$, $\langle \text{PNUE} \rangle_c$ and $\langle \text{LMA} \rangle_c$, all shift exponentially with temperature across the gradient (Table 2; Supporting Information Table S6). Potential exponential temperature

dependences (e.g., a modified 'Arrhenius plot'; see Gillooly et al., 2001; White, Xiao, Isaac, & Sibly, 2012) are revealed by plotting the natural logarithm of biological response (here the community mean trait value or GPP, NPP) versus the inverse product of the Boltzmann constant and temperature as measured in kelvin ($1/kT$). The fitted linear slope then is an estimate of E or how sensitive the biological response is to temperature. For these traits, we estimate E to be 0.16, 0.15 and 0.19 eV, respectively (Table 2). Consideration of the 95% CIs for $\langle \text{P:N} \rangle_c$ indicates that E ranges from 0.03 to 0.28 eV.

Across the elevation gradient, analyses of the shape of the community distribution (variance, skewness and kurtosis), as estimated by our trait bootstrapping method, show significant trait structuring (Figure 3; Supporting Information Figure S3; Table S7). All community trait distributions, except for %C, are characterized by positive kurtosis (see Figure 3), indicating strongly peaked trait distributions. Furthermore, except for %C, all traits also show positive skewness, with %P and LMA showing the strongest positive skewness. Note that symmetrical distributions are characterized by skewness values of zero, and kurtosis values greater than zero indicate a more 'peaked' distribution than a normal distribution characterized by skewness and kurtosis of zero.

The observed patterns in the higher moments of the trait distributions are consistent with several predictions from theory (Box 1; Table 1). First, consistent with theory (Box 1a), traits associated with growth rate tended to cluster or converge to a common site 'optimal' specific value. Furthermore, community trait distributions tended to be unimodal (Supporting Information Figures S3 and S4), with many

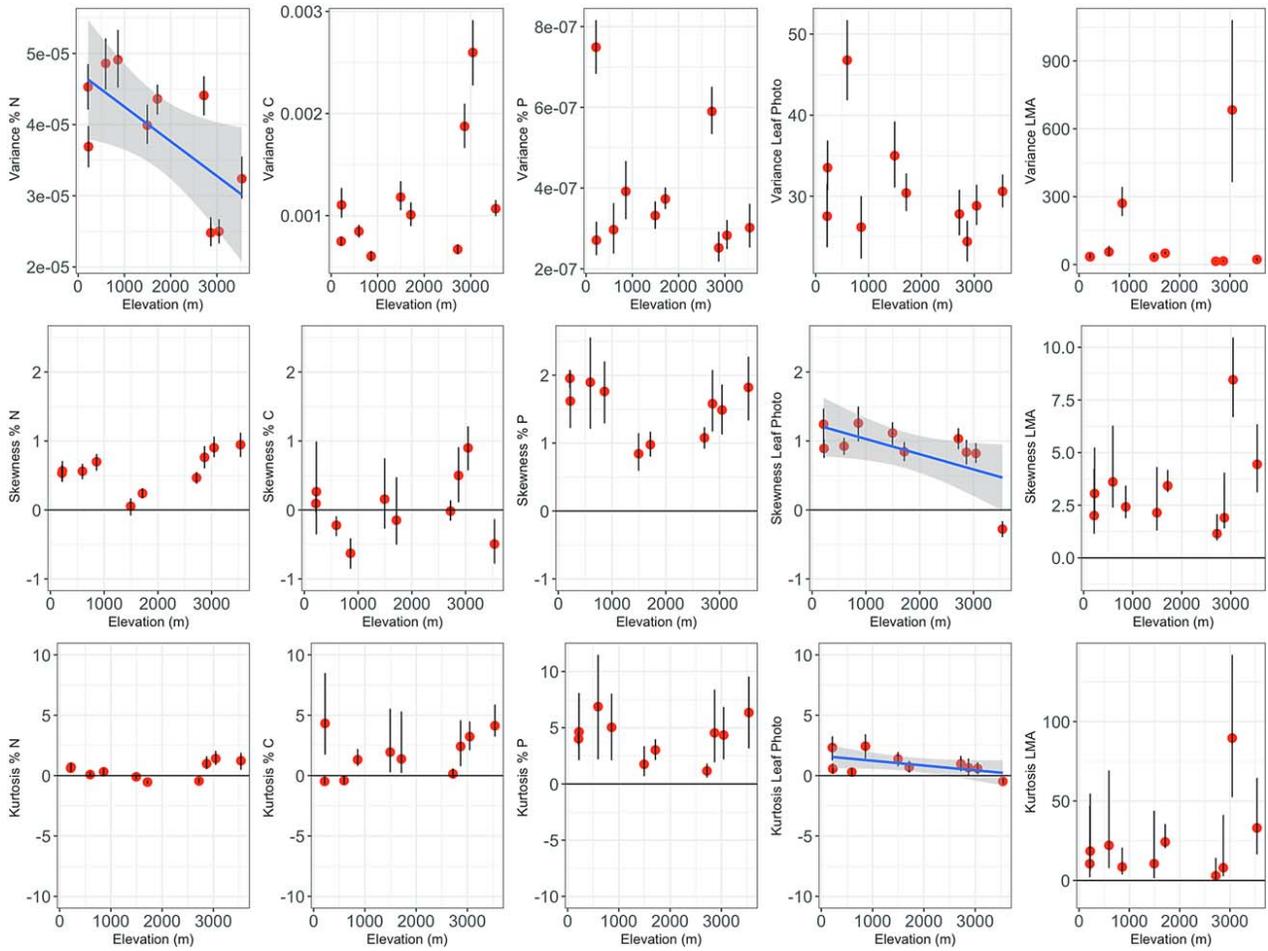


FIGURE 3 Assessing shifts in the statistical moments (mean, variance, skewness and kurtosis) of the community trait distribution across elevation. Moments were generated for five community leaf traits (N, P, C, photosynthesis and LMA) for each of the 10 forest plots sampled for traits across the Perú elevational gradient. We generated 1,000 bootstrapped community-wide trait distributions for each plot by sampling from each species' intraspecific trait distribution for individuals of species measured across the same Peruvian gradient. The moments describing the shape of the trait distributions (variance, skewness and kurtosis) and their 95% confidence intervals (shown by the dark vertical lines) are reported around each moment value. Confidence intervals are calculated based on the 1,000 bootstrap replicates for each plot (see Materials and methods). Across all forest plots, all traits, except for leaf C, were characterized by skewed community distributions (skewness > 0) and distributions that were more peaked than expected by normal distribution (kurtosis > 0) or even a uniform or even distribution (kurtosis = -1.2)

traits (C, P, photosynthesis and LMA) showing positive kurtosis (Figure 3). Second, consistent with the expectations of Feeley et al. (2011) and predictions from theory (Box 1b and c), the community mean values of LMA (as well as P, N and photosynthesis) show skewed distributions (see Figure 3), indicating that forests along the elevational gradient are directionally shifting in trait composition in response to directional shifts in temperature but that the trait composition and dominance are lagging the shift in temperature attributable to changing climate; see Box 1 and Table 1 III). Third, as a result, consistent with theory (Box 1c), the skewness values of $\langle \text{LMA} \rangle_c$ for all forest plots were positive, indicative of a dynamical shifting community in response to changing temperature. Few of the traits showed directional trends in the higher moments with elevation. Exceptions included photosynthesis, which showed decreases in skewness and kurtosis with increasing elevation, and the variance in N decreased with elevation.

To assess predictions of H2 (Figure 1) further, we next assessed whether the observed elevational shifts in community trait means were associated with shifts in the metabolic traits that underlie the plant growth normalization b_0 (see Supporting Information Equation S16). Specifically, we assessed whether the observed covariation in community trait values with elevation and temperature reflect selection for temperature adaptation and acclimatization, resulting in equalization of leaf photosynthesis and plant growth rates. In short, if the traits of the tree growth normalization b_0 [PNUE (ϕ_L^A), LMA ($\frac{m_L}{a_L}$) and P:N; see Supporting Information Equation S15] covary with temperature (T), they may negate or diminish the expected kinetic effects of temperature on ecosystem production (GPP and NPP) where $\text{NPP} \propto \text{GPP} \propto e^{-\frac{0.65}{kT}}$ (see Equation 2; Supporting Information Equation S16).

To assess whether the observed covariation in plant growth traits with temperature is consistent with H2 (Figure 1), we estimated the community or plot average value of b_0 (see Equation 3) by multiplying

TABLE 2 Boltzmann–Arrhenius fits of variation in the community mean trait values and NPP and GPP as an inverse function of temperature ($1/kT$)

Dependent variable	$\ln(<P:N>_j)$	$\ln(<PNUE>_j)$	$\ln(<N>_j)$	$\ln(<LMA>_j)$	$\ln(NPP/M_{Tot}^{3/5})$	$\ln(GPP/M_{Tot}^{3/5})$
Temperature sensitivity, E (eV)	0.21	0.19*	-0.10*	0.29***	-0.19***	-0.13**
95% CI	(-0.02 to 0.44)	(0.02-0.35)	(-0.21 to 0.0004)	(0.18-0.39)	(-0.31 to -0.06)	(-0.24 to -0.03)
Fitted intercept	-11.44**	-5.99	4.86**	-6.70**	7.00**	5.98**
95% CI	(-20.57 to -2.32)	(-12.54 to 0.56)	(0.70-9.02)	(-10.92 to -2.48)	(2.09-11.92)	(1.70-10.27)
Observations	10	10	10	10	16	16
r^2	0.29	0.38	0.32	0.78	0.39	0.30

Note. Community weighted trait mean values were estimated by our community subsampling routine. Estimates of the temperature sensitivities of each trait, E , are from fitting the Boltzmann function, $e^{-E/kT}$. The associated 95% confidence intervals (CIs) for E are given in parentheses. Consistent with our theory (see Supporting Information Equation S5), because of the similar estimates for E observed for LMA and PNUE, $\ln <Photo>$ should remain approximately constant with temperature, as observed. Nonetheless, biomass-corrected values of NPP and GPP [$\ln(NPP/M_{Tot}^{3/5})$ and $\ln(GPP/M_{Tot}^{3/5})$, respectively] decrease slightly with temperature. * $p < .1$; ** $p < .05$; *** $p < .01$.

the community abundance weight of five growth traits $b_0 \sim (\langle \phi_L^A \rangle \cdot \langle \frac{m_L}{a_L} \rangle^{-1} \cdot \langle \frac{P}{N} \rangle \cdot \langle \beta_L \rangle)$, but here we did not include the expected temperature dependency, $e^{-\frac{0.65}{kT}}$. For trees, we used an estimate of β_L , the leaf mass fraction, using a value of 0.1 from Poorter et al. (2012). We plotted this estimate of the growth normalization (b_0) as a function of temperature. Our results indicate that (b_0) is independent of temperature (Figure 4). If decreases in temperature reduced tree growth rates then we would have expected a negative relationship in Figure 5, with a slope approximating -0.65 . But this is not what we see. Indeed, our results support hypothesis H2, indicating that the observed shifts in plant growth traits with temperature in part negate the kinetic effects of temperature on plant growth.

Theory also predicts that $NPP \propto GPP \propto \langle b_0 \rangle e^{-E/kT} [\frac{5}{3} M_{Tot}]^\alpha$, where the value of α should approximate 3/5 or 0.60 (see Table 1 IV) in forests close to resource and demographic steady state (Duncanson, Dubayah, & Enquist, 2015; Enquist et al., 2009). Also, NPP and GPP is expected to vary exponentially with temperature as $NPP \propto GPP \propto e^{-E/kT}$ with an estimate of E of c. 0.65 eV; (Allen et al., 2005; Enquist et al., 2003; Gillooly et al., 2001; Perkins et al., 2012; Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010). These predicted relationships should become more apparent after controlling for covariation between temperature and standing biomass, as well as potential variation in b_0 . Tables 2 and 3, Supporting Information Tables S8 and S9 show the results of fitting various models where the values of α and E could vary as well as assessing the relative importance of other potential drivers of variation in NPP and GPP. For the models that best explained variation in NPP and GPP (using either adjusted R^2 or AICc), the observed value of the scaling exponent α overlapped with the theoretical prediction of 3/5 or 0.6 (see Equation 2). The observed values of α were much closer to prediction and the models with higher adjusted R^2 values occurred when the covariate of site temperature was included (Supporting Information Table S5; Figure 5).

Consistent with theory (H2), variation in stand biomass is a primary determinant of variation in ecosystem functioning (Figure 4; model r^2 values range from .65 to .49; Table 3). Adding temperature improves the predictive ability of the model (adjusted R^2 values of .66 and .71), indicating that the best predictors of variation in NPP and GPP are stand biomass followed by temperature. These results also support the prediction that two variables, stand biomass and environmental temperature, are the best predictors of variation in ecosystem production (Figures 4 and 5). The above results are also supported by assessing 18 separate models that include different potential combinations of categories (stand biomass, traits and environmental drivers) as well as each category separately (Supporting Information Tables S1, S8 and S9).

5 | DISCUSSION

Previous work by Malhi et al. (2017) has shown that across this elevation gradient, tropical forest NPP and GPP decrease with elevation and correspondingly increase with temperature. However, this past work has also shown that the total forest biomass also covaries with temperature across the elevation gradient. Our results also show that the trait

TABLE 3 Scaling of NPP and GPP with total stand biomass and multiple model with Boltzmann temperature

Dependent variable	GPP	NPP	NPP	GPP
Predicted scaling exponent, $\alpha=3/5$	0.6	0.6	0.6	0.6
Observed scaling exponent, α	0.79***	0.73***	0.49**	0.59***
95% CI	(0.50–1.07)	(0.36–1.10)	(0.15–0.83)	(0.31–0.88)
Predicted temperature sensitivity, E (eV)			0.65–0.32	0.65–0.32
Observed temperature sensitivity, E (eV)			0.21**	0.16**
95% CI			(0.07–0.35)	(0.04–0.28)
Fitted intercept	–0.20	–1.05	8.38**	7.02**
95% CI	(–1.48 to 1.09)	(–2.70 to 0.59)	(1.78–14.98)	(1.48–12.57)
Observations	16	16	16	16
Adjusted R^2	0.65	0.49	0.66	0.73

Note. Variation in NPP and GPP are well fitted by models that include either standing biomass alone (first two columns) or standing biomass and environmental temperature (last two columns). Estimates of the scaling exponent, α , come from fitting the scaling of NPP or GPP with total stand biomass. Temperature sensitivities of each trait, E , are from fitting the Boltzmann function, $e^{-E/kT}$. The associated 95% confidence intervals (CIs) for E and the metabolic scaling exponent are given in parentheses. Models with both total stand biomass and temperature resulted in better fits (higher adjusted R^2 and lower corrected Akaike information criterion value). Theoretical predicted values for α and E are also listed. The predicted value of $E = 0.65$ – 0.32 eV is when growth traits in the growth normalization b_0 do not covary with temperature. * $p < .1$; ** $p < .05$; *** $p < .01$.

composition, the total biomass and ecosystem productivity all covary with each other and shift directionally with temperature (Tables 2 and 3; Supporting Information Tables S4–S6; Figures 3 and 5). These changes reflect an overall multivariate shift in physiological functioning of tropical forests (Figure 2) best predicted by temperature (Figure 1b; Supporting Information Figures S1 and S2). Compared with warmer lower elevation forests, colder high-elevation forests are composed of leaves with higher values of LMA, greater amounts of P relative to N, and higher PNUE. These results are consistent with several recent studies documenting some trait correlations in tropical forest canopy traits across elevation (Asner & Martin, 2016; Malhi et al., 2017) where tropical forest canopy LMA, PNUE, non-structural carbohydrates (NSC) and P concentrations tend to increase with elevation, but the mean foliar N declines. Sometimes these studies found that foliar P showed no trend with elevation (Asner et al., 2014), as we find here. Although these studies did not assess shifts in leaf P:N, our results do generally support the finding that leaf P:N increases with decreases in temperature (Elser et al., 2010; Hedin, 2004; Swenson et al., 2012).

Generally, the underlying drivers of several of the traits we have measured here, including LMA and leaf chemistry, include a diverse array of climate and soil fertility factors (Asner & Martin, 2016; Poorter, Niinemets, Poorter, Wright, & Villar, 2009). For example, Cordell, Goldstein, Mueller-Dombois, Webb, and Vitousek (1998) have shown that temperature and radiation, and perhaps humidity, are among the most important drivers of LMA on tropical elevation gradients (Cordell et al., 1998). Our analyses indicate that these shifts in community trait means are approximately exponential with temperature (Table 2). Fitting a Boltzmann–Arrhenius function to these relationships reveals that these community traits are characterized by temperature responses (E) of c. 0.15 (see Table 2). Importantly, these shifts have resulted in approximately constant rates of leaf photosynthesis (Figure 3).

Our results support, in part, the predictions of hypothesis H1 (see Figure 1). First, a fit of the predicted equation from MST, $\ln(\text{GPP}) \propto \ln(\text{NPP}) = b - \frac{E}{kT} + \alpha \ln(M_{\text{Tot}})$, where b is a constant and α is the ecosystem scaling exponent hypothesized to be c. 3/5 or 0.6 (Enquist et al., 2009; Michaletz, Cheng, Kerkhoff, & Enquist, 2014), explains 68 and 73% of the variation in GPP and NPP, respectively (see Table 3). All the other potential hypothesized drivers of NPP and GPP variation did not explain as much variation and did not compete as well as the model with only stand biomass and temperature (see Supporting Information Tables S7 and S8). Second, after controlling for covariation with temperature, the fitted value of α was indistinguishable from the predicted value of 3/5 or 0.60 (Figures 1 and 5; Table 3; Supporting Information Tables S7 and S8). However, although we did find that temperature had a significant effect on variation in NPP and GPP as hypothesized in H1, the functional response was significantly shallower than predicted by H1. Specifically, the predicted temperature response of NPP and GPP did not support the a priori hypothesis (H1; Figure 1) of E c. 0.65 eV or even E c. 0.32 eV if photosynthesis exhibited differing temperature responses. Instead, the observed change in NPP and GPP is characterized by a much shallower temperature function with E c. 0.16 and 0.20 eV for GPP and NPP (95% CI = 0.07–0.32 and 0.05–0.26, respectively; Table 2; Supporting Information Tables S7 and S8).

Support for H2 (Figure 1) is given by the observed directional shift in the many growth traits that underlie the growth normalization, b_0 (Figure 2), the resulting approximate constancy of the community tree growth normalization $\langle b_0 \rangle$ across the gradient (Figure 5c), and the very shallow temperature response of NPP and GPP (Figure 5a,b). Hypothesis H2 states that a shift in growth traits such as $\langle \text{LMA} \rangle$ will help to stabilize leaf temperatures around their physiological optima (Michaletz et al., 2016), and a shift in growth traits such as $\langle \text{P:N} \rangle$ and $\langle \text{PNUE} \rangle$ can also compensate rates of growth with decreases in

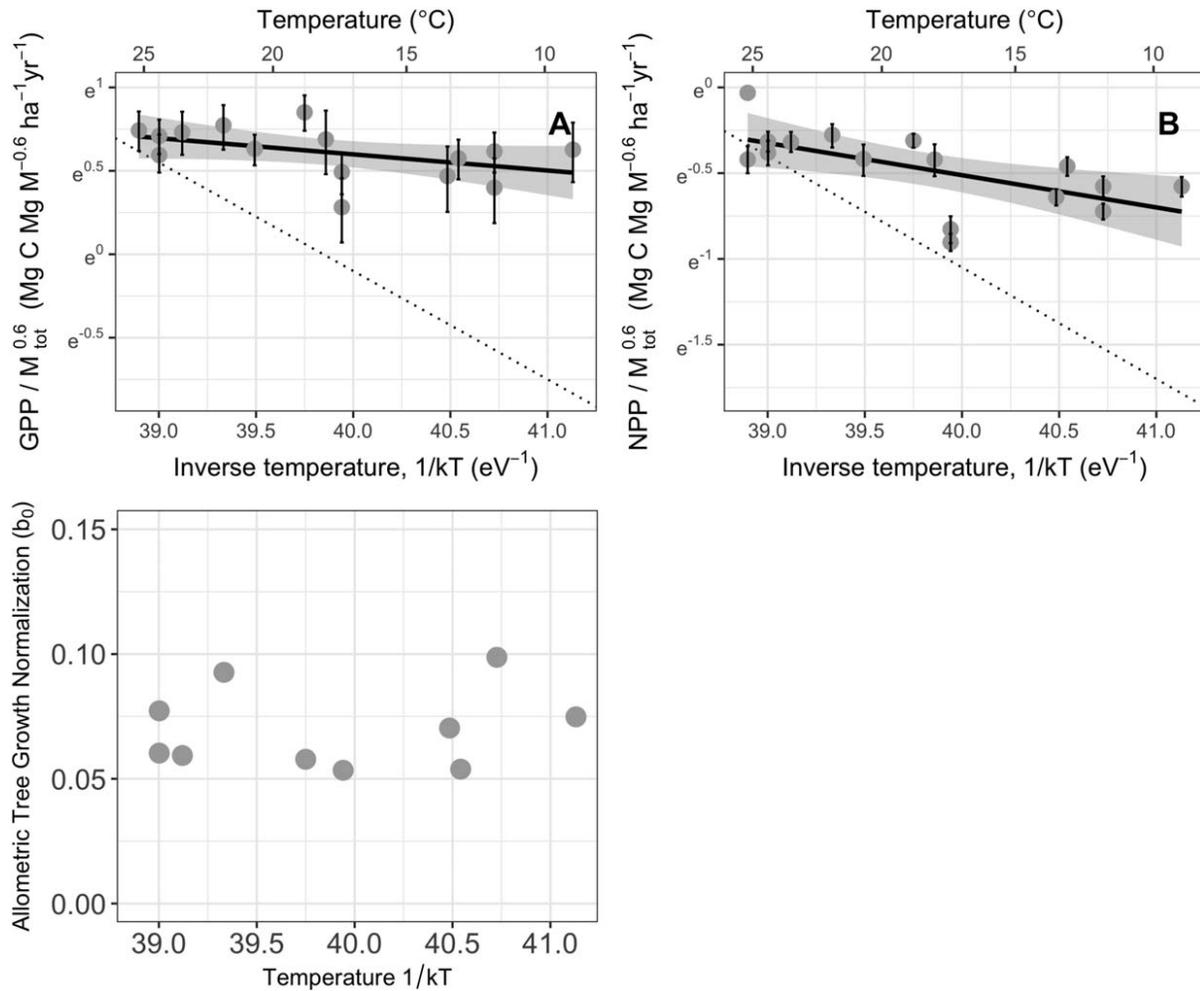


FIGURE 4 Modified Arrhenius plots of variation in forest biomass-corrected variation in GPP, NPP and the metabolic normalization, b_0 . These plots reveal the functional role of temperature on variation in (a) GPP, (b) NPP and (c) the metabolic normalization, b_0 , between forest plots (White et al., 2012). In (a) and (b), the y axes plot the natural logarithm of the quotient of annual GPP or NPP and $M_{\text{Tot}}^{0.6}$ obtained from rearrangement the predicted scaling function in Equation 2 (i.e., $\ln \left(\frac{\text{GPP}}{M_{\text{Tot}}^{0.6}} \right) \propto \ln \left(\frac{\text{NPP}}{M_{\text{Tot}}^{0.6}} \right) = -E \cdot \frac{1}{kT}$, with slope E and independent variable $1/kT$). The fitted slopes yield an estimate of the temperature sensitivity, E , for GPP and NPP where $E_{\text{GPP}} = 0.158$ (95% CI 0.045–0.270; $r^2 = .349$) and $E_{\text{NPP}} = 0.195$ (95% CI = 0.0619–0.329; $r^2 = .371$), respectively. The observed temperature sensitivities for both GPP and NPP are much shallower than the expectation of E_{GPP} and $E_{\text{NPP}} = 0.65$ (the dotted line in both graphs). In (c), the value of b_0 , the tree growth rate normalization, was estimated by multiplying the community average of the three traits $b_0 \sim \left(\langle \phi_L^A \rangle \cdot \langle \frac{m_L}{a_L} \rangle^{-1} \cdot \langle \frac{P}{N} \rangle \cdot \langle \beta_L \rangle \right)$. For trees, we used an estimate of β_L , the leaf mass fraction of 0.1 (Poorter et al., 2012). As b_0 does not significantly change with temperature, the observed shifts in the traits that underlie b_0 with temperature (Figure 3) support hypothesis H2, where covariation in these traits with temperature will lower the kinetic effects of temperature on plant growth, which will then decrease E_{GPP}

temperature (Kerkhoff et al., 2005). Indeed, consistent with this expectation, we find that the community average rate of leaf photosynthesis does not vary significantly with temperature. According to the 'growth rate hypothesis' (Elser et al., 2000; Kerkhoff et al., 2005), selection to increase growth rates because of shorter growing seasons and/or to upregulate metabolism and growth is reflected in organismal P:N ratios. Together, shifts in these traits could then lead to a maintenance of approximately constant rates of photosynthesis and rates of whole-plant growth rate despite changes in temperature (Kerkhoff et al., 2005; Niklas et al., 2005), as we observe here.

Our estimates of the temperature sensitivity of NPP and GPP are reflected by the fitted values of E . The observed values of E are lower

than the proposed range of value of b . 0.65–0.32 eV, indicating that the temperature response of forest productivity is very shallow. Accounting for covariation with total biomass, M_{Tot} , shows that the temperature sensitivity or E of for both GPP and NPP as c. 0.15–0.21 eV (see Tables 2 and 3; and Supporting Information Tables S7 and S8; Figure 5). In other words, going from our coldest high-elevation site ($1/kT = 41$) to our hottest lowland site ($1/kT = 39$), a value of E of c. 0.15 eV would equate to a 1.35-fold increase in productivity attributable to increases in temperature. In contrast, if plant growth traits did not covary with temperature and the temperature sensitivity of productivity was $E = 0.65$ eV then this would lead to a 3.67-fold proportional increase in NPP and GPP. Thus, we estimate that the NPP and GPP observed in

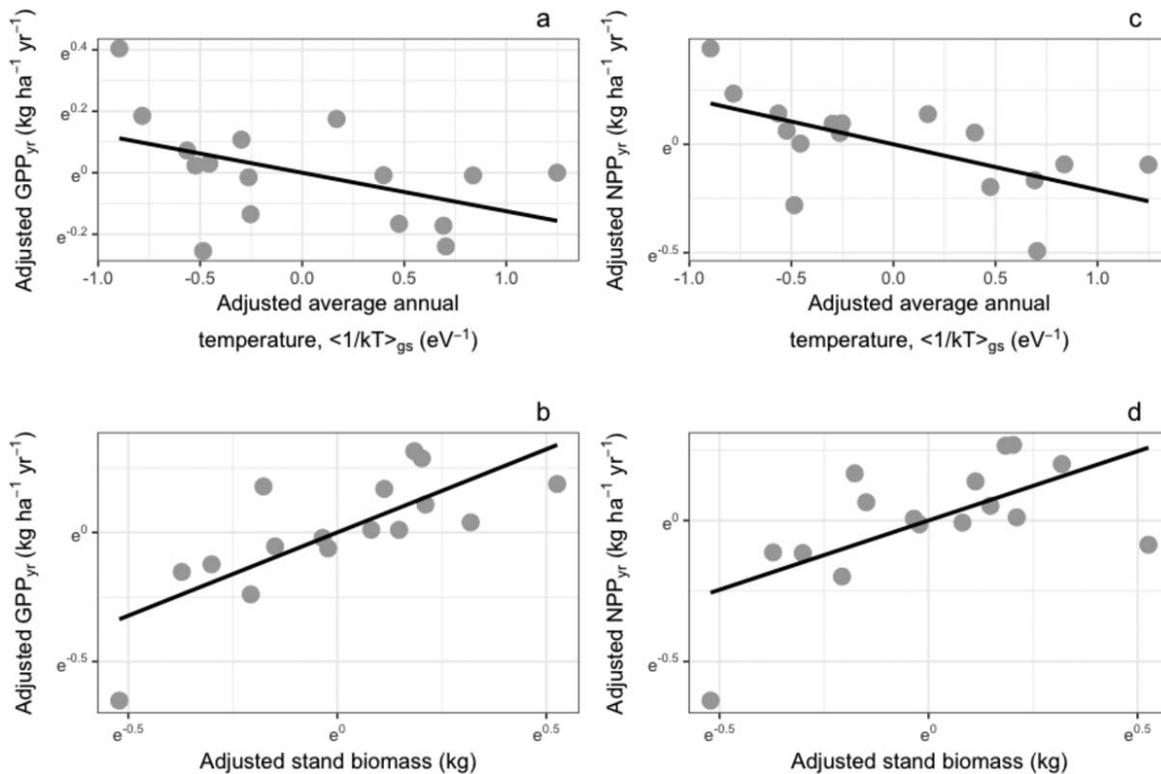


FIGURE 5 Partial regression plots illustrating relationships between annual gross primary productivity (GPP), net primary production (NPP) and individual covariates from Equation 8 for 18 woody plant communities across the Peruvian elevational gradient. Plots show the direct relationship (slope and variance) between GPP, NPP and each covariate while controlling for the influence of all other model covariates. (a, c) Annual temperature, T . (b, d) Stand biomass, M_{Tot} . In general, variation in above-ground biomass and mean annual temperature explain most of the variation in ecosystem NPP and GPP. The predicted scaling function $\text{NPP} \propto \text{GPP} \propto e^{-E/KT} M_{\text{Tot}}^{\alpha}$ explains 71 and 66% of the variation in NPP and GPP, respectively, and the fitted scaling exponent, α , for the scaling of NPP and GPP with total above-ground biomass is indistinguishable from the value of 0.6 predicted by theory (see Tables 1–3; Supporting Information Tables S8 and S9). However, the influence of temperature on NPP and GPP is much more muted than expected. The fitted value of the temperature sensitivity, E , is significantly lower than the expectation of $E = 0.65\text{--}0.32$ eV, and c. 0.21 and 0.16, respectively (see Supporting Information Tables S8 and S9)

our coldest sites is c. 2.3 times more than what would be expected if there was not the observed covariation in community growth traits.

Our results also support claims by Feeley et al. (2011) that increases in historical temperature attributable to climate change appear to be responsible for observed elevational shifts in the distribution of tree species (see also Bush, Silman, & Urrego, 2004). However, Feeley et al. (2011), working across this same elevational gradient, did not provide a mechanistic basis for these conclusions. The assumption is that observed upward migration of trees is driven by species sorting because of their different trait–temperature optima (Bush et al., 2004). An important finding is that the observed mean rate of change in the species composition of these plots is less than predicted from the temperature increases for the region (Feeley, 2012; Feeley et al., 2011). Thus, according to theory (Box 1), for traits more closely matched to plant growth, upwardly migrating tree species would result in skewed community trait distributions (Figure 3), consistent with the prediction that the trait composition of these forests is not matched to the local climate. As predicted, the skewness values for LMA are positive across the gradient, consistent with the expectation that these forest communities are currently shifting directionally to match their LMA at a given temperature (Box 1).

An important question raised by our analysis is, given the approximate constancy of b_0 (Figure 5) that supports H2, why do we still observe a shallow temperature dependence to variation in NPP and GPP (Figures 4 and 5)? Three possibilities might explain the shallow but non-zero temperature response of NPP and GPP:

First, other climate and historical constraints, such as increased disturbance history associated with landslides at higher elevations and/or increased importance of fog inundation and cloud cover at the higher elevations (see Malhi et al., 2017), may further reduce productivity at higher elevations.

Second, recent analysis of an individual-based forest model (Fyllas et al., 2014), applied to these same forest plots and using a carbon-based version of the MST growth function, suggests that differences in light availability across the gradient may explain residual variation in NPP not explained by total biomass and temperature (Fyllas et al., 2017). Thus, the weak temperature response of NPP could be driven by the interaction between resource availability and the kinetic temperature response of photosynthesis (see Supporting Information). For example, there is an indication that when light, nutrients and/or CO_2 are limiting, the temperature dependence of photosynthesis may be much weaker (see figs 3 and 4 in Berry and Bjorkman, 1980). Although

our results do not support a conclusion of Fyllas et al. (2017) indicating an important role of solar radiation in explaining the decrease in forest productivity (Supporting Information Tables S2, S8 and S9), we do show that both solar radiation and temperature are important predictors of the observed shift in community-level traits ($PCA1_d$) in mean community trait values (see Discussion).

Third, a shallow temperature response of NPP and GPP may reflect a lagging community response to directional climate change and increasing temperature. For example, the observed rate of trait shift across the temperature gradient is approximately exponential across the temperature gradient (Table 2), but the reported rates of tree migration in response to observed warming in the study by Feeley et al. (2011) are approximately constant across the gradient. A difference between these two rates would then increasingly lead to higher elevation forests being more 'lagged' between the new trait 'optimal' trait value, Z_{opt} , in a warming world (Box 1) and the current mean trait value, Z_{mean} , of the community. If correct, then the lower NPP and GPP in the colder forests reflects the dominant trait composition of higher elevation communities being more lagged in their trait values and further away from trait–environment optimal matching. Thus, we speculate that the observed shallow temperature dependence of NPP and GPP (Figure 5) might reflect an increasing hysteresis in the functioning of higher elevation, colder forests in response to climate change.

6 | CONCLUSIONS

The Peruvian elevation gradient provides a novel natural laboratory for assessing several predictions of trait-based scaling theory. The theory (Box 1; Table 1; Figure 1) is unique because it provides a general theoretical framework for trait-based ecology by integrating ecology, stoichiometry, allometry, metabolic scaling theory and physiological approaches to plant ecology and global change studies. Furthermore, it underscores the importance of the shapes of two distributions, namely the frequency distribution of plant sizes (via the ecosystem scaling exponent) and the frequency distribution of traits (via the moments of distribution), as being central to 'scaling up from traits' and predicting variation in ecosystem metabolism (Enquist et al., 2003; Michaletz et al., 2014). Indeed, our results indicate that variation in ecosystem productivity is characterized by a common allometric scaling relationship predicted by theory (Figure 5; Kerkhoff & Enquist, 2006; Michaletz et al., 2014). The theory also provides a quantitative foundation to show how (a) the diversity of plant form and function and (b) directional shifts in climate are reflected in the shape of trait distributions.

Our results highlight the fundamental role of temperature as a critical driver of tropical forest trait composition. More importantly, the theoretical foundation detailed here and the empirical results indicate that knowledge of stand biomass and canopy chemistry can predict variation in NPP and GPP in consistent and predictable ways that could be integrated into dynamic global vegetation models (DGVMs; Fisher et al., 2015; Fyllas et al., 2014). However, such insights have yet to be incorporated into global vegetation models (Marthens et al., 2012) as these models predict a high sensitivity of tropical GPP to temperature

(Galbraith et al., 2010). Our work indicates that global change models incorporating information about the shape of community trait distributions and the size distribution via the total stand biomass can improve predictions of future ecosystem function (see also Fyllas et al., 2017).

Together, our results and those of Fyllas et al. (2017) show that the observed shifts in leaf traits almost entirely compensate for the expected physiological decline of canopy photosynthetic rates with elevation, leading to a less-than-expected decline of productivity with elevation. However, the two studies differ in posited explanations for the residual observed slight decline in productivity with temperature. Fyllas et al. (2017) fitted the carbon-based trait growth equation from MST (Enquist et al., 2007) with additional assumptions of light limitation on photosynthesis. The present study does not make these assumptions. Our approach instead: (i) extends MST to provide new mechanistic analytical derivations to link how differences in leaf physiology, plant tissue nutrient stoichiometry and tree size influence tree growth and forest productivity; (ii) questions the primary role of solar radiation on directly driving variation in productivity across this elevational gradient via reductions in photosynthesis; and (iii) points to the importance of covariation between photosynthetic nutrient use efficiency, ϕ , or PNUE, and environmental temperature in mediating variation in tropical forest productivity observed across this gradient.

Combined with the findings of Kerkhoff et al. (2005) and Enquist et al. (2007), our results are consistent with the hypothesis (H2; Figure 1) that many directional changes in organismal traits across geographical gradients can be linked to the plant growth rate normalization, b_0 . An approximate constancy of b_0 means that trees in the warm lowlands grow at about the same mass-corrected rate as trees in the colder high-elevation forests. Ultimately, the observed approximate constancy of b_0 across an impressive c. 16.2 °C temperature gradient reflects how selection and/or community species sorting has resulted in the up- or downregulation of metabolism via respiration and/or photosynthesis. Thus, a more powerful test of several of our findings is to link the observed shift in traits ultimately to the temperature dependencies of respiration and photosynthesis (Yvon-Durocher et al., 2012) and to our understanding of how temperature influences photosynthesis and respiration within and across environments (Atkin, Loveys, Atkinson, & Pons, 2006, 2015; Berry & Bjorkman, 1980; Heskell et al., 2016). In addition, future work should assess the generalities of our findings by asking whether similar trait shifts in communities and ecosystem responses occur across other broad temperature gradients. Several studies do suggest that similar trait shifts are observed across tropical elevation and latitudinal (temperature) gradients (Asner & Martin, 2016; Hedin, 2004; Kerkhoff et al., 2005; Reich & Oleksyn, 2004). Nonetheless, our paper and the study by Fyllas et al. (2017; who also worked along this same Perú gradient) are the only studies so far to test predictions from trait-based scaling theory.

In sum, the observed shifts in tropical forest trait distributions are consistent with the expectations from trait-based ecology that (I) trait matching with the environment is widespread in both space and time (Ackerly, 2003; Westoby, Cunningham, Fonseca, Overton, & Wright,

1998); and that (ii) it originates from evolutionary and ecological processes that lead to the local dominance of specific phenotypes that maximize leaf carbon gain and whole-plant growth rates in variable environments (Chabot & Hicks, 1982; Pearcy et al., 1987); but that (iii) recent climate change has probably resulted in tropical forest communities with species trait composition increasingly in disequilibrium with the current climate (Blonder et al., 2015; Davis & Shaw, 2001; Svenning & Sandel, 2013). Together, trait-based scaling theory provides a quantitative framework to link pattern and process in communities and ecosystems via traits. It also allows us to assess the role of temperature as a primary driver of plant functional turnover.

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DATA ACCESSIBILITY

All data files used in these analyses and R code used for the analyses, graphs and tables presented in this paper are available as separate files in the Supporting Information.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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