Supplemental document

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

Brian J. Enquist1,2*, Lisa Patrick Bentley3, Alexander Shenkin3, Brian Maitner1, Van Savage4, Sean Michaletz1,5, Benjamin Blonder3, Vanessa Buzzard1, Tatiana Erika Boza Espinoza6, William Farfan-Rios7,8, Chris Doughty9, Gregory R. Goldsmith10, Roberta E. Martin11, Norma Salinas3,8, Miles Silman8, Sandra Diaz12, Gregory P. Asner11, Yadvinder Malhi3

*Corresponding author: Brian J. Enquist, email: benquist@email.arizona.edu

1 Department of Ecology and Evolutionary Biology, University of Arizona, AZ 85721, USA.
2 The Santa Fe Institute, 1399 Hyde Park Rd, Santa Fe, New Mexico 87501, USA.
3 Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, Oxford, OX1 3QY, UK.
4 Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, UCLA
5 Earth and Environmental Sciences Division, Los Alamos National Laboratory, MS J495, Los Alamos, New Mexico 87545, USA.
6 Institute of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland
7 Biology of Biology, Wake Forest University, Winston Salem, NC, USA
8 Sección Química, Pontificia Universidad Católica del Perú, San Miguel, Lima, Perú
9 School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ. 86011, USA
10 Ecosystem Fluxes Group, Laboratory for Atmospheric Chemistry, Paul Scherrer Institute, 5232 Villigen PSI, Switzerland
11 Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305, USA.
12 Instituto Multidisciplinario de Biología Vegetal (IMBIV, CONCIET-UNC), and FCEFYN, Universidad Nacional de Córdoba, Argentina
• Theory – Overview trait-based scaling theory
  • Parameterizing trait-based scaling theory – A stoichiometric and metabolic scaling based growth function
    o Linking Functional Traits to Tree Growth: Tissue Stoichiometry
    o Stoichiometric effects and interactions with plant size
    o Scaling from traits to ecosystems

• Methods
  o Traits Measured
  o Trait Measurement Protocol
  o Generation of trait distributions: Hierarchical bootstrapping method using intra and interspecific trait values.

• Supplemental Tables
  o Table S1 Environmental characteristics of 1ha plots across the elevation transect.
  o Table S2. Overview of the three differing cases of possible explanatory drivers for climate, biomass and climate, and traits and biomass.
  o Table S3. Loadings of community mean trait values for the traits of the most abundant species, <trait>, across the Peru elevation gradient.
  o Table S4. Loadings of community mean trait values, <trait> across the Peru elevation gradient for all individuals in the community.
  o Table S5. Change in Community Weighted Plot Traits with Elevation (Abundant Species) – Assessing shifts in the mean trait value of the community trait distribution across elevation.
  o Table S6. Change in Community Plot Traits with Elevation (Trait distribution subsampling method) – Assessing shifts in the mean trait value of the community trait distribution across elevation.
  o Table S7. Assessing shifts in the statistical moments (mean, variance, skewness, and kurtosis) of the community trait distribution, <c> across elevation.
  o Table S8 Competing differing models to best predict variation in GPP. Model competition based on AICc.
  o Table S9. Competing which models best predict variation in NPP. Model competition based on AICc.

• Supplemental Figures
  o Figure S1. Multivariate analyses of weighted mean trait values within each forest plot across the Peru elevation gradient.
  o Figure S2. Correlation table between PCA1, PCA 2 and climatic variables and the weighted mean trait values for the abundant species and the entire community.
  o Figure S3. Community frequency distributions of five foliar traits across the Peruvian elevational gradient generated using statistical subsampling of intra-and interspecific trait distributions.
  o Figure S4. Assessment of if trait distributions tend to be unimodal. Plots of the bimodality coefficient for each of the trait distributions plotted against elevation.

• Appendix
  o Appendix S1 Listing of the central notation, description, and units of the central mathematical variables.

• Bibliography
Theory – Overview of trait-based scaling theory

Trait-based scaling theory (Norberg et al., 2001; Savage et al., 2007; Enquist et al., 2015) outlines several predictions for scaling from traits to communities and ecosystems. As outlined in Box 1, and discussed in the main text, the theory is based on two set assumptions:

First, across an environmental gradient, $\varepsilon$, organisms will tend to have a unimodal functional response in their performance and fitness functions (Box 1). This stems from the assumption that organisms will tend to have a unimodal functional response in their performance and fitness functions (see Norberg et al. 2001).

It then follows that for a constant environment, $\varepsilon$, there are optimal trait values, $z_{opt}$, that maximize the growth rate of an individual given the environment (Norberg et al. 2001; Savage et al. 2007). However, a shift in the environment, $\varepsilon$, will affect the per capita population biomass production rate and thus which traits are dominant in the community or assemblage (Davis & Shaw, 2001). For a more detailed treatment of how species interactions and other community and landscape level processes can influence organismal functional responses see Norberg et al. (2001), Savage et al. (2007) and Enquist et al. (2015).

Second, trait-based scaling theory further predicts that the shape of the trait distribution will reflect various biotic processes and the dynamics of how communities respond to changing climate (Box 1). For example, the strength of local biotic forces is revealed via trait variance and kurtosis. Differing biotic community assembly hypotheses can differentially influence the spacing of trait values within the range of filtered phenotypes. If a given climate selects for a few optimal traits that maximize local performance (Norberg et al. 2001), competition for a common limiting resource would ultimately lead to dominance of individuals with similar trait values (e.g. see (Tilman, 1982) resulting in a convergence of ‘superior competitor’ phenotypes (Abrams & Chen, 2002; Savage et al., 2007; Mayfield & Levine, 2010). This convergence would be reflected by decreasing variance and an increase in unimodal ‘peakedness’ of the trait distribution or an increase in positive kurtosis (Navas & Violle, 2009).

In contrast, if traits map onto niche differences, increased niche (trait) differentiation will lead to increasing coexistence of individuals with differing traits (Chesson, 2000). These classical niche partitioning models predict that competition could also limit functional (trait) similarity (MacArthur & Levins, 1967) and thus increase the spacing between co-occurring phenotypes (see (MacArthur, 1958; Diamond, 1975)). Alternatively, biological enemies (Kraft & Ackerly, 2010), facilitation (Brooker et al., 2008) and frequent disturbance (Grime, 1998) can maintain trait diversity (e.g. an over-dispersion of phenotypes). Niche-based models result in either a broader or evenly dispersed trait distribution (high variance) or even a multimodal trait (negative kurtosis) distribution; (Box 1). Nonetheless, trait-based scaling theory, because of the strong assumption of local trait optima would predict unimodal trait distributions that tend toward positive kurtosis.

As shown in Box 1 (see main text), shifts in climate should be reflected in skewed trait distributions. Because of time lags between environmental change and the time scale of organismal responses (growth, demography etc.), the trait distribution of an assemblage will not
be able to instantaneously track environmental change. As a result, skewness in the trait
distribution will develop. The implication is that trait-based ecology can infer the dynamics of
trait assemblages by assessing the shape of contemporary trait distributions. Any shifts in $\varepsilon$ (or
temperature) would be expected to also shift the trait distribution, but we would also expect to
observe skewed trait distributions for communities responding to climate change. As discussed
below, changes in the shape of the trait distribution or a shift in the distribution will have
implications for ecosystem functioning.

**Parameterizing trait-based scaling theory – A stoichiometric and metabolic scaling based growth function**

Here we parameterize trait-based scaling theory by first incorporating a central organismal trait,
body size. Indeed, a central prediction of metabolic scaling theory (MST) is that variation in the
rate of metabolism, $B$, of an organism (i.e. respiration rates, gross photosynthesis) is due to the
combined effects of two variables, its body size, $m$ (West *et al.*, 1997) and the absolute
temperature, $T$ in kelvin (K; (Gillooly *et al.*, 2001), where

$$B = B_0 e^{-E/kT} m^\theta$$  \hspace{1cm} (S1)  

and $B_0$ is the metabolic normalization constant (units of Watts $m^{m^\theta}$) that is independent of
body size and temperature. The value of $B_0$ has also been linked to several tissue and cellular
traits (Enquist *et al.*, 2007b; Allen & Gillooly, 2009; Elser *et al.*, 2010). The value of $\theta$ is
predicted to approximate $\sim 3/4$, reflecting how natural selection has optimized the scaling of the

The importance of temperature is given by the Van’t Hoff/Boltzmann factor, $e^{-E/kT}$, and
describes the temperature dependence of metabolic rate, where $E$ is the sensitivity of metabolism
to temperature and $k$ is Boltzmann’s constant, $k = 8.62 \times 10^{-5}$ eV K$^{-1}$ (Gillooly *et al.*, 2001).

Previous research has indicated that the activation energy, $E$, is approximately constant for
respiration and approximates 0.65 eV for both animals and plants (Gillooly *et al.*, 2001; Enquist
*et al.*, 2003; Yvon-Durocher *et al.*, 2010; Anderson-Teixeira & Vitousek, 2012), the two groups
which comprise most biomass in terrestrial ecosystems.

*Estimates of $E$ and the sensitivity of photosynthesis to temperature*

The kinetics of net photosynthesis are determined by multiple rate-limiting processes (Medlyn *et al.*, 2002; Sage & Kubien, 2007; Bernacchi *et al.*, 2009). These include several temperature-
dependent limitations on photosynthesis such as the maximum rate of electron transport
(Farquhar *et al.*, 1980; Sage & Kubien, 2007), inactivation of Rubisco (Crafts-Brandner &
Salvucci, 2000), or stomatal closure (Berry & Bjorkman, 1980; Sage & Kubien, 2007; Bernacchi
*et al.*, 2009). These processes, each with unique temperature-dependencies, are ultimately
integrated into a single temperature response curve for net photosynthesis that can be
characterized by an overall effective activation energy $E_p$ (Michaletz in review).

Past hypotheses for the value of the activation energy for photosynthesis, $E_p$, stem from two
approaches. First, Kerkhoff *et al.* (2005) averaged the mean values for $E$ for $V_{\text{cmax}}$ and $J_{\text{max}}$
from Table 2 of (Leuning, 2002), which gives $E_p \sim 0.65$ eV. This first approximation may be an
overestimate as the averaging method does not account for interactions of multiple limitations on
net photosynthesis. For example, $V_{\text{cmax}}$ and $J_{\text{max}}$ were obtained under ideal conditions of
saturating, non-limiting light and CO$_2$. In real forest canopies, however, photosynthesis may become limited by light and/or CO$_2$, making it less sensitive to temperature (Berry and Bjorkman 1980). Alternatively, to incorporate the multiple rate limitations, a second approach (Allen et al., 2005) (Allen et al. 2005) assumed that photosynthesis: i) can be characterized as C3, ii) is limited by Rubisco-catalyzed carboxylation ($V_{\text{max}}$), and iii) occurs at operative temperatures below the optimal temperature for photosynthesis. The activation energy of photosynthesis was then calculated using a model for carboxylation-limited C3 photosynthesis (Farquhar et al., 1980) parameterized with empirical activation energies (Bernacchi et al., 2001) based on data from one species (transgenic tobacco) for the four model parameters. This yielded an estimate of $E_p = 0.32$ eV and was applied across terrestrial plants. Nonetheless, the approach implicitly comprises several interactive kinetic processes (cf. (Farquhar et al., 1980)). The predictions from each of the different methods for estimating $E_p$ have not been adequately evaluated using leaf-level data for net photosynthesis (but see Michaletz in review). This is an outstanding research need. Additional work is needed to better understand and characterize the role of photosynthetic kinetics for macroecological patterns and processes.

### Visualizing temperature sensitivities - Arrhenius Plots

Equation S1 can be linearized as $\ln \left( \frac{B}{m^\theta} \right) = \frac{E}{kT} + \ln \left( (B_0) \right)$ so that a modified ‘Arrhenius Plot’ of the natural log of $B$ versus the inverse of temperature as measured in Kelvins will reveal a slope of that is equal to $E$ (see also (White et al., 2012) The value of $E$ is then a quantitative measure of the temperature sensitivity of metabolism with lower values of $E$ reflecting lower temperature sensitivities. Note, plotting $B$ as the quotient of $\frac{B}{m^\theta}$ removes the allometric or mass dependency on $B$.

### Linking functional traits to tree growth via tissue stoichiometry

We start by reviewing and further refining a general mechanistic trait-based scaling model to quantitatively link variation in net primary production, environmental temperature, biomass, and functional traits. Plant functioning is affected by stoichiometric composition, that is the relative concentrations of various macro- and micronutrients in plant tissues (Chapin et al., 1986; Aoren, 1988; Ågren, 2004). Variation in organismal nutrient content can be linked to variation in organism growth rates (Sterner & Elser, 2002) using the following formalism,

$$\frac{C}{X} = \frac{\phi}{\mu} \tag{S2}$$

Here $C$ is the mass of carbon, and $X$ is the mass of a nutrient such as nitrogen (N) or phosphorous (P) and $\phi$ is the efficiency of using $X$ to generate $C$ (e.g. photosynthetic nutrient use efficiency or PNU). PNU or $\phi$ is defined as net photosynthetic rate ($\dot{A}_L$) per unit leaf N content ($E^N_L$)),

while $\mu$ is mass-specific growth rate (dm/mdt). Eq. S2 assumes balanced growth, i.e.,

$dC/Cdt = dX/Xdt = dM/Mdt$ and can be rearranged to show how organismal mass-specific growth rate will change as a function of organismal stoichiometry, $\mu \propto \phi \left( \frac{X}{C} \right)$. This relation should apply whenever availability of $X$ limits growth rate. When another aspect of growth is limiting, $\mu$ may saturate in its response to increasing $X$, as is often the case in plants.

Carbon (C), nitrogen (N) and phosphorus (P) are critical important elements for organisms (Sterner and Elser 2002). The relative concentrations of C, N, and P in biomass reflects multiple biological, ecological, and evolutionary processes as well as patterns of element supply from the
environment (Sterner and Elser 2002). Increasingly, the values and ranges of C:N:P ratios in an organism are important determinants of the ecological niche (Elser et al., 2000) and reflect multiple ecological processes (Elser et al., 2000; Kerkhoff et al., 2005).

For Eqn S2, variation in $x$ has been primarily linked to ratio of nitrogen (N) and phosphorus (P). Variation in N and P are important as they are the nutrients that most commonly limit plant growth and primary productivity (Güsewell, 2004). The role of N and P in the component processes of growth likely depends on the relative availability of the two resources as well as the underlying biochemistry (Chapin et al., 1986; Aoren, 1988; Ågren, 2004). Further, the effects of nutrient concentrations (i.e., dry mass fractions, g nutrient $\cdot$ g biomass$^{-1}$) on the terms of eq. (S2) may be either independent of or collinear with the effects of whole plant mass (Neilson, 1995; Elser et al., 1996; Cebrian, 1999). Distinguishing these two types of effects requires an explicit hypothesis about how whole-plant nutrient concentration, $F_p$, varies with whole-plant size or mass.

The growth rate hypothesis, proposed by Elser et al. (Elser et al., 2010), can be parameterized in MST with specific traits and nutrient stoichiometry and nutrient use efficiencies that underlie $\phi$. Because carbon makes up an approximately constant fraction of dry biomass (Sterner and Elser 2002), the growth rate hypothesis states that one can substitute the mass concentration of P and N for the $X/C$ term in equation S2. Combined with eq. (S1), this makes the explicit the linkage with variation in plant tissue ratio of phosphorus to nitrogen where
d$M/Mdt = \mu \propto \phi(P:N) m^{-1/4} e^{-E/kT}$. However, $\phi$ or PNUE is linked mainly to variation in tissue nitrogen via the photosynthesis per unit nitrogen (Kerkhoff et al. 2005). Thus, the relative growth rate, $\mu$, is predicted to increase as plant tissues become relatively more enriched in P relative to N and as $\phi$ increases (Niklas et al., 2005; Yu et al., 2012; Raven, 2015). As we discuss below, several additional traits can also be linked to the normalization constant $B_0$ of Eqn. S1 and hence can also potentially influence plant metabolism and relative growth rate.

Variation in P:N can reflect variation in how the total body nitrogen $N_T$ is allocated to protein construction and the proportion of the total body phosphorus $P_T$ that is allocated to rRNA (responsible for maintaining any specific quantity of protein). Further, variation in leaf tissue P, can reflect the importance of upregulation of plant growth via protein synthesis, ADP phosphorylation and triose phosphate production (Amthor, 1989; Stitt, 1990). Variation in the amount of triose phosphate translocators which requires phosphorus then directly impacts variation in the rate of phloem loading (Geiger, 1979; Sharkey, 1985). Eqn. S2 can then be stated to relate variation in relative growth rates to plant tissue P : N stoichiometry (Kerkhoff et al., 2005; Niklas et al., 2005) as $\mu \propto \phi \left(\frac{P}{N}\right)$ where increases in P relative to N and or $\phi$ (or PNUE). However, as we show below a more formal integration of traits that underlie variation in tree growth requires more detailed consideration of the traits that underly growth.

Stoichiometric effects and interactions with plant size and the growth rate normalization $B_0$

Next, we more formally integrate tissue stoichiometry with other traits that underlie variation in the scaling of metabolism and growth. Metabolic scaling theory or MST links how changes in organismal body size with several traits that are associated with the metabolic scaling normalization (Enquist et al., 1999; West et al., 1999a; Niklas & Enquist, 2001). This work starts
with the observation that whole-plant growth \( \frac{dm}{dt} \) is directly proportional to total leaf mass, \( M_L \), of individual plants, where

\[
\frac{dm}{dt} \propto B_0 m^{3/4} \propto (A_{L}^{M})M_L
\]  

(S3)

Here, \( B_0 \) is the metabolic growth normalization, \( m \) again is plant biomass, and \( A_{L}^{M} \) is the net leaf photosynthetic rate per unit leaf mass. The brackets \(<>\) indicate the abundance weighted average. Note, as discussed below the growth rate normalization is assumed to be directly proportional to the metabolic normalization \( B_0 \).

The growth normalization \( B_0 \) can be shown to comprise several traits. The value of \( A_{L}^{M} \) can be related to two additional leaf traits as

\[
A_{L}^{M} \equiv \left( \frac{1}{A_{L}^{A}} \cdot \frac{m_L}{a_L} \right)
\]

where \( \frac{m_L}{a_L} \) is the quotient of leaf mass, \( m_L \), and leaf area, \( a_L \) (the leaf mass per unit area, LMA) and, \( A_{L}^{A} \) is the photosynthetic rate per unit leaf area. Thus, variation in \( A_{L}^{M} \) can be linked to the leaf traits \( A_{L}^{A} \) and LMA as

\[
\frac{dm}{dt} \propto \left( \frac{1}{A_{L}^{A}} \cdot \frac{m_L}{a_L} \right)M_L
\]  

(S4)

Variability in the leaf mass-specific production can be linked to nutrient content and can reflect both environmental influences and differences in leaf photosynthetic capacity (see below). Variation in additional functional traits can be integrated into Eqn. S4 via a generalized function relating leaf nitrogen concentration, \( F_{L}^{N} \) to whole-plant production rates (Kerkhoff et al., 2005; see also (Agren & Bosatta, 1996; Elser et al., 2010). Specifically, \( \frac{dm}{M_L dt} \), the leaf mass-specific photosynthetic production rate or \( \mu_L \) (g \( \times \) g leaf\(^{-1} \times \) time\(^{-1} \)) is related to the leaf nitrogen content, \( F_{L}^{N} \) and \( \phi_{L} \), the photosynthetic nutrient use efficiency, PNUE,

\[
\frac{dm}{M_L dt} = \mu_L \propto \phi_{L}^{M} F_{L}^{N} = \phi_{L}^{A} \frac{a_L}{m_L} F_{L}^{N}
\]  

(S5)

Here, we can more formally define the photosynthesis nutrient use efficiency \( \phi_{L} \), or PNUE from eqn S2 as the rate of total biomass production per unit leaf mass, \( \mu_L \) is influenced by \( \phi_{L} \) a measure of the efficiency of leaves in using nutrients to assimilate mass. Note, PNUE can be measured two different ways:

- PNUE on a per unit leaf mass basis, \( \phi_{L}^{M} \) (g C \( \cdot \) g leaf\(^{-1} \cdot \) g nutrient\(^{-1} \cdot \) time\(^{-1} \)),
- PNUE on a per unit leaf area basis, \( \phi_{L}^{A} \) (g C \( \cdot \) m\(^2\) leaf \( \cdot \) g nutrient\(^{-1} \cdot \) time\(^{-1} \)).

Previous studies have shown that variation in PNUE may change with tissue nutrient concentration (Field & Mooney, 1986; Reich et al., 1997). Indeed, given the above we have,

\[
\phi_{L}^{M} = \mu_L / F_{L}^{N}
\]

and with substitution, \( \phi_{L}^{M} = (A_{L}^{A} \cdot \frac{a_L}{m_L}) / (F_{L}^{N}) \). This links how variation in PNUE measured on a per leaf mass basis or on a per leaf area basis, \( \phi_{L}^{A} = \langle A_{L}^{A} \rangle / (F_{L}^{N}) \), is tied to potential variation in \( F_{L}^{N} \), \( A_{L}^{A} \), and \( \frac{m_L}{a_L} \).

Variation in plant physiology and performance can also be linked to the importance of plant size or allometry. First, whole-plant growth rate, \( \frac{dm}{dt} \) (kg s\(^{-1} \)), where \( m \) is whole-plant mass, \( m \), can be linked to variation in whole-plant respiration rate \( \dot{R} \) (kg s\(^{-1} \)), whole-plant gross carbon assimilation rate \( \dot{A} \) (kg s\(^{-1} \)), xylem flow rate \( \dot{Q} \) (L s\(^{-1} \)), and the total number of leaves \( n_L \).
(dimensionless). A central prediction of MST is that we can link variation in whole-plant growth and physiological performance with variation in plant size and the allometry where
\[\frac{dm}{dt} \propto R \propto \dot{A} \propto \dot{Q} \propto n_L \propto m^\theta.\] Further, difference in allocation of the total organismal leaf mass, \(M_L\), varies allometrically with whole-plant mass, \(m\), as \(M_L \propto n_L, M_L = \beta_L m^{3/4}\) where the allometric coefficient \(\beta_L\) is the leaf mass fraction that reflects variation in allocation to leaf biomass and \(\theta\) is the allometric scaling exponent. From the common allometric scaling of net growth and photosynthetic production, the above arguments imply that plant respiration must also scale as the 3/4 power of whole plant mass, as predicted by allometric theory and observed in almost all organisms, i.e., \(\frac{dm}{dt} \propto R \propto m^{3/4}\) (Ernest et al., 2003; Savage, 2004b) but see also discussion in (Reich et al., 2006; Enquist et al., 2007a).

Rearranging we have, a generalized stoichiometry and trait based growth model for an individual

\[\frac{dm}{dt} \propto \phi_L^M F_L^N M_L \propto (\dot{A}_L^A \cdot \frac{a_L}{m_L})/(F_L^N) \cdot \beta_L m^{3/4}\] (S6)

Assuming Eqn S1 and S2 apply under conditions of constant mass and temperature, we can substitute for \(\phi \left(\frac{X}{C}\right)\) as proportional to \(B_0\) and if \(\theta = \frac{3}{4}\) then, with substitution, we can next show how variation in plant relative growth rate, is linked to plant size and temperature,

\[\frac{dm}{m dt} = \mu \propto \phi_L^M \left(\frac{X}{C}\right) e^{-E/kT} m^{-1/4}\] (S7)

Eqn. S7 shows that variation in relative growth rate, \(\mu\) will be influenced by plant size, \(m\), temperature \(T\), tissue nutrient stoichiometry, \(X/C\), the nutrient use efficiency and the metabolic normalization \(b_0\). The model implicitly assumes that no other resources are limiting (water availability, etc.). Eqn S7 states that the relative growth rate of a plant will decrease to the -1/4 power with increases in plant size, but that the growth rate will increase exponentially with increases in temperature and can be modified by changes in nutrient concentrations.

Given the growth rate hypothesis of Elser et al. (Elser et al., 2010), we can parameterize MST with specific traits and nutrient stoichiometry and nutrient use efficiencies that underlie \(\phi\) to predict the relative biomass growth rate (\(\mu\)) as

\[\mu \propto B_0 e^{-E/kT} m^{-1/4}\] (S8)

\[\mu \propto \left[ h \cdot \phi_L^M \cdot \beta_L \cdot \left(\frac{\rho}{N}\right) \right] e^{-E/kT} m^{-1/4}\] (S9)

\[\mu \propto \left[ h \cdot \phi_L^A \cdot \frac{a_L}{m_L} \cdot \beta_L \cdot \left(\frac{\rho}{N}\right) \right] e^{-E/kT} m^{-1/4}\] (S10)

where \(\phi_L^M = \langle A_L^M \rangle / \langle F_L^N \rangle\) and \(\phi_L^A = \langle A_L^A \rangle / \langle F_L^N \rangle\) and \(h\) is a constant reflecting the carbon use efficiency of plant growth and the carbon fraction of plant tissue (see Enquist et al., 2007b). Because carbon use efficiency, \(h\), does not change across our study plots (Malhi et al. 2016) we estimate the value of the growth normalization \(b_0\) that includes the hypothesized importance of temperature

\[b_0 \propto \left[ h \cdot \phi_L^A \cdot \frac{a_L}{m_L} \cdot \beta_L \cdot \left(\frac{\rho}{N}\right) \right] e^{-E/kT}\] (S11)

Noting that \(\phi\) can be expressed on a per unit leaf mass, \(\phi_L^M\) or per unit leaf area, \(\phi_L^A\) both then will be influenced by the traits Eqns. S5-S7 shows that it is possible to predict how variation in plant growth rates are influenced by measuring plant size, and the various traits that underlie the
scaling of growth rate. From above, PNUE or $\phi$ will be influenced by potential variation in $\dot{A}_L^A$ (photosynthesis per unit leaf area) and $\frac{m_L}{a_L}$ (leaf mass per unit area or LMA).

The influence of the environment on plant growth will be expressed differently. For example, short-term changes in light availability and water availability etc. will be reflected in potential changes in the traits listed in Eqns S8 – S10. Leaf level photosynthetic rates $\dot{A}_L$ will respond quickly to changes in water and light. Further, the effect of short- and long-term variation in temperature on plant growth will be captured by the Boltzmann term. However, longer-term shifts in water, nutrient, and light supply could then be reflected in potential shifts in many of the traits listed in Eqns S8-S10. As shown by several researchers, many of the traits listed these equations do tend to vary across gradients of temperature, light, nutrient, and water supply e.g. see (Poorter et al., 2009; Elser et al., 2010; Asner et al., 2014; Wang et al., 2016). As we discuss in the main text, this feedback between the environment and the traits of individuals and their dominance in communities can ramify to influence the production of biomass and the flux of water, carbon, and nutrients.

Scaling from traits to ecosystems

Next, we integrate how variation in the traits of individuals, the abundance of a trait in a community, and variation in the total biomass of a community can then influence how we scale from traits to ecosystems. Grime (1998) argued that the dominant traits in a community were likely the ones that best predicted ecosystem functioning. Thus, trait-based ecology aims to identify the trait, $z$, and the abundance or biomass, $m$, of the individuals with a given trait value. Trait-based scaling theory builds on Grime by focusing on the trait frequency distribution $m(z)$ — the histogram of biomass across individuals characterized by a given trait value, $z$, summed across all individuals within and across species. Thus, $m(z)$ captures both intra- and interspecific trait differences.

Recent work (Norberg et al., 2001; Savage et al., 2007; Enquist et al., 2015) provides a framework to scale from the distribution of traits associated with plant relative growth rate to the gross and net primary productivity. Specifically,

$$m(z) = \int dm M_{Tot}(z,m) = \int dm N(z,m)m$$

(S12)

where $M_{Tot}$ is biomass and $C(z,m)$ is the mass density of individuals with both trait value $z$ and individual mass $m$, while $N(z,m)$ is the number density of individuals that have both trait value $z$ and individual mass $m$. Most assemblages of organisms will be characterized by a distribution of sizes. For plants, following the arguments in Enquist et al. (2009), the distribution of the number of individuals, $N$, as a function of their size, $m$ or the size-spectra, $N(m)$ can be linked to the trait distribution. For the allometrically idealized case of $\theta \approx 3/4$ (see Eqn S1), and in communities that are in approximate resource and demographic steady state, the size distribution $N(m)$ characterizes how the number of individuals, $N$, per unit area will scale inversely with their size or mass, $m$, as

$$N(m) \propto m^{-11/8}$$

(S13)
Enquist et al. (2009; 2015) then show how to combine the distribution of sizes and the
distribution of traits that underlie the growth function, \( f(z) \) to predict the net primary productivity
or NPP (\( dM_{\text{Tot}}/dt \)). Specifically, linking traits to growth occurs via the metabolic normalization
\( b_0 \). The total community rate of production or the net primary production, NPP, is the
summation of the growth rates of all individuals where
\[
\frac{dM_{\text{Tot}}}{dt} = \int b_0(z) M(z) dz
\]
(S14)

Next, as shown in Enquist et al. (2009), see also (Enquist et al., 2016) to show explicitly how
total forest carbon, energy, and resource fluxes scale with total stand biomass. For the total
energy flux of all individuals, we have
\[
NPP \propto GPP \propto B_{\text{Tot}} = \left( b_0 \right) c_m^{\theta/5} c_n^{2/5} \left[ \frac{5}{3} M_{\text{Tot}} \right]^{3/5}
\]
(S15)

where \( c_m \) (m kg\(^{-3/8}\)) is a normalization constant relating stem radius to plant mass and, \( c_n \) (m) is
another normalization constant reflecting the how densely trees are packed in the forest (see
Enquist et al. 2009). The brackets denote the average, denoted by brackets \(< > \) is taken with
respect to the abundances of individuals within the community (see Enquist et al. 2015).

Equation S14 is derived in Enquist et al. (2015) and assumes a community steady state
approximation where \( N(z, M) \) is not changing in time. If this is violated (e.g. the community trait
abundance or number distribution \( N(z, M) \) is changing), then deviations are expected. Further,
the values of the exponents in Eqn S15 assume ‘quarter-power’ scaling of organismal
metabolism and growth and form (West et al., 2009). Nonetheless, the above equations provide
a basis for linking the scaling of organismal growth rate and trait variation of individuals with
ecosystem-level processes. For all of these equations and cases, the functions inside the averages
can be expanded in terms of additional moments of the distribution of \( b_0 \) within a given forest as
done for trait-based scaling theory for biomass-weighted averages or as done in Savage (Savage,
2004a) for abundance-weighted averages.

From above, we can derive the traits that underlie the metabolic normalization \( b_0 \) as
\[
b_0 = \left[ \phi_L^{\theta} \cdot \left( \frac{m_{l^{-1}}}{a_L} \right) \cdot \beta_L \cdot \left( \frac{P}{N} \right) \right] e^{-E/kT} = \left[ h \cdot \phi_L^{M} \cdot \beta_L \cdot \left( \frac{P}{N} \right) \right] e^{-E/kT}
\]
(S16)

\[
NPP \propto \left[ \left( h \cdot \phi_L^{\theta} \cdot \left( \frac{m_{l^{-1}}}{a_L} \right) \cdot \beta_L \cdot \left( \frac{P}{N} \right) \right) \right] e^{-E/kT} \left[ \frac{5}{3} M_{\text{Tot}} \right]^{3/5}
\]
(S17)

where \( h \) is carbon use efficiency. Eqn (S17) predicts that shifts in \( < b_0 > \) due to potential shifts in
the traits that underlie \( < b_0 > \) will lead to corresponding shifts in NPP or \( dM_{\text{Tot}}/dt \). This will
occur whenever the community mean trait value, \( < b_0 > \), is near the maximum of the organismal
growth function (Norberg et al. 2001). So, shifts in \( < b_0 > \) will lead to corresponding shifts in
\( dM_{\text{Tot}}/dt \). For example, increases in the abundance weighted mean trait value will lead to an
increase in NPP.
We can simplify Eqn. S17 to reveal a prediction for how variation in temperature should influence variation in forest productivity,

\[ \ln\left(\frac{NPP}{M^{3/5}_{TOT}}\right) \propto \frac{-E}{kT} + \ln\left(\langle h \cdot \phi_0 \cdot \left(\frac{m_L}{a_L}\right)^{-1} \cdot \beta_L \cdot \left(\frac{P}{N}\right)\rangle\right) \]

(S18)

where \(\frac{NPP}{M^{3/5}_{TOT}}\) is a measure of biomass corrected net primary productivity. This model provides several important predictions concerning variability in terrestrial production. The quotient of \(\frac{NPP}{M^{3/5}_{TOT}}\) removes the allometric effects of productivity and plotting its value against \(1/kT\) will reveal the direct kinetic influence of temperature on NPP, as well as the role of possible variation in community trait distributions, \(\langle b_0, Net(z)\rangle\).

If we assume that none of the plant parameters vary with temperature and that productivity is limited by the kinetics of photosynthesis, then per Eqn S17 a plot of \(\ln\left(\frac{NPP}{M^{3/5}_{TOT}}\right)\) versus \((1/kT)\), a modified “Arrhenius plot”, will yield a linear relationship with a slope of \(-E \approx -0.65\) eV. This reflects the activation energy of individual plant metabolism (Gillooly et al., 2001; Kerkhoff et al., 2005). Under this restrictive assumption, the predicted slope should be \(-E \approx -0.65\) eV, all else being equal, with residual variation related to the other variables.

**Trait-based Scaling Theory: Temperature as a Driver of Functional Turnover Across Gradients**

There are two lines of research that hypothesize that several leaf traits should covary with temperature. First, building on the ‘growth rate hypothesis’ (Elser et al., 2000), Kerkhoff et al. (2005) hypothesized that selection to minimize the kinetic effects of temperature on plant metabolism has resulted in covariation in the traits that underlie \(b_0\) in Eqn 2 and temperature (see \(H_1\) in Fig. 1). As a result, the relationship between net primary productivity and inverse temperature, \(\ln(NPP)\) and \(1/kT\), will depart from the expected temperature sensitivity (e.g. where \(E \approx 0.65\) eV; see Eqn 2). Thus, systematic changes in the leaf traits P:N, PNUE, and LMA with temperature are adaptive and will modify the temperature dependence of plant growth and ultimately whole-forest NPP (see Supplemental Document). Second, Michaletz et al. (2015, 2016), used energy budget theory to hypothesize that natural selection to buffer transient changes in leaf temperatures and maintain photosynthesis near a photosynthetic optimum could be reflected in shifts in leaf mass per unit area (LMA), and several other leaf traits with temperature. Thus, despite shifts in air temperature, variation in LMA can help modulate variation in leaf temperatures to maximize rates of leaf net carbon assimilation.

**Phosphorus - The ‘Growth Rate’ hypothesis versus potential edaphic controls**

An increasing number of macroecological studies have indeed shown that leaf stoichiometry and other functional traits, including LMA, are now known to vary across temperature gradients (Körner, 1989; Yin, 1993; Wright et al., 2006; Swenson et al., 2012; Asner & Martin, 2016). Further, these studies have shown that environmental temperature appears to be a key correlate to shifts in plant traits across gradients. There are several lines of work indicating that coordinated acclamatory and adaptive shifts in plant traits across temperature gradients can influence the importance of temperature in explaining variation in GPP and NPP. Building on the ‘growth rate hypothesis’ (Elser et al., 2000), Kerkhoff et al. (2005) proposed that temperature acclimation and adaptation could be accomplished via the upregulation of plant metabolism by
selection on the P:N content of plant tissue. The growth yield of plants will increase with an increasing fraction of cellular [P:N]. Thus, as temperatures decrease, potential reductions in metabolism and growth rates due to low temperatures may be offset in part by upregulation via intra- and interspecific increases in biosynthesis via increased P investment in ribosomes (per unit protein; Kerkhoff et al. 2005; Yu et al., 2012) and/or increased cold tolerance by allocation to phospholipids for energy storage as observed (Horvath et al., 1980; Yu et al., 2012; Strimbeck et al., 2015). In colder environments, relative increases in leaf P to N would suggest a proportionate need for more P relative to N due to selection for increased cold tolerance mechanisms and/or additional lipid energy storage.

Alternatively, variation in some plant traits including plant nutrient concentrations and LMA may also reflect gradients in soil nutrient availability (Yin, 1993; Conover & Schultz, 1995; Wright et al., 2002; Woods et al., 2003; McGroddy et al., 2004; Reich & Oleksyn, 2004; Asner & Martin, 2016). In the tropics, we would expect that lower elevation forest soils to be relatively lower in P and high elevation soils relatively enriched in P (Lovelock et al., 2007; Fisher et al., 2013). Thus, any shift in P:N ratios of plant tissue may reflect underlying shifts in soil P availability relative to N.

Methods

Forest Plots

The field-plots are located across the Andes-Amazon elevation gradient, including upper TMCF, lower TMCF and lowland rainforest (For illustration of locations see (Malhi et al., 2016). Mean annual temperature (MAT) declines with increasing elevation from 24.4 to 13.1°C. Mean annual precipitation (MAP) increases from 1900 mm yr\(^{-1}\) in the lowlands to 5302 mm yr\(^{-1}\) in the lower TMCF close to the cloud base (ca. 1500 m asl; Halladay et al., 2012) and then declines again to 1560 mm yr\(^{-1}\) in the upper TMCF (Rapp & Silman, 2012; Girardin et al., 2014a; Huacara Huasco et al., 2014; Malhi et al., 2014a). There is a distinct seasonality in the amount of precipitation, with 200-800 mm month\(^{-1}\) precipitation occurring during the November-March wet season and ~100 mm month\(^{-1}\) in the June-August dry season (Rapp & Silman, 2012; Girardin et al., 2014a). In the montane forest plots, cloud immersion is most common in the dry season (April-September).

Climate data

We obtained climate data from a set of weather stations located nearby to each one of the study sites (as described by (Malhi et al., 2017)). The most complete annual time series for most weather stations were for year 2013 and incoming radiation, temperature, precipitation and relative humidity were recorded at 30 min intervals. We used these time series to estimate average daily climate. For days where data were not available, the average daily values were obtained by interpolating the daily parameters of the previous and following 3 days. We corrected temperature for altitudinal differences using an adiabatic rate of 6 °C km\(^{-1}\) elevation and assumed no change of radiation and precipitation with altitude. Data are summarized in Table S1.

Ecosystem Net Primary Productivity Data
We used the data for above ground stand biomass, NPP, and GPP reported in (Malhi et al., 2017). For some plots, above ground biomass data was updated following protocol in Malhi et al. 2017. A complete listing of the methodology and description of these plots is given in Malhi et al. (2017). A total of 16 1ha plots have both GPP and NPP estimates. As discussed below, the ecosystem plot network consists of more plots than the network of plots where traits were sampled. Thus, 10 plots had NPP and GPP and associated trait measurements. Data are summarized in Table S1.

**Traits Sampled**

Based on census data for 2013 or the most recent year before 2013, a sampling protocol was adopted wherein species were sampled that maximally contributed to the total plot basal area (a proxy for plot biomass or leaf area), including tree ferns and palms. Following Pérez-Harguindeguy et al. (2013), we aimed to sample the minimum number of species that contributed to 80% of basal area (see Supplemental Document).

For each sampled species in each plot, 5 individual trees in upland sites and 3 individual trees in lowland sites were chosen for sampling. If an insufficient number of individuals was available, we sampled additional individuals of the same species from an area immediately surrounding the plot. 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. Across all plots, approximately 40% of trees also had shade branches sampled (some trees had no shade branches available). From each branch, we measured 5 leaves from simple-leaved species, or 5 individual leaflets from compound-leaved species (both referred to as ‘leaf’ below) for trait measurements. Branches and leaves with minimal damage were chosen.

All trait data were accessed using the gemtraits database and R package (Shenkin et al., 2017).

The five traits we measured include:

- **Leaf Mass per unit Area or LMA** - LMA is defined as the dry mass of the leaf divided by the light capturing surface area per unit (LMA; g m⁻²) and has been shown to correlate with net photosynthetic capacity, leaf longevity, relative growth rate and competitive ability (Poorter & Lambers, 1991; Reich et al., 1997). In addition, increasing values of LMA are associated with a shift from slow to fast growth strategies. LMA responds to both abiotic factors such as gradients of precipitation, temperature, and soil nutrients (Reich et al., 1997; Westoby, 1998) as well as biotic factors such as neighboring height and density (Navas & Violle, 2009). LMA is, therefore, a key trait indicative of plant physiological processes ranging from light capture (Ninemets et al., 1999) to growth rates (Poorter et al., 2009) as well as plant life strategies (Westoby et al., 2002).

- **Phosphorus** - The total phosphorus per unit of dry leaf mass (mg g⁻¹) is a fundamental component of nucleic acids, lipid membranes and bioenergetic molecules such as ATP, is an essential nutrient in photosynthetic carbon assimilation and protein synthesis (Field & Mooney, 1986). Increasing P also generally indicates high nutritional quality to consumers in food webs (Cornelissen et al., 2003) (Cornelissen et al. 2003). Leaf P is positively correlated with growth and assimilation rates (Niklas et al., 2005; Wright et al., 2006).
Nitrogen - (total nitrogen per unit of dry leaf mass; mg g⁻¹) or nitrogen content within a leaf is an integral component to the proteins of the photosynthetic machinery responsible for drawdown of carbon dioxide (CO₂) inside the leaf. Thus, variation in both N and P content have been directly linked to variation in rates of leaf photosynthetic activity (Raaimakers et al., 1995; Evans & Poorter, 2001; Reich et al., 2008).

Carbon - (total carbon per unit of dry leaf mass; mg g⁻¹) or carbon content within a leaf is a major component of cellulose and lignin, which in turn, are used to build the cell walls of tissues (Kokaly et al., 2009).

Leaf photosynthetic nitrogen use efficiency – per Eqn S11, we calculated PNUE on a per unit area basis (PNUE = µmol CO₂ × % N⁻¹× m⁻² × sec⁻¹) by dividing the leaf photosynthesis (per unit area), φL, by the leaf nitrogen. PNUE is the efficiency of leaves in using nitrogen to assimilate CO₂, which itself may change with nutrient concentration (Field & Mooney, 1986; Reich et al., 1997; Sterner & Elser, 2002; Wright et al., 2004). Changes in PNUE have been indicated as a key trait driving temperature adaptation in plants and has been shown to be inversely related to growing season temperature (Kerkhoff et al. 2005).

Trait Measurement Protocol

Leaf mass per unit area – We measured LMA (m² g⁻¹) by imaging the adaxial surface of each leaf (or leaflet, for compound leaves) in the field immediately after collection using a digital scanner (Canon LiDE 110⁰®). Leaves too large to fit on the scanner were cut into smaller pieces that were scanned separately. All leaves were then oven-dried at 72°C until constant weight was reached (around 72h), and their dry mass then was measured. Leaf area images were processed using Matlab (code available via GitHub github.com/OxfordEcosystemsLab/gemtraits_misc). Each image was first binarized using an automatic threshold, visually checked and the threshold then set manually to fit the leaf shape as accurately as possible. When the leaf was damaged due to herbivory, the holes were not filled to obtain the true area.

LMA was calculated on a whole-leaf basis, including both laminas and petioles. In cases where dry petioles had a mass of zero (due to a balance with limited precision) the dry masses were corrected by the site-level ratio of fresh mass/dry mass. Leaf areas from images with folded leaves were not included. Leaves that caused the tree to have variances >2000 for LMA were also not included (i.e., single leaves from groups of 5 leaves were removed as outliers). LMA was calculated separately for each leaf before calculating the mean LMA per individual tree. At the species and plot levels, LMA was calculated from individual tree (and not leaf) values.

Leaf Photosynthesis - Maximum photosynthetic rate per unit area (Amax; µmol m⁻² s⁻¹) was measured on mature, healthy individual leaves (5 leaves per individual tree) from each sunlit canopy branch. Leaves were measured while still attached to the branch (which was re-cut under water after collection). Rates of photosynthesis were measured using the Li-COR 6400XT portable photosynthesis system (Li-COR, Lincoln, NE, USA) under ambient temperature and humidity, saturating light (1200-2000 µmol m⁻² s⁻¹) and saturating [CO₂] (1200-1500 ppm).

Leaf stoichiometry - Nutrient content for all leaves were measured at the University of Arizona. All dry leaf samples were then homogenised and ground to a fine powder. For elemental
analysis, all leaf samples were homogenized and ground to a fine powder at the species level. Leaf phosphorus concentrations were determined using triplicates consisting of 3.5 – 4.0 mg of finely ground leaf material. Total phosphorus content was determined using persulfate oxidation followed by the acid molybdate technique (APHA 1992) and phosphorus concentration was then measured colorimetrically with a spectrophotometer (ThermoScientific Genesys20, USA). Carbon and nitrogen content were measured on a continuous-flow gas-ratio mass spectrometer (Finnigan Delta PlusXL) coupled to an elemental analyzer (Costech). Samples of 1.0 mg (+/- 0.2 mg) were combusted in the elemental analyzer. Leaf carbon and nitrogen contents were measured by the Department of Geosciences Environmental Isotope Laboratory at the University of Arizona.

Statistical Analyses
All statistical analyses were conducted in R 3.3.3 (R Core Team, 2017). To assess general multivariate responses of community trait distributions to the environmental gradient, we utilized Principle Component Analysis using the R function princomp() on the correlation matrix. Model selection was done using general linear models (glm) and then comparing AICc values using the R package glmulti, leaps, MASS, and lme4 (Calcagno, 2013; Bates et al., 2015; Lumley, 2017) All plots were completed using ggplot2 (Wickham, 2009). To determine the explanatory value of these models, we used the R package ‘MuMln’ to calculate marginal and conditional r^2 values (Barton, 2015). Functional forms of relationships were also assessed using partial residual plots obtained using crPlots() from the R package car (Fox & Weisberg, 2011). Partial regression statistics were obtained using lm.sumSquares() from the R package lmSupport, and partial regression plots were prepared using avPlots() from the R package car (Fox et al., 2016). Linear relationships between model covariates in our various models may be compromised by potential collinearity between variables (Dormann et al., 2013). We tested potential collinearity using calculated variance inflation factors (VIFs) for each covariate in each model using vif() from the R package car.

To assess the importance of metabolic drivers and to assess the predictions of metabolic scaling theory we included measures of temperature and total stand biomass as specified by the theory. Temperature was expressed as the Boltzmann factor exponent 1/kT, where k is the Boltzmann constant (8.617 x 10^-25 eV K^-1) and T is temperature (K), and calculated as the annual averages <1/kT>. In assessing the kinetic role of temperature on variation in NPP and GPP within the context of trait-based scaling theory all other variables were natural log transformed.

Next, we assessed the relative importance of different drivers of NPP and GPP by testing 16 different models with different numbers of predictor variables that characterized three separate classes of models – models with differing (i) climate drivers; (ii) biomass and climate drivers; and (iii) biomass, traits, and climate drivers (see Table S1). We assessed the predictions of trait-based scaling theory (Box 1 and Fig. 1) by assessing the ranking of these models based on AICc and AdjR^2 as well as the overlap of the fitted parameters of these models to the specific values of the exponents predicted by the theory. For each model, we assessed predicted values of GPP and NPP using differing variables environmental drivers, stand biomass, as well as several community weighted trait means and variances.
In competing each associated model with differing combinations of environmental drivers, stand biomass, and community trait distributions we used AICc. Aikaike weight values, and Adj$R^2$ values. AICc was used because of relatively low sample sizes (forest plots with adequate NPP, GPP, environmental, and trait data ranged from 9-10 plots). Models with $\Delta$AICc values greater than 3 have considerably less support (Burnham and Anderson 2002). Akaike weight values are the estimated probability of a given model being the actual best model. Relationships between NPP and mean annual temperature or precipitation were described using ordinary least squares (OLS) linear and glm regression.

**Estimating trait distributions**

We estimated the shape of trait distributions using two methods:

**Community Weighted Mean** - The first method utilized trait information from the most abundant species that comprise 80% of the forest biomass. Here, for each trait, the species proportional contributions to the community were based on the abundance of each species from taxonomic inventories collected between 2009 and 2014. The community weighted mean or CWM (Garnier et al., 2004; Violle et al., 2007; Hulshof et al., 2013) was calculated for each plot:

$$CWM_k = \sum \mu_i f_i$$

where $k$ = plot, $i$ = species, and $\mu_i$ and $f_i$ are the mean trait value and relative abundance of the species $i$. Due to sampling constraints, the total sampled abundances differed among plots; that is, the sum of all $f_i$ varied. To account for this variation, the final CWM for each plot was normalized by the sum of total abundances.

**Estimating the shape of trait distributions by bootstrapping** - The second method utilized parametric bootstrapping. This method was implemented because our CHAMBASA trait sampling protocol sampled traits of the most abundant species within each plot. This meant that the less abundant and rare species did not have trait measures sampled within a given plot. Following a protocol outlined by Enquist et al. (2015) community trait distributions were estimated by local sampling and intra and interspecific variation. We estimated the community trait distribution for each plot by applying a hierarchical bootstrapping method that emphasized traits sampled locally over traits sampled from distant CHAMBASA plots and traits from global compilations.

To estimate traits for the rare species in each community we constrained the selection of their traits based on a hierarchical method consisting of two levels – spatial and taxonomic. Spatial sampling selected traits found either within a given plot, traits found between plots, or global trait values. The other hierarchy that informed our sampling is taxonomic (trait values that were measured within species or a given genus, or a given family). When a trait value was present for a given species then we assigned that value and followed the spatial sampling hierarchy (e.g. traits for a given individual within a given species were chosen as locally as possible). If a trait value was not present for a species, we then assigned a genus mean and if there were no genus means we assigned a family mean trait value. These two hierarchical constraints enabled us to estimate trait distributions by emphasizing traits found locally and traits sampled within species and underemphasized traits sampled at larger geographic scales and traits sampled in more distantly related taxa.
Next, we generated the community trait distribution by randomly selecting traits from each species’ intraspecific trait distribution that was unique to each community or plot. Each species’ trait distribution consisted of traits constrained by the hierarchical sampling rules. When there were multiple trait values per species in that community then our sample of traits per species consisted of all available sampled traits. For species where there was only 1 trait record per species per community (e.g. 1 individual with a trait value) then just that point measure was used. If two or more trait measurements were available a distribution was fitted, which was then sampled once per individual. When an individual had multiple traits, all those measurements were used to fit the species’ distribution. For trait values that were percentages (N, P, C; e.g. bounded between 0 to 1) we fit a beta distribution. For all other traits, we used a gamma distribution (bounded by zero and positive infinity).

For each species, intra-specific trait distributions were fit using the R package Fitdistrplus using the function fitdist. For each species within each plot we then extracted the associated parameters for each fitted trait distribution. For example, for the beta distribution we saved the shape1 and shape2 parameters (alpha and beta). For the gamma distribution, we extracted the fitted ‘shape’ and ‘rate’ parameters. Thus, per community, each species consisted of an intraspecific trait distribution as described by these parameters.

We estimated each overall community trait distribution by sampling one trait per individual from the corresponding set of species and plot-specific trait distributions. For a given species found within a given plot, we randomly drew a trait value for each individual within the local population from each species’ trait distribution (e.g. the beta or gamma distribution). This resulted in a randomly selected trait for each individual. We iterated this process 1,000 times, generating 1,000 bootstrap replicates for each plot, informed by the trait hierarchy sampling design.

If traits were estimated that exceeded the observed trait maximum and minimum for the entire Peru CHAMBASA trait data set (for example with SLA, data ranged from 2.11 m² g⁻¹ and 421.28 m² g⁻¹ in Peru) the sampled trait was then set to the corresponding maximum or minimum value. This occurred for less than 1% of the subsampled estimated trait values and visual inspection of the plots and data did not reveal any piling up of individuals. For each of those 1,000 distributions we then calculated the statistical moments of the trait distribution (mean, variance, skewness, and kurtosis). Our method enabled us to then calculate the 95% confidence intervals for each moment, for each plot, and for each trait. We then plotted the estimated trait distribution using the density function in the stats R package using the s3 generic function. We used the default kernel and bandwidth for plotting the community trait distribution for all traits.

Calculation of Kurtosis
In comparing kurtosis values of each community trait distribution or \( \beta_2 \) we used \( \beta_2 - 3 \) in order to standardize our measurements to the normal distribution as it is defined with a kurtosis of 0 (DeCarlo, 1997). Thus, \( \beta_2 - 3 > 0 \) indicates a more peaky or leptokurtic distribution and \( \beta_2 - 3 < 0 \) is platykurtic. A flat or uniform distribution \( \beta_2 - 3 = -1.2 \) and a bimodal or multimodal distribution will be characterized by \( \beta_2 - 3 \leq 1.2 \).
Assessing unimodality of trait distributions

To assess if trait distributions were unimodal or multimodal we calculated the bimodality coefficient (BC). The BC is based on an empirical relationship between bimodality and the third (skewness, $s$) and fourth (kurtosis, $k$) statistical moments of a distribution. It is proportional to the division of squared skewness with uncorrected kurtosis, $BC \propto (s^2 + 1) / k + 3$. A bimodal distribution will have low kurtosis, and/or asymmetric, or both. These conditions will increase the value of BC. The values range from 0 and 1, with distributions characterized by $BC < .555$ (the value representing a uniform distribution) tending to be unimodal while values $BC > .555$ tending to be bi- or multimodal (Freeman & Dale, 2013; Pfister et al., 2013).

Discussion

Our results support the prediction that two variables, stand biomass and environmental temperature, are the best predictors of variation in ecosystem production (Figs 4-5). These results are also supported by assessing eighteen separate models that include different potential combinations of categories (stand biomass, traits, and environmental drivers) as well as each category separately (Tables 3-4). In addition, these comparisons assessed the relative importance differing potential biotic and environmental drivers including different trait combinations as well as variation in solar radiation, soil moisture, and precipitation. The results listed in Tables S7-S8 again support a key prediction of trait-based scaling theory – stand biomass is a primary driver of variation in NPP and GPP (Kerkhoff & Enquist, 2006; Enquist et al., 2009). Models that include just stand biomass or $M_{Tot}$ best explain variation in NPP and GPP based on either Adj $R^2$ or $AIC_c$ criteria. Again, our analyses indicate that together, both temperature and stand biomass best explain variation in GPP and NPP – with biomass having a larger partial coefficient of determinant explaining about 56% and 41% of the variation in ecosystem production while temperature had a partial coefficient of determinant explaining about 34% and 39.6% respectively. The combined effect of both variables explaining 73% of the variation in GPP and 68% of the variation in NPP (Figs 5 and 6). The fitted scaling exponents for the top three models for NPP and GPP (m12, m9, m8 and m9, m14, and m10 respectively; see Table S1, S7, S8) all include the predicted value of 3/5. However, again, the functional scaling relationship was significantly shallower than the predicted value $E \approx 0.65eV$. Indeed, the fitted value $eV \approx 0.21$ for NPP and $\approx 0.15$ for GPP indicate a significant but shallow temperature response of tropical forests to changes in temperature.

Support for $H_2$ (Fig. 1) is given by the observed directional shift in the many growth traits that underlie the growth normalization, $b_0$ (Fig. 2). We point to three specific findings in support of $H_2$ (Fig. 1).

First, both leaf $<P:N>$ and $<PNUE>$ decreased exponentially with temperature, $T$. The observed covariation between $<P:N>$ and $T$ would lead to an increase in tree growth rates and a corresponding modulation of the temperature sensitivity of productivity (NPP and GPP).

Second, Asner et al. (2016) reported increases in leaf canopy non-structural carbohydrates (NSC) with elevation along this same gradient. An increase in NSCs with decreases in temperature is consistent with the $H_2$ and the 'growth rate' hypothesis as increases in NSC can reflect upregulation of plant growth rates (Chapin et al., 1990). Variation in NSC is a measure of the
carbon source-sink relationship within a plant (Chapin et al., 1990; Hoch, 2007). Also, consistent
with cold adaptation, the presence of more NSCs in colder climates also reduces the freezing
point of intracellular leaf components (Thomashow, 1999).

Third, our estimate of the biomass growth normalization \( b_0 \), where

\[
b_0 = \left( \left( \phi^d \cdot \left( \frac{m_d}{a_d} \right)^{-1} \right) \cdot \left( \frac{p}{N} \cdot \langle \beta_L \rangle \right) \right),
\]

shows that \( b_0 \) does not significantly vary with temperature. This finding is consistent with H2 where adaptive shifts these traits with temperature, in

particular leaf LMA, PNUE and leaf P:N and or leaf N can minimize the kinetic effects of
temperature on plant metabolism and ultimately growth. Indeed, recent work across this same
gradient has showed that intraspecific variation in tree growth of many species of *Weinmannia* (a
dominant and widespread genus of cloud forest trees in the Andes) was largely insensitive to site
temperature (Rapp et al., 2012). Further, Zaka et al. show similar shifts in these same growth
traits with temperature as plants acclimate to different growing temperatures to maintain similar
levels of leaf photosynthesis (Zaka et al., 2016). Nonetheless, as we discuss below, we still
observe a significant effect of temperature on forest productivity.
Table S1 Environmental characteristics of 1ha plots along a tropical elevation transect. Units include elevation (m), Solar Radiation (GJ m$^{-2}$ yr$^{-1}$), Mean annual air temperature. C°, Precipitation mm yr$^{-1}$, and Aboveground biomass (kg). Values of GPP and NPP (kg yr$^{-1}$) are from Malhi et al. 2017, biomass values from Malhi et al. 2017 and more recent updated values.

<table>
<thead>
<tr>
<th>Plot Name</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation</th>
<th>Solar Radiation</th>
<th>Temperature</th>
<th>Precipitation</th>
<th>Biomass</th>
<th>GPP</th>
<th>NPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acjanaco I</td>
<td>-13.15</td>
<td>-71.63</td>
<td>3,537</td>
<td>4.60</td>
<td>9</td>
<td>1,980</td>
<td>81.90</td>
<td>26.31</td>
<td>7.89</td>
</tr>
<tr>
<td>Allpahuayo A</td>
<td>-3.95</td>
<td>-73.43</td>
<td>120</td>
<td>NA</td>
<td>25.20</td>
<td>2,689</td>
<td>130.40</td>
<td>39.05</td>
<td>12.21</td>
</tr>
<tr>
<td>Allpahuayo C</td>
<td>-3.95</td>
<td>-73.43</td>
<td>150</td>
<td>5.22</td>
<td>25.20</td>
<td>2,689</td>
<td>88.50</td>
<td>41.88</td>
<td>14.27</td>
</tr>
<tr>
<td>Esperanza</td>
<td>-13.18</td>
<td>-71.59</td>
<td>2,868</td>
<td>NA</td>
<td>13.10</td>
<td>1,560</td>
<td>65.03</td>
<td>21.76</td>
<td>7.73</td>
</tr>
<tr>
<td>Pantiacolla II</td>
<td>-12.65</td>
<td>-71.26</td>
<td>595</td>
<td>3.82</td>
<td>23.50</td>
<td>2,366</td>
<td>97.42</td>
<td>32.41</td>
<td>11.34</td>
</tr>
<tr>
<td>Pantiacolla III</td>
<td>-12.64</td>
<td>-71.27</td>
<td>859</td>
<td>NA</td>
<td>21.90</td>
<td>2,835</td>
<td>66.61</td>
<td>26.90</td>
<td>9.42</td>
</tr>
<tr>
<td>San Pedro 1500</td>
<td>-13.05</td>
<td>-71.54</td>
<td>1,713</td>
<td>4.36</td>
<td>17.40</td>
<td>5,302</td>
<td>144.37</td>
<td>32.33</td>
<td>8.01</td>
</tr>
<tr>
<td>San Pedro 1750</td>
<td>-13.05</td>
<td>-71.54</td>
<td>1,494</td>
<td>4.08</td>
<td>18.80</td>
<td>5,302</td>
<td>106.67</td>
<td>38.57</td>
<td>12.08</td>
</tr>
<tr>
<td>Tambopata VI</td>
<td>-12.84</td>
<td>-69.27</td>
<td>223</td>
<td>NA</td>
<td>24.40</td>
<td>1,900</td>
<td>142.20</td>
<td>35.47</td>
<td>14.28</td>
</tr>
<tr>
<td>Tambopata V</td>
<td>-12.83</td>
<td>-69.30</td>
<td>215</td>
<td>4.80</td>
<td>24.40</td>
<td>1,900</td>
<td>112.10</td>
<td>34.47</td>
<td>11.60</td>
</tr>
<tr>
<td>Tono</td>
<td>-12.96</td>
<td>-71.57</td>
<td>1,000</td>
<td>NA</td>
<td>20.70</td>
<td>3,087</td>
<td>91.48</td>
<td>28.27</td>
<td>9.90</td>
</tr>
<tr>
<td>Trocha Union IV</td>
<td>-13.11</td>
<td>-71.59</td>
<td>2,719</td>
<td>3.49</td>
<td>13.50</td>
<td>2,318</td>
<td>88.52</td>
<td>23.54</td>
<td>7.77</td>
</tr>
<tr>
<td>Trocha Union III</td>
<td>-13.11</td>
<td>-71.60</td>
<td>3,044</td>
<td>NA</td>
<td>11.80</td>
<td>1,776</td>
<td>59.08</td>
<td>17.23</td>
<td>5.61</td>
</tr>
<tr>
<td>Trocha Union VII</td>
<td>-13.07</td>
<td>-71.56</td>
<td>2,020</td>
<td>NA</td>
<td>17.40</td>
<td>1,827</td>
<td>50.65</td>
<td>13.97</td>
<td>4.61</td>
</tr>
<tr>
<td>Trocha Union VIII</td>
<td>-13.07</td>
<td>-71.56</td>
<td>1,885</td>
<td>3.96</td>
<td>18</td>
<td>2,472</td>
<td>64.22</td>
<td>24.19</td>
<td>7.98</td>
</tr>
<tr>
<td>Wayqecha</td>
<td>-13.19</td>
<td>-71.59</td>
<td>3,045</td>
<td>3.51</td>
<td>11.80</td>
<td>1,560</td>
<td>81.32</td>
<td>25.93</td>
<td>7.86</td>
</tr>
</tbody>
</table>
**Table S2.** Overview of the three differing cases of possible explanatory drivers for climate, biomass and climate, and traits and biomass. These three differing classes of models were further broken down into 16 different sub-models with different numbers of predictor variables that characterized three separate classes of models. Temperature (MAinvBT) was expressed as the Boltzmann factor exponent $1/kT$, where $k$ is the Boltzmann constant ($8.617 \times 10^{-25}$ eV K$^{-1}$) and $T$ is the mean annual temperature of the forest plot. We assessed the importance of community trait values as measured by the mean and variance of the community trait distributions of SLA, and leaf P, N, C, Photosynthesis, and the calculated values of N:P and P:NUE (or PhotosynthesisPerLeafN). Per trait-based scaling theory (Enquist et al. 2015), for each trait, we calculated the abundance weighted average and variance. We used two measures of abundance weighted trait values were calculated. First, to assess the shift in community mean trait values of the dominant (abundant) species that were sampled in each plot, we calculated the abundance weighted measure of the dominant community trait by calculating the arithmetic mean values of all traits measured within each plot.

(i) Climate;

\begin{align*}
m1 & < \text{lm(ln(GPP) ~ MAinvBT);} \\
m2 & < \text{lm(ln(GPP) ~ Precipitation.mm.yr.1.;)} \\
m3 & < \text{lm(ln(GPP) ~ ln(Precipitation.mm.yr.1.));} \\
m4 & < \text{lm(ln(GPP) ~ ln(Precipitation.mm.yr.1.) + MAinvBT);} \\
m5 & < \text{lm(ln(GPP) ~ ln(SolarRadiation.GJ.m.2.yr.1.));} \\
m6 & < \text{lm(ln(GPP) ~ ln(SolarRadiation.GJ.m.2.yr.1.) + MAinvBT);} \\
m7 & < \text{lm(ln(GPP) ~ ln(SolarRadiation.GJ.m.2.yr.1.) + ln(Precipitation.mm.yr.1.) + MAinvBT);}
\end{align*}

(ii) Biomass and Climate;

\begin{align*}
m8 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass));} \\
m9 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + MAinvBT)} \\
m10 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(Precipitation.mm.yr.1.) + MAinvBT);} \\
m11 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(mean_sla_lamina_petiole) + ln(mean_n_percent));} \\
m12 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(mean_sla_lamina_petiole) + ln(mean_n_percent) + ln(SLAVarianceMean));} \\
m13 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(mean_sla_lamina_petiole) + ln(mean_n_percent) + ln(NVarianceMean));} \\
m14 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(PhotosynthesisPerLeafN));} \\
m15 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(PhotosynthesisPerLeafN) + ln(PlotNtoP));}
\end{align*}

(iii) Traits and Biomass;

\begin{align*}
m16 & < \text{lm(ln(GPP) ~ ln(Aboveground_biomass) + ln(PhotosynthesisPerLeafN) + ln(PlotNtoP));}
\end{align*}
**Table S3.** Loadings of community mean trait values for the traits of the most abundant species, \(<\text{trait}>_a\), across the Peru elevation gradient. The first three principle components explain 85.9% of the variation in traits across the gradient with components 1, 2 and 3 explaining 41.9, 26.5, and 17.4% of the variation respectively.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Comp.1</th>
<th>Comp.2</th>
<th>Comp.3</th>
<th>Comp.4</th>
<th>Comp.5</th>
<th>Comp.6</th>
<th>Comp.7</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;LMA&gt;_a</td>
<td>-0.426</td>
<td>-0.220</td>
<td>-0.016</td>
<td>-0.163</td>
<td>0.861</td>
<td>-0.056</td>
<td>0.000</td>
</tr>
<tr>
<td>&lt;N&gt;_a</td>
<td>0.082</td>
<td>-0.570</td>
<td>0.530</td>
<td>-0.423</td>
<td>-0.148</td>
<td>0.425</td>
<td>-0.076</td>
</tr>
<tr>
<td>&lt;C&gt;_a</td>
<td>0.264</td>
<td>-0.235</td>
<td>0.395</td>
<td>0.814</td>
<td>0.234</td>
<td>0.037</td>
<td>0.013</td>
</tr>
<tr>
<td>&lt;P&gt;_a</td>
<td>-0.335</td>
<td>0.318</td>
<td>0.628</td>
<td>-0.069</td>
<td>-0.106</td>
<td>-0.302</td>
<td>0.534</td>
</tr>
<tr>
<td>&lt;Photo&gt;_a</td>
<td>-0.474</td>
<td>-0.404</td>
<td>0.027</td>
<td>0.154</td>
<td>-0.342</td>
<td>-0.529</td>
<td>-0.437</td>
</tr>
<tr>
<td>&lt;P:N&gt;_a</td>
<td>-0.446</td>
<td>0.465</td>
<td>0.205</td>
<td>0.172</td>
<td>-0.031</td>
<td>0.527</td>
<td>-0.485</td>
</tr>
<tr>
<td>&lt;PNUE&gt;_a</td>
<td>-0.454</td>
<td>-0.303</td>
<td>-0.354</td>
<td>0.271</td>
<td>-0.231</td>
<td>0.408</td>
<td>0.532</td>
</tr>
</tbody>
</table>
Table S4. Loadings of community mean trait values, $<trait>_c$ across the Peru elevation gradient for all individuals in the community. Species include abundant and rare species. The first three principle components explain 87.9% of the variation in traits across the gradient with components 1, 2 and 3 explaining 41.7, 28.8, and 17.5% of the variation respectively.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Comp.1</th>
<th>Comp.2</th>
<th>Comp.3</th>
<th>Comp.4</th>
<th>Comp.5</th>
<th>Comp.6</th>
<th>Comp.7</th>
</tr>
</thead>
<tbody>
<tr>
<td>$&lt;\text{LMA}&gt;_c$</td>
<td>0.489</td>
<td>-0.079</td>
<td>0.006</td>
<td>0.529</td>
<td>0.685</td>
<td>0.061</td>
<td>0.038</td>
</tr>
<tr>
<td>$&lt;\text{N}&gt;_c$</td>
<td>-0.382</td>
<td>-0.024</td>
<td>-0.420</td>
<td>0.615</td>
<td>-0.253</td>
<td>0.418</td>
<td>0.247</td>
</tr>
<tr>
<td>$&lt;\text{C}&gt;_c$</td>
<td>-0.360</td>
<td>-0.062</td>
<td>-0.591</td>
<td>-0.424</td>
<td>0.579</td>
<td>0.034</td>
<td>0.023</td>
</tr>
<tr>
<td>$&lt;\text{P}&gt;_c$</td>
<td>0.070</td>
<td>-0.689</td>
<td>-0.265</td>
<td>0.126</td>
<td>-0.177</td>
<td>-0.618</td>
<td>0.142</td>
</tr>
<tr>
<td>$&lt;\text{Photo}&gt;_c$</td>
<td>0.387</td>
<td>0.285</td>
<td>-0.575</td>
<td>0.059</td>
<td>-0.244</td>
<td>-0.084</td>
<td>-0.607</td>
</tr>
<tr>
<td>$&lt;\text{P:N}&gt;_c$</td>
<td>0.280</td>
<td>-0.615</td>
<td>0.003</td>
<td>-0.265</td>
<td>-0.114</td>
<td>0.653</td>
<td>-0.184</td>
</tr>
<tr>
<td>$&lt;\text{PNUE}&gt;_c$</td>
<td>0.502</td>
<td>0.234</td>
<td>-0.270</td>
<td>-0.268</td>
<td>-0.168</td>
<td>0.070</td>
<td>0.718</td>
</tr>
</tbody>
</table>
Table S5. Change in Community Weighted Plot Traits with Elevation (Abundant Species) – Assessing shifts in the mean trait value of the community trait distribution across elevation.
Mean community trait values were generated for five community leaf traits (N, P, C, LMA, and photosynthesis) for each of the 10 forest plots sampled across the Perú elevational gradient for all individuals per plot. Trait distributions were generated by randomly subsampling 1,000 times local within plot measured inter- and intraspecific trait variation for the most dominant species and sampling trait values for individuals of species measured across the same Peruvian gradient and across the globe from a global trait database for the rarer species not sampled within each plot.

<table>
<thead>
<tr>
<th>Elevation</th>
<th>&lt;%N&gt;</th>
<th>&lt;%P&gt;</th>
<th>&lt;P:N&gt;</th>
<th>&lt;%C&gt;</th>
<th>&lt;LMA&gt;</th>
<th>&lt;Photo&gt;</th>
<th>&lt;PNUE&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>-0.0001</td>
<td>0.0000</td>
<td>-0.003*</td>
<td>0.0002</td>
<td>0.02***</td>
<td>0.001</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>(-0.0003 -</td>
<td>(-0.0000 -</td>
<td>(-0.01 -</td>
<td>(-0.001 -</td>
<td>(0.02 -</td>
<td>(-0.001 -</td>
<td>(0.0000 -</td>
<td></td>
</tr>
<tr>
<td>0.0000)</td>
<td>0.0000)</td>
<td>0.0001)</td>
<td>0.001)</td>
<td>0.03)</td>
<td>0.002)</td>
<td>0.001)</td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>2.41***</td>
<td>0.11***</td>
<td>0.04***</td>
<td>47.93***</td>
<td>88.47***</td>
<td>8.69***</td>
<td>3.51***</td>
</tr>
<tr>
<td>(2.11 - 2.71)</td>
<td>(0.07 -</td>
<td>(0.03 -</td>
<td>(46.47 -</td>
<td>(71.07 -</td>
<td>(5.97 -</td>
<td>(2.37 - 4.66)</td>
<td></td>
</tr>
<tr>
<td>0.14)</td>
<td>0.06)</td>
<td>49.40)</td>
<td>105.87)</td>
<td>11.41)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observations</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>r²</td>
<td>0.29</td>
<td>0.05</td>
<td>0.31</td>
<td>0.03</td>
<td>0.79</td>
<td>0.10</td>
<td>0.35</td>
</tr>
</tbody>
</table>

Note: *p < 0.1; **p < 0.05; ***p < 0.01
Table S6. Change in Community Plot Traits with Elevation (Trait distribution subsampling method) – Assessing shifts in the mean trait value of the community trait distribution across elevation. Mean community trait values were generated for five community leaf traits (N, P, C, LMA, and photosynthesis) for each of the 10 forest plots sampled across the Perú elevational gradient for all individuals per plot. Trait distributions were generated by randomly subsampling 1,000 times local within plot measured inter- and intraspecific trait variation for the most dominant species and sampling trait values for individuals of species measured across the same Peruvian gradient and across the globe from a global trait database for the rarer species not sampled within each plot.

<table>
<thead>
<tr>
<th>Elevation Parameter</th>
<th>&lt;%N&gt;_c</th>
<th>&lt;%P&gt;_c</th>
<th>&lt;P:N&gt;_c</th>
<th>&lt;%C&gt;_c</th>
<th>&lt;LMA&gt;_c</th>
<th>&lt;Photo&gt;_c</th>
<th>&lt;PNUE&gt;_c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-0.0001**</td>
<td>0.0000</td>
<td>-0.002**</td>
<td>-0.0003*</td>
<td>0.0000***</td>
<td>0.0004</td>
<td>0.04*</td>
</tr>
<tr>
<td>Observations</td>
<td>(2.38 - 2.77)</td>
<td>(0.09 - 0.14)</td>
<td>(0.04 - 0.05)</td>
<td>(48.46 - 49.69)</td>
<td>(0.06 - 0.09)</td>
<td>(6.51 - 9.52)</td>
<td>(235.89 - 374.34)</td>
</tr>
<tr>
<td>r²</td>
<td>0.47</td>
<td>0.08</td>
<td>0.44</td>
<td>0.33</td>
<td>0.45</td>
<td>0.12</td>
<td>0.40</td>
</tr>
</tbody>
</table>

Note: *p < 0.1; **p < 0.05; ***p < 0.01
Table S7. Assessing shifts in the statistical moments (mean, variance, skewness, and kurtosis) of the community trait distribution, <c> across elevation. Moments were generated for five community leaf traits (N, P, C, SLA, and photosynthesis) for each of the 10 forest plots sampled across the Peru elevational gradient. Trait distributions were generated by randomly subsampling 1,000 times local within plot measured inter- and intraspecific trait variation for the most dominant species and sampling trait values for individuals of species measured across the same Peruvian gradient and across the globe from a global trait database for the rarer species not sampled within the plot.

<table>
<thead>
<tr>
<th>Dependent variable:</th>
<th>%N Mean</th>
<th>%N Variance</th>
<th>%N Skewness</th>
<th>%N Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>-0.0001**</td>
<td>-0.00**</td>
<td>0.0001</td>
<td>0.0002</td>
</tr>
<tr>
<td>Constant</td>
<td>2.58***</td>
<td>0.0000***</td>
<td>0.41**</td>
<td>3.12***</td>
</tr>
<tr>
<td>Observations</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>R²</td>
<td>0.47</td>
<td>0.45</td>
<td>0.18</td>
<td>0.11</td>
</tr>
<tr>
<td>Adjusted R²</td>
<td>0.41</td>
<td>0.39</td>
<td>0.08</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

Note: *p<0.1; **p<0.05; ***p<0.01

<table>
<thead>
<tr>
<th>Dependent variable:</th>
<th>%P Mean</th>
<th>%P Variance</th>
<th>%P Skewness</th>
<th>%P Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>0.0000</td>
<td>-0.00</td>
<td>-0.0001</td>
<td>-0.0001</td>
</tr>
<tr>
<td>Constant</td>
<td>0.12***</td>
<td>0.0000***</td>
<td>1.64***</td>
<td>7.43***</td>
</tr>
<tr>
<td>Observations</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>R²</td>
<td>0.08</td>
<td>0.08</td>
<td>0.07</td>
<td>0.01</td>
</tr>
<tr>
<td>Adjusted R²</td>
<td>-0.03</td>
<td>-0.04</td>
<td>-0.05</td>
<td>-0.11</td>
</tr>
</tbody>
</table>

Note: *p<0.1; **p<0.05; ***p<0.01
### Dependent variable: %C

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>%C Mean</th>
<th>%C Variance</th>
<th>%C Skewness</th>
<th>%C Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-0.0003*</td>
<td>0.0000</td>
<td>0.0001</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>(-0.001 - 0.000)</td>
<td>(-0.0000 - 0.0000)</td>
<td>(-0.0002 - 0.0003)</td>
<td>(-0.0003 - 0.0001)</td>
</tr>
<tr>
<td>Constant</td>
<td>49.07***</td>
<td>0.001**</td>
<td>-0.09</td>
<td>3.84***</td>
</tr>
<tr>
<td></td>
<td>(48.46 - 49.69)</td>
<td>(0.0001 - 0.001)</td>
<td>(-0.61 - 0.43)</td>
<td>(1.97 - 5.71)</td>
</tr>
</tbody>
</table>

| Observations | 10 | 10 | 10 | 10 |
| R²           | 0.33 | 0.27 | 0.04 | 0.16 |
| Adjusted R²  | 0.25 | 0.18 | -0.08 | 0.05 |

### Note:
* p<0.1; ** p<0.05; *** p<0.01

### Dependent variable: Photo

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>Photo Mean</th>
<th>Photo Variance</th>
<th>Photo Skewness</th>
<th>Photo Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.0004</td>
<td>-0.002</td>
<td>-0.0002</td>
<td>-0.0004*</td>
</tr>
<tr>
<td></td>
<td>(-0.0003 - 0.001)</td>
<td>(-0.01 - 0.001)</td>
<td>(-0.0004 - 0.0000)</td>
<td>(-0.001 - 0.0000)</td>
</tr>
<tr>
<td>Constant</td>
<td>8.02***</td>
<td>34.50***</td>
<td>1.25***</td>
<td>4.65***</td>
</tr>
<tr>
<td></td>
<td>(6.51 - 9.52)</td>
<td>(27.65 - 41.36)</td>
<td>(0.86 - 1.64)</td>
<td>(3.76 - 5.49)</td>
</tr>
</tbody>
</table>

| Observations | 10 | 10 | 10 | 10 |
| R²           | 0.12 | 0.15 | 0.40 | 0.31 |
| Adjusted R²  | 0.01 | 0.04 | 0.32 | 0.22 |

### Note:
* p<0.1; ** p<0.05; *** p<0.01

### Dependent variable: SLA

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>SLA Mean</th>
<th>SLA Variance</th>
<th>SLA Skewness</th>
<th>SLA Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-0.001*</td>
<td>0.04</td>
<td>0.001</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>(-0.003 - 0.0001)</td>
<td>(-0.07 - 0.15)</td>
<td>(-0.0005 - 0.002)</td>
<td>(-0.005 - 0.02)</td>
</tr>
<tr>
<td>Constant</td>
<td>13.16***</td>
<td>51.79</td>
<td>2.25*</td>
<td>12.04</td>
</tr>
<tr>
<td></td>
<td>(10.62 - 15.71)</td>
<td>(-187.56 - 291.14)</td>
<td>(0.002 - 4.51)</td>
<td>(-14.91 - 38.99)</td>
</tr>
</tbody>
</table>

| Observations | 10 | 10 | 10 | 10 |
| R²           | 0.36 | 0.06 | 0.12 | 0.16 |
| Adjusted R²  | 0.28 | -0.06 | 0.01 | 0.05 |

### Note:
* p<0.1; ** p<0.05; *** p<0.01
Table S8 Competing differing models to best predict variation in GPP. Model competition based on AICc. Also, each models Adj-R2 value are also reported. We competed 18 models that together characterized the central hypotheses of trait-based scaling theory, models that consisted just of environmental variables, and models that consist of just trait community mean values for the most abundant species in the community. Each model is listed in the methods. Numeric values listed under each variable are the parameter fits of that variable within the context of the given model, m. Consistent with theory, model m9 had the lowest AICc indicating that forest above ground biomass and temperature best explained variation in NPP. The fitted scaling exponent for the scaling of GPP with total above-ground biomass for the models within ΔAICc of 3 are all indistinguishable from the value of 0.6 predicted by theory.

However, the fitted activation energy for the effect of temperature is shallower than expected. Shaded cells indicate the p values for the top three models. Note, models with ΔAICc values greater than 3 have considerably less support. Akaike weight values are the estimated probability of a given model being the actual best model. Models m12 and m9 are essentially equivocal based on AICc, and Akaike weight values but m12 has a much higher Adj-R2 value.

<table>
<thead>
<tr>
<th></th>
<th>(Intercept)</th>
<th>Bollmann</th>
<th>Temp</th>
<th>ln(T)</th>
<th>ln(Med)</th>
<th>Precip</th>
<th>ln(Annual)</th>
<th>ln(Precip)</th>
<th>ln(Solar Radiation)</th>
<th>ln(N%)</th>
<th>ln(SLA Var)</th>
<th>ln(PNUE)</th>
<th>ln(NP)</th>
<th>df</th>
<th>logLik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
<th>Adj-R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>m9</td>
<td>5.420</td>
<td>-0.125</td>
<td>0.645</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>4.00</td>
<td>7.980</td>
<td>-4.323</td>
<td>0.000</td>
<td>0.317</td>
<td>0.707</td>
</tr>
<tr>
<td>m8</td>
<td>-0.196</td>
<td>NA</td>
<td>0.787</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3.00</td>
<td>5.964</td>
<td>-3.928</td>
<td>0.395</td>
<td>0.260</td>
<td>0.650</td>
</tr>
<tr>
<td>m12</td>
<td>1.071</td>
<td>NA</td>
<td>0.476</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.174</td>
<td>1.110</td>
<td>5.00</td>
<td>16.118</td>
<td>-2.236</td>
<td>2.087</td>
<td>0.112</td>
<td>0.922</td>
</tr>
<tr>
<td>m11</td>
<td>1.444</td>
<td>NA</td>
<td>0.603</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.176</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>4.00</td>
<td>8.770</td>
<td>-1.541</td>
<td>2.782</td>
<td>0.079</td>
<td>0.604</td>
<td></td>
<td></td>
</tr>
<tr>
<td>m13</td>
<td>1.444</td>
<td>NA</td>
<td>0.603</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>4.00</td>
<td>8.770</td>
<td>-1.541</td>
<td>2.782</td>
<td>0.079</td>
<td>0.604</td>
<td></td>
<td></td>
</tr>
<tr>
<td>m17</td>
<td>1.353</td>
<td>NA</td>
<td>0.518</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.227</td>
<td>4.00</td>
<td>8.634</td>
<td>-1.268</td>
<td>3.055</td>
<td>0.069</td>
<td>0.593</td>
</tr>
<tr>
<td>m10</td>
<td>4.726</td>
<td>-0.121</td>
<td>0.597</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.095</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>5.00</td>
<td>8.316</td>
<td>-0.632</td>
<td>3.691</td>
<td>0.050</td>
<td>0.696</td>
<td></td>
</tr>
<tr>
<td>m14</td>
<td>7.365</td>
<td>-0.134</td>
<td>0.386</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>4.00</td>
<td>7.579</td>
<td>0.842</td>
<td>5.164</td>
<td>0.024</td>
<td>0.497</td>
<td></td>
</tr>
<tr>
<td>m6</td>
<td>8.319</td>
<td>-0.145</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.610</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>4.00</td>
<td>6.887</td>
<td>4.225</td>
<td>8.548</td>
<td>0.004</td>
<td>0.561</td>
</tr>
<tr>
<td>m1</td>
<td>13.54</td>
<td>NA</td>
<td>0.257</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3.00</td>
<td>1.083</td>
<td>5.835</td>
<td>10.157</td>
<td>0.002</td>
<td>0.356</td>
</tr>
<tr>
<td>m4</td>
<td>9.752</td>
<td>-0.216</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.277</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>4.00</td>
<td>2.634</td>
<td>6.369</td>
<td>10.692</td>
<td>0.002</td>
<td>0.429</td>
</tr>
<tr>
<td>m18</td>
<td>1.033</td>
<td>NA</td>
<td>0.523</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.198</td>
<td>5.00</td>
<td>8.921</td>
<td>7.157</td>
<td>11.480</td>
<td>0.001</td>
<td>0.551</td>
</tr>
<tr>
<td>m3</td>
<td>0.168</td>
<td>NA</td>
<td>0.405</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3.00</td>
<td>8.708</td>
<td>9.416</td>
<td>13.739</td>
<td>0.000</td>
<td>0.194</td>
<td></td>
</tr>
<tr>
<td>m16</td>
<td>-1.021</td>
<td>NA</td>
<td>0.529</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.223</td>
<td>1.350</td>
<td>NA</td>
<td>NA</td>
<td>0.184</td>
<td>NA</td>
<td>6.00</td>
<td>21.877</td>
<td>10.246</td>
<td>14.569</td>
<td>0.000</td>
<td>0.973</td>
<td></td>
</tr>
<tr>
<td>m2</td>
<td>3.016</td>
<td>0.00</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3.00</td>
<td>-1.135</td>
<td>10.305</td>
<td>14.628</td>
<td>0.000</td>
<td>0.148</td>
<td></td>
</tr>
<tr>
<td>m7</td>
<td>6.575</td>
<td>-0.130</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.152</td>
<td>0.578</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>5.00</td>
<td>8.383</td>
<td>13.235</td>
<td>17.558</td>
<td>0.000</td>
<td>0.622</td>
<td></td>
</tr>
<tr>
<td>m15</td>
<td>0.453</td>
<td>NA</td>
<td>0.449</td>
<td>NA</td>
<td>NA</td>
<td>0.066</td>
<td>1.235</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>6.00</td>
<td>17.989</td>
<td>18.022</td>
<td>22.345</td>
<td>0.000</td>
<td>0.935</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table S9. Competing which models best predict variation in NPP. Model competition based on AICc. We competed 18 models that together characterized the central hypotheses of trait-based scaling theory, models that consisted just of environmental variables, and models that consist of just trait community mean values for the most abundant species (see methods for a listing of these models). Models include the same numbered models as are listed in Table 3. Numeric values listed under each variable are the parameter fits of that variable within the context of the given model, m. Consistent with theory, model m9 had the lowest AICc indicating that forest above ground biomass and temperature best explained variation in GPP. Shaded cells indicate the parameter fit values for the top three models. Note, models with ΔAICc values greater than 3 have considerably less support. Akaike weight values are the the estimated probability of a given model being the actual best model. Models m92 and m14 are essentially equivocal based on AICc, and Akaiki weight values but m12 has a much higher Adj-$R^2$ value. Consistent with trait-based scaling theory, stand biomass consistently came out as a key predictor of variation in GPP followed by temperature. The fitted scaling exponent for the scaling of GPP with total above-ground biomass for the models within ΔAICc of 3 are all indistinguishable from the value of 0.6 predicted by theory. However, the fitted activation energy for the effect of temperature is shallower than expected. Shaded cells indicate the parameter fit values for the top three models. Note, models with ΔAICc values greater than 3 have considerably less support.

| Model | (Intercept) | Plantation Temp | ln(Mass) | Precip | ln(Annual Precip) | ln(Solar Radiation) | ln(SLA) | ln(N%) | ln(Photo Var) | ln(SLA Var) | ln(N Var) | ln(PNUE) | ln(PNUE) | df | logLik | AICc | ΔAICc | weight | Adj-$R^2$ |
|-------|-------------|----------------|---------|--------|------------------|---------------------|---------|-------|--------------|-------------|-----------|----------|----------|---------|-----|--------|-------|-------|--------|----------|
| m9    | 8.380       | -0.210         | 0.491   | NA     | NA               | NA                  | NA      | NA    | NA           | NA          | NA        | NA       | NA       | 4.000  | 5.985 | -0.334 | 0.000  | 0.422 | 0.661   |
| m14   | 9.905       | -0.218         | NA      | NA     | NA               | NA                  | NA      | NA    | NA           | NA          | NA        | NA       | NA       | 4.000  | 7.970 | 0.059  | 0.393  | 0.347 | 0.680   |
| m1    | 14.569      | -0.310         | NA      | NA     | NA               | NA                  | NA      | NA    | NA           | NA          | NA        | NA       | NA       | 3.000  | 2.133 | 3.733  | 4.067  | 0.055 | 0.491   |
| m10   | 8.829       | -0.213         | 0.522   | NA     | 0.006           | NA                  | NA      | NA    | NA           | NA          | NA        | NA       | NA       | 5.000  | 6.093 | 3.813  | 4.147  | 0.053 | 0.638   |
| m8    | -1.055      | NA             | 0.730   | NA     | NA               | 0.399               | NA      | NA    | NA           | NA          | NA        | NA       | NA       | 3.000  | 2.076 | 3.847  | 4.182  | 0.052 | 0.488   |
| m6    | 10.510      | -0.221         | NA      | NA     | NA               | NA                  | NA      | NA    | NA           | NA          | 0.394     | NA       | 4.000   | 6.491 | 5.017  | 5.351  | 0.029 | 0.642   |
| m17   | 1.118       | NA             | 0.411   | NA     | NA               | NA                  | NA      | NA    | NA           | NA          | NA        | -0.495  | 4.000  | 4.959 | 6.081  | 6.415  | 0.017 | 0.415   |
| m1   | 13.223      | -0.296         | NA      | 0.098  | NA               | NA                  | NA      | NA    | NA           | NA          | NA        | -0.945  | 4.000  | 4.959 | 6.081  | 6.415  | 0.011 | 0.466   |
| m11   | 1.019       | NA             | 0.554   | NA     | 0.279           | NA                  | NA      | NA    | NA           | NA          | NA        | 4.000  | 3.904 | 8.192  | 8.526  | 0.006 | 0.277   |
| m13   | 1.019       | NA             | 0.554   | NA     | 0.279           | NA                  | NA      | NA    | NA           | NA          | NA        | 4.000  | 3.904 | 8.192  | 8.526  | 0.006 | 0.277   |
| m18   | -0.012      | NA             | 0.429   | NA     | NA               | 0.279               | NA      | NA    | NA           | NA          | NA        | -0.394 | 3.000  | 6.985 | 11.030 | 11.364 | 0.001 | 0.545   |
| m3    | 0.077       | NA             | 0.574   | NA     | 0.274           | 1.464               | NA      | NA    | NA           | NA          | NA        | 3.000  | -3.288 | 14.577 | 14.911 | 0.000 | 0.038   |
| m2    | 2.027       | NA             | NA      | 0.000  | NA               | NA                  | NA      | NA    | NA           | NA          | 3.000     | NA      | 3.000  | -3.288 | 14.577 | 14.911 | 0.000 | 0.038   |
| m12   | 0.542       | NA             | 0.382   | NA     | 0.274           | 1.464               | NA      | NA    | NA           | NA          | NA        | 5.000  | 6.094 | 16.192 | 16.526 | 0.000 | 0.583   |
| m7    | 10.462      | -0.221         | NA      | NA     | 0.004           | 0.399               | NA      | NA    | NA           | NA          | NA        | 5.000  | 6.492 | 17.016 | 17.350 | 0.000 | 0.570   |
| m16   | -2.828      | NA             | 0.467   | NA     | NA               | 0.353               | 1.850   | NA    | NA           | NA          | NA        | -0.296 | 6.000  | 8.150 | 37.700 | 38.034 | 0.000 | 0.605   |
| m15   | 1.779       | NA             | 0.438   | NA     | NA               | 0.491               | 1.215   | NA    | NA           | NA          | NA        | -0.071 | 6.000  | 7.775 | 38.450 | 38.784 | 0.000 | 0.570   |
**Figure S1. Multivariate analyses of weighted mean trait values within each forest plot across the Perú elevation gradient.** (A) PCA 1 and 2 for the abundant species, <trait>\(_a\), (B) the weighted mean trait value of the entire community species, <trait>\(_c\), (C, D) Correlations between the best environmental variables explaining variation in plot trait values of of PCA1 and PCA2 for both <trait>\(_a\) and <trait>\(_c\) respectively. Principle component analyses (PCA) using plot mean traits include: leaf mass per unit area (LMA); leaf % Nitrogen, N; % Phosphorus, P; % leaf maximum photosynthesis, photo; the ratio of leaf P:N, the photosynthetic N use efficiency, PNUE. Numbers represent each Perú community plot value where 1 = ACJ-01, 4 = ESP-01, 5 = PAN-02, 6 = PAN-03, 7= SPD-01, 8= SPD-02, 9= TAM-05, 12= TRU-04, 16= WAY-01. Mean community trait loadings for the traits of the dominant species and the entire community along the CHAMBASA Perú gradient show that along PCA1, variation in trait values reflect a shift along a continuum of leaf traits that underlie the scaling of plant growth. These shifts along PCA1 are best predicted by the change in the mean annual temperature across the elevational gradient (C and D). Along PCA1, <LMA>\(_a\), and P:N show the most negative loadings while PNUE and Photosynthesis show the most positive loadings. These results show, compared to warmer forests, colder high elevation forests tend to be comprised of leaves with higher values of LMA, greater amounts of P relative to N, and higher PNUE. For the abundant species in the community variation in PCA2 trait loadings was not significantly related to any of the other environmental variables including annual precipitation (C). However, for the entire community, shifts in mean community traits along PCA2 was significantly correlated with soil moisture (D); see also Figure S2.
**Figure S2.** Correlation table between PCA1 and PCA 2 and several climatic variables and the weighted mean trait values for the abundant species and the entire community. Numeric values are the pair-wise correlation coefficients. Abiotic values include Mean Annual Air Temperature (°C), SolarRadiation (GJ.m\(^{-2}\).yr\(^{-1}\) yr\(^{-1}\)), Elevation (m), and Soil moisture %, Non-significant correlations are given with a ‘x’. Positive correlations are colored blue while negative correlations are colored red.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>PCA1.Community</td>
<td>1</td>
<td>0.82</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PCA2.Community</td>
<td>1</td>
<td>-0.19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PCA1.Dominant</td>
<td>1</td>
<td>0.52</td>
<td>-0.53</td>
<td>-0.48</td>
<td>-0.55</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PCA2.Dominant</td>
<td>1</td>
<td>-0.47</td>
<td>-0.57</td>
<td>-0.6</td>
<td>-0.74</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>1</td>
<td>-0.46</td>
<td>-1</td>
<td>-0.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solar.Radiation</td>
<td>1</td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAT</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil.Moisture</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure S3. Community frequency distributions of five foliar traits across the Peruvian elevational gradient generated using statistical subsampling of intra- and interspecific trait distributions. Color scheme ranges from warm lower elevation sites (red) to colder high elevation sites (blue). Traits include leaf Carbon, Nitrogen, phosphorus as well as leaf photosynthesis and leaf mass per unit area (or LMA). All traits show approximate unimodal distributions (see Fig. S3) but only LMA and N (and the ratio of P to N or P:N) show significant differences between sites.
Figure S4. Assessment of if trait distributions tend to be unimodal. Plots of the bimodality coefficient for each of the trait distributions plotted against elevation. To assess if trait distributions were unimodal or multimodal we calculated the bimodality coefficient (BC). The BC is based on an empirical relationship between bimodality and the third (skewness, $s$) and fourth (kurtosis, $k$) statistical moments of a distribution. It is proportional to the division of squared skewness with uncorrected kurtosis, $BC = (s^2 + 1)/k+3$. The values range from 0 and 1, with distributions characterized by $BC < .555$ (the value representing a uniform distribution) tending to be unimodal. Except for the highest elevation plot for the LMA distribution, all trait distributions across plots have $BC < .555$ indicating that they tend to be unimodal and are more peaked than a flat or uniform distribution.
## Appendix S1 Listing of the central notation, description, and units of the central mathematical variables.

<table>
<thead>
<tr>
<th>Notation</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$B$</td>
<td>Whole organismal metabolism</td>
<td>Watts</td>
</tr>
<tr>
<td>$B_0$</td>
<td>Metabolic normalization constant</td>
<td>Watts $m^{(-\theta)}$</td>
</tr>
<tr>
<td>$b_0$</td>
<td>Biomass growth rate normalization constant</td>
<td>g $m^{(-\theta)}$</td>
</tr>
<tr>
<td>$m$</td>
<td>Whole organismal mass</td>
<td>g</td>
</tr>
<tr>
<td>$E$</td>
<td>activation energy</td>
<td>eV</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Allometric scaling exponent for growth rate or metabolism</td>
<td></td>
</tr>
<tr>
<td>$k$</td>
<td>Boltzmann’s constant</td>
<td>$= 8.62 \times 10^5$ eV K$^{-1}$</td>
</tr>
<tr>
<td>$\mu$</td>
<td>mass-specific growth rate, $= \frac{dm}{mdt}$</td>
<td>g $\cdot$ g$^{-1} \cdot$ time$^{-1}$</td>
</tr>
<tr>
<td>$A_L^M$</td>
<td>net leaf photosynthetic rate per unit leaf mass</td>
<td>g CO$_2$ $\cdot$ g leaf$^{-1}$</td>
</tr>
<tr>
<td>$A_L^A$</td>
<td>net leaf photosynthetic rate per unit leaf area</td>
<td>g CO$_2$ $\cdot$ m$^{-2}$ leaf $\cdot$ time$^{-1}$</td>
</tr>
<tr>
<td>$m_L$</td>
<td>Leaf mass</td>
<td>g</td>
</tr>
<tr>
<td>$a_L$</td>
<td>Leaf area</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$M_L$</td>
<td>Total leaf mass per plant</td>
<td>g</td>
</tr>
<tr>
<td>$m_L$</td>
<td>leaf mass per unit area, LMA</td>
<td>g $\cdot$ m$^{-2}$</td>
</tr>
<tr>
<td>$a_L$</td>
<td>leaf nitrogen content</td>
<td>g</td>
</tr>
<tr>
<td>$\phi_L$</td>
<td>leaf mass-specific photosynthetic production rate</td>
<td>g $\times$ g leaf$^{-1} \times$ time$^{-1}$</td>
</tr>
<tr>
<td>$F_L^N$</td>
<td>leaf phosphorus content</td>
<td>g</td>
</tr>
<tr>
<td>$\beta_L$</td>
<td>leaf mass fraction or the proportion of total plant biomass that is in leaves</td>
<td></td>
</tr>
<tr>
<td>$\phi$</td>
<td>Photosynthetic nutrient use efficiency or PNUE</td>
<td>g CO$_2$ $\cdot$ g leaf$^{-1} \cdot$ g nutrient$^{-1} \cdot$ time$^{-1}$</td>
</tr>
<tr>
<td>$\phi_L^M$</td>
<td>Photosynthesis Nutrient Use Efficiency (PNUE)</td>
<td>g CO$_2$ $\cdot$ g leaf$^{-1} \cdot$ g nutrient$^{-1} \cdot$ time$^{-1}$</td>
</tr>
<tr>
<td>$\phi_L^A$</td>
<td>Photosynthesis Nutrient Use Efficiency (PNUE)</td>
<td>g CO$_2$ $\cdot$ m$^{-2}$ leaf $\cdot$ g nutrient$^{-1} \cdot$ time$^{-1}$</td>
</tr>
<tr>
<td>$P$</td>
<td>Phosphorus</td>
<td>g</td>
</tr>
<tr>
<td>$N$</td>
<td>Nitrogen</td>
<td>g</td>
</tr>
<tr>
<td>$h$</td>
<td>constant reflecting the carbon use efficiency of plant growth and the carbon fraction of plant tissue</td>
<td></td>
</tr>
<tr>
<td>$z$</td>
<td>a given trait value</td>
<td></td>
</tr>
<tr>
<td>$M_{Tot}$</td>
<td>Total biomass of a stand or vegetation</td>
<td>g</td>
</tr>
<tr>
<td>$B_{Tot}$</td>
<td>Total metabolism of a stand or vegetation</td>
<td></td>
</tr>
<tr>
<td>$N$</td>
<td>Number density of individuals</td>
<td></td>
</tr>
</tbody>
</table>
Bibliography


the temperature-dependence of primary productivity. *Global Ecology and Biogeography*, 14, 585–598.


7 R Core Team (2017) R: A Language and Environment for Statistical Computing.


15 Savage, V.M. (2004a) Improved approximations to scaling relationships for species, populations, and ecosystems across latitudinal and elevational gradients. Journal of theoretical biology,


