Supporting Information

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SI Materials and Methods

Panama Leaf Trait Measurements. Traits were measured on mature but not senescent leaves. Gas exchange rates ($A_{\max}$, R_{dark}) were measured in 2007 during the early rainy season. Gas exchange was measured midmorning, the optimal time for photosynthesis, from the canopy crane gondola on attached leaves (in situ) with an LI-6400 portable photosynthesis system (LI-COR Biosciences) at ambient temperature and carbon dioxide concentration. $A_{\max}$ and R_{dark} were estimated by fitting photosynthesis light response curves. Leaves used for these gas exchange measurements were immediately collected, and their fresh leaf area and dry mass (after oven drying at 60 °C) were measured. *LMA*, leaf thickness (*LT*), and leaf density (*LD*) were measured using methods described in refs. 47 and 48. *LL* was measured using methods described in Kitajima et al. (49), with sample sizes for *LL* reported in Table S1. Cellulose per unit leaf volume was measured using methods in Kitajima et al. (21). Leaves collected for *N* and *P* were oven dried at 60 °C and then sent to the Louisiana State University Soil Testing and Plant Analysis Laboratory for analysis.

Ecuador Leaf Trait Measurements. Traits were measured on mature but not senescent leaves. Methods for leaf *N* and specific leaf area (the inverse of *LMA*) are described in the works by Kraft et al. (44, 45, 50). Leaf lamina thickness (*LT*) was measured on field-collected leaves with a digital micrometer by averaging measurements from three points along the central axis of each leaf while avoiding the midrib or other major raised veins (additional details are in ref. 50). Leaf density (*LD*) was then calculated as *LMA*/*LT*.

Generalized Form of Eq. 1 to Quantify Area and Mass Dependence of Leaf Traits. Eq. **1** quantifies how the total amount of trait i in a species j leaf (X_{ij}) depends on area (Area_j) and mass (Mass_j):

$$X_{ij} = a_i \left(\text{Area}_j\right)^{1-b_i} \left(\text{Mass}_j\right)^{b_i} \varepsilon_{ij},$$

where ε_{ij} is a lognormally distributed random variable (e.g., with a mean or median of one) that represents both measurement error and interspecific variation that is not explained by leaf mass or area. The exponent b_i is an index of mass proportionality across species (e.g., if $b_i = 0$, then trait i is purely area proportional, whereas if $b_i = 1$, then trait i is purely mass proportional in that leaf assemblage). In principle, the sum of the exponents for area and mass does not need to be one. A more general form of the equation is

$$X_{ij} = a_i \text{Area}_j^{b_{1i}} \text{Mass}_j^{b_{2i}} \varepsilon_{ij}. \qquad \textbf{[S1]}$$

The exponents b_{1i} and b_{2i} quantify how X_{ij} increases with leaf area and mass, respectively. We used maximum likelihood estimation to fit Eq. **S1** for $A_{\max}$, R_{dark}, *N*, and *P* using a modified Glopnet dataset (2) that included leaf area and leaf mass values for a subset of leaves (area and mass data were not available in the original Glopnet dataset published in ref. 2 but were obtained by P.B.R. for a subset of Glopnet records). Using this enhanced dataset, we fit Eq. **S1** for the global flora and functional groups with at least 25 observations for a given trait. The sum of the estimates for b_{1i} and b_{2i} is close to one for all traits and groups (Table S2), justifying the simpler model represented by Eqs. **1**–**3**.

Partitioning Traits into Mass- and Area-Proportional Fractions Using Model-M&A. Here, we present an alternative method (referred to in ref. 11 as "Model-M&A") to Eqs. **1**–**3** to quantify interspecific mass vs. area proportionality. Model-M&A has a clear biological motivation, but unlike Eqs. **1**–**3**, it is not easily extended to the intraspecific case with the available data (one sun and one shade sample for each species). We present Model-M&A here for its heuristic value in understanding the concept of mass vs. area proportionality and to show the robustness of the estimates of interspecific mass proportionality presented in the text. Osnas et al. (11) showed that Eqs. **1**–**3** (referred to as "Model-LN" in the supporting information in ref. 11) also yield similar quantitative results to a third method ("Model-C" in the supporting information in ref. 11), which further supports the robustness of the interspecific estimates in the text.

Model-M&A quantifies how interspecific trait variation depends on leaf mass and area. The explanation of Model-M&A below closely follows the supporting information in ref. 11 and is presented here for the reader's convenience. Let $\bar{X}_{Mi}$ and $\bar{X}_{Ai}$ be constants that quantify mass and area proportionality, respectively, across species for trait i. The units of $\bar{X}_{Mi}$ and $\bar{X}_{Ai}$ are the amounts of trait i per unit mass and per unit area, respectively. The expected value of the total amount of trait i in a species j leaf is $\text{Mass}_j\bar{X}_{Mi} + \text{Area}_j\bar{X}_{Ai}$. The model has three mathematically identical forms depending on how data are normalized:

$$X_{ij} = \left(\text{Mass}_j\bar{X}_{Mi} + \text{Area}_j\bar{X}_{Ai}\right)\varepsilon_{ij} \qquad \textbf{[S2]}$$

$$X_{Mij} = \left(\bar{X}_{Mi} + \bar{X}_{Ai} LMA_j^{-1}\right)\varepsilon_{ij} \qquad \textbf{[S3]}$$

$$X_{Aij} = \left(LMA_j\bar{X}_{Mi} + \bar{X}_{Ai}\right)\varepsilon_{ij}, \qquad \textbf{[S4]}$$

where X_{ij}, X_{Mij}, and X_{Aij} are the total, mass-normalized, and area-normalized amounts, respectively, of trait i in a species j leaf; and ε_{ij} is a species-specific, unitless random variable with a mean of one that quantifies interspecific variation. According to this model, a trait is purely mass proportional if the mass-proportional constant ($\bar{X}_{Mi}$) is greater than zero but the area-proportional constant ($\bar{X}_{Ai}$) is zero. In this case, Eq. **S2** shows that interspecific variation in the total amount of trait in a leaf is due to two factors alone: interspecific variation in leaf mass (Mass_j) and interspecific variation in the amount of trait per unit leaf mass (ε_{ij}). If a trait is purely mass proportional, the total trait amount (X_{ij}) may increase across leaves as area increases but only due to the positive correlation between area and mass. Thus, if traits are purely mass proportional, then mass-normalized trait values are uncorrelated with mass, area, or *LMA* (Eq. **S3** with $\bar{X}_{Ai} = 0$), whereas area-normalized trait values are, on average, proportional to *LMA* (Eq. **S4** with $\bar{X}_{Ai} = 0$). Conversely, according to this model, a trait is purely area proportional if the area-proportional constant ($\bar{X}_{Ai}$) is greater than zero but the mass-proportional constant ($\bar{X}_{Mi}$) is zero. Area-normalized values of purely area-proportional traits are uncorrelated with mass, area, or *LMA* (Eq. **S4** with $\bar{X}_{Mi} = 0$), but mass-normalized values of purely area-proportional traits are, on average, inversely proportional to *LMA* (Eq. **S3** with $\bar{X}_{Mi} = 0$). Leaf traits may be purely mass proportional, be purely area proportional, or have both mass- and area-proportional components (in which case, both $\bar{X}_{Mi}$ and $\bar{X}_{Ai}$ are greater than zero).

We fit Model-M&A to trait data for Glopnet functional groups and for canopy and understory leaves from Panama and Ecuador using the maximum likelihood methods described in ref. 11. To simplify the text below, we refer to each Glopnet record as a "species j," although in reality, 17% of species in Glopnet are represented by more than one data record. Our analysis was based on area-normalized traits (Eq. **S4**), but equivalent results may be obtained from mass-normalized traits (Eq. **S3**) or from nonnormalized traits (Eq. **S2**) if leaf mass and area values are available (11). For comparison with estimates of mass proportionality presented in the text (b_i in Eqs. **1–3**), we converted the mass- and area-based constants in Model-M&A, $\bar{X}_{Mi}$ and $\bar{X}_{Ai}$, to the mass-proportional trait fraction p_{Mij} for trait i and species j as

$$p_{Mij} = \frac{\mathrm{Mass}_j \bar{X}_{Mi}}{\mathrm{Mass}_j \bar{X}_{Mi} + \mathrm{Area}_j \bar{X}_{Ai}} = \frac{\bar{X}_{Mi}}{\bar{X}_{Mi} + \bar{X}_{Ai} LMA_j^{-1}}. \quad \textbf{[S5]}$$

In Fig. S2, we report the median value of p_{Mij} from its estimated distribution, which reflects both the distribution of LMA values in Glopnet as well as uncertainty in the maximum likelihood estimates (MLEs) of $\bar{X}_{Mi}$ and $\bar{X}_{Ai}$. Specifically, we approximated the sampling distribution of the two parameters as multivariate normal with mean given by the MLEs and variance–covariance matrix estimated from the second derivatives of the likelihood function. For each of 1,000 parameter sets drawn at random from this multivariate normal distribution, we generated a p_{Mij} value for each Glopnet species j using its reported LMA value. We then pooled all p_{Mij} values to yield a distribution of p_{Mi} values across species in each Glopnet functional group. Each functional group was analyzed separately, and the median of the p_{Mi} distribution for each functional group is reported in Fig. S2.

Estimates of interspecific mass proportionality for different traits ($A_{\max}$, R_{dark}, N, and P) within Glopnet functional groups are very similar whether obtained from Eqs. **1–3** (parameter b_i) or from Eq. **S5** (Fig. S2). Note that all available Glopnet values were used in the analyses summarized in Fig. S2, whereas the analyses in Fig. 4 only use Glopnet records for which a leaf lifespan (LL) value was reported. Excluding Glopnet records lacking an LL value typically has a small effect on the estimates of mass proportionality (Table S4) and does not qualitatively affect our results or conclusions.

Quantifying Intraspecific Mass vs. Area Proportionality Between Canopy Layers. Here, we present two models to complement Eqs. **5** and **6** to test whether traits are more area or mass proportional within species between canopy layers. These models test the conservation of either mass- or area-normalized intraspecific trait values across canopy layers. If traits are purely mass proportional, then mass-normalized values should be conserved across canopy layers, and area-normalized values should be proportional to LMA. In contrast, if traits are purely area proportional, then area-normalized values should be conserved across canopy layers, and mass-normalized values should be inversely proportional to LMA.

The first model considered here assumes that the understory and canopy mass-normalized values are, on average, equal. According to this assumption, the understory mass-normalized trait value (UM; representing one of $A_{\max}$, R_{dark}, N, or P) has the same expectation as the canopy mass-normalized value (CM):

$$UM = CM \times \varepsilon_M, \quad \textbf{[S6a]}$$

where ε_M is a lognormally distributed error term with a mean of one that represents measurement error as well as variation between understory and canopy leaves in their mass-normalized trait values. Eq. **S6a** can be expressed in terms of the area-normalized understory trait value (UA) by multiplying both sides of the equation by the understory LMA value (LMA_u):

$$UA = CM \times LMA_u \times \varepsilon_M. \quad \textbf{[S6b]}$$

As an alternative to the mass-proportional model (Eq. **S6**), the second model considered here assumes that the understory and canopy area-normalized values are, on average, equal. According to this assumption, the understory area-normalized trait value has the same expectation as the canopy area-normalized value:

$$UA = CA \times \varepsilon_A, \quad \textbf{[S7a]}$$

where ε_A is a lognormally distributed error term with a mean of one that represents measurement error as well as variation between understory and canopy leaves in their area-normalized trait values. Eq. **S7a** can be expressed in terms of the mass-normalized understory trait value by dividing both sides of the equation by the understory LMA value:

$$UM = \left(\frac{CA}{LMA_u}\right) \times \varepsilon_A. \quad \textbf{[S7b]}$$

The only unknown parameter values in Eqs. **S6** and **S7** are the SDs of ε_M and ε_A. If mass-normalized trait values are more nearly conserved across layers than area-normalized values, then Eq. **S6** will fit the understory data better than Eq. **S7** (i.e., ε_M will have a smaller SD than ε_A). Conversely, if area-normalized values are more nearly conserved than mass-normalized values, then Eq. **S7** will fit the data better.

We used the mle2 function in the bbmle package (51) in R (52) to estimate ε_M and ε_A using maximum likelihood and to calculate the Akaike Information Criterion (AIC) values for these two models (Eqs. **S6** and **S7**) for $A_{\max}$, R_{dark}, and P from Panama and N from both Panama and Ecuador. In Fig. S3, we report results for Eqs. **S6b** and **S7b**, but equivalent results could be obtained from Eqs. **S6a** and **S7a**. Similar qualitative results may also be obtained by treating the canopy trait values as the response and the understory trait values as the predictor.

Results of these analyses show that $A_{\max}$, R_{dark}, N, and P are primarily mass proportional across canopy layers within tropical tree species. Specifically, Eq. **S6** (mass-proportional model) provides a highly significantly better fit to data on intraspecific variation (from sun to shade) than Eq. **S7** (area-proportional model) for all traits (Fig. S3). For every trait, the estimated SD of the error term ε_M in Eq. **S6** is much lower than the estimated SD of the error term ε_A in Eq. **S7**, leading to much lower AIC values for Eq. **S6** compared with Eq. **S7** (AIC difference >46 in all cases). This means that, across canopy layers within species, traits are more nearly mass proportional than area proportional. This result is consistent with the results presented in Fig. 3 (gray bars), which reports estimates of within-species mass proportionately from Eqs. **5** and **6** (parameter w_i).

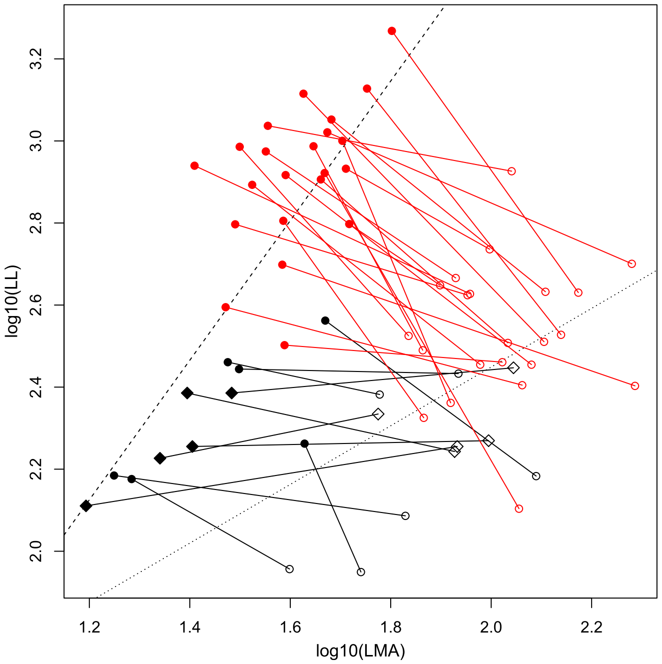

Fig. S1. Leaf lifespan (*LL*; days) vs. leaf mass per area (*LMA*; grams per square meter) for canopy (sun: open symbols) and understory (shade: closed symbols) leaves at dry (black) and wet (red) sites in Panama for the 33 species with both canopy and understory *LL* and *LMA* values. Circles represent evergreen species, and diamonds represent deciduous species. Solid line segments connect sun and shade leaves of a given species. These line segments show that, as *LMA* increases from shade to sun, there is no systematic change in *LL* at the dry site (black), but *LL* decreases at the wet site (red). These intraspecific patterns contrast with interspecific trends shown by the dotted and dashed lines, which are OLS regressions for sun and shade leaves, respectively, pooled across both sites. These regressions show that, across species in Panama, *LL* increases with *LMA*. The log–log slope for sun leaves is 0.72 (SEM = 0.14; *P* value = 0.005), and the log–log slope for shade leaves is 1.70 (SEM = 0.26; *P* value < 0.0001). For comparison, the log–log slope for tropical tree species in Glopnet (primarily sun leaves) is 0.71 (SEM = 0.15; *P* value < 0.0001; *n* = 96 species). Note that the difference in *LL* units (Panama: days; Glopnet: months) does not affect the log–log slopes.

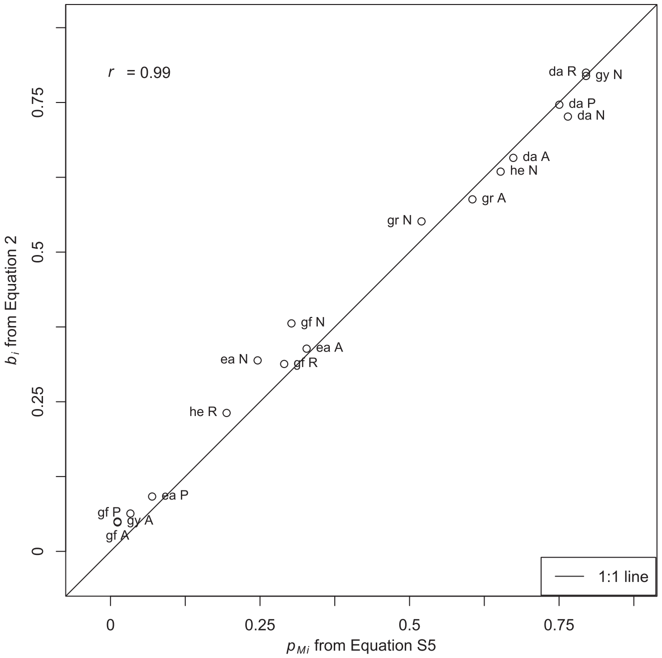

Fig. S2. Relationship between two independent estimates of mass proportionality: b_i from Eq. **2** and p_{Mi} from Eq. **S5**. Each point is labeled by a Glopnet functional group (da, deciduous woody angiosperms; ea, evergreen woody angiosperms; gf, global flora; gr, graminoids; gy, gymnosperms; he, herbs) and a trait (A, maximum net photosynthetic rate A_{max}; N, nitrogen concentration *N*; P, phosphorus concentration *P*; R, dark respiration rate R_{dark}). The figure only shows results for analyses with a sample size (*n*) of at least 25, where *n* is the number of Glopnet records that include trait values needed for a given analysis. The clustering of estimates along the 1:1 line and the high correlation (Pearson's $r = 0.99$) indicate consistent estimates from the two methods, which support the use of Eq. **2** and its extensions to estimate mass proportionality within and among species (Eqs. **5**–**8**). Sample sizes are in Table S4.

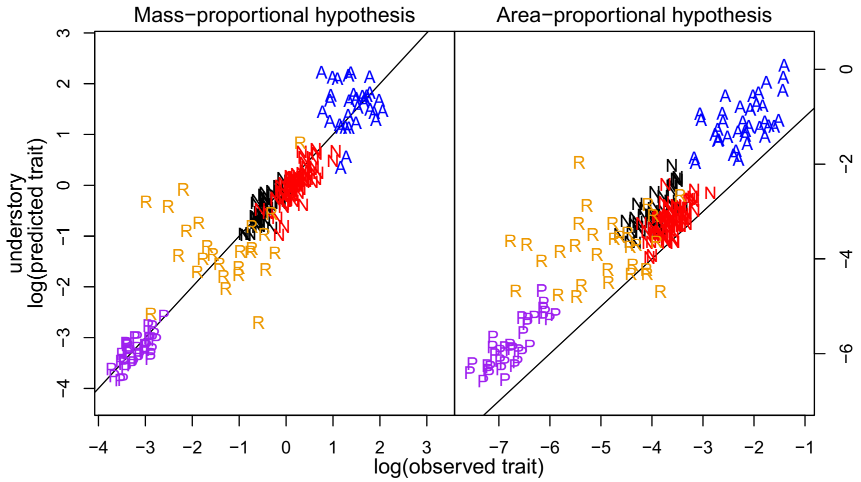

Fig. S3. Results from Eq. **S6** (mass-proportional hypothesis; *Left*) and Eq. **S7** (area-proportional hypothesis; *Right*) for intraspecific variation across canopy layers for four traits measured in Panama (wet and dry sites combined: blue A, maximum net photosynthetic rate A_{max}; orange R, dark respiration rate R_{dark}; black N, nitrogen concentration N; and purple P, phosphorus concentration P) and one in Ecuador (red N, nitrogen concentration). Values are predicted and observed understory trait values (*Left*: area-normalized traits, Eq. **S6b**; *Right*: mass-normalized traits, Eq. **S7b**). Eqs. **S6b** and **S7b** were fit to trait values without logarithmic transformation (units are in Fig. S4), and the predicted and observed values were then natural log transformed for plotting. The 1:1 line is shown. Note that equivalent results are obtained for either mass- or area-normalized trait data, because Eq. **S6a** (mass-normalized) is converted to Eq. **S6b** (area-normalized) by multiplying by a constant, and similarly for Eq. **S7a** (area-normalized) and Eq. **S7b** (mass-normalized). Predictions from the mass-proportional model (*Left*) are distributed evenly across the 1:1 line (indicating conservation, on average, of mass-normalized trait values across canopy layers within species), whereas predictions from the area-proportional model (*Right*) tend to be greater than the observed values (because canopy leaves tend to have greater area-normalized values than understory leaves within a given species) (Fig. S4). These results support the analyses presented in the text (Fig. 3, grays bars), which indicate that, within species, traits are more nearly mass proportional than area proportional. Samples sizes (number of species) for Eq. **S6** (*Left*) for Panama: A_{max} ($n = 32$), R_{dark} ($n = 26$), N ($n = 37$), and P ($n = 37$). Sample sizes for Eq. **S7** (*Right*) for Panama: A_{max} ($n = 37$), R_{dark} ($n = 31$), N ($n = 37$), and P ($n = 37$). Sample size for Eqs. **S6** and **S7** for Ecuador: N ($n = 67$). Sample sizes differ between Eq. **S6**, Eq. **S7**, and other analyses (e.g., Fig. S4) due to missing values for area- or mass-normalized trait values or *LMA*.

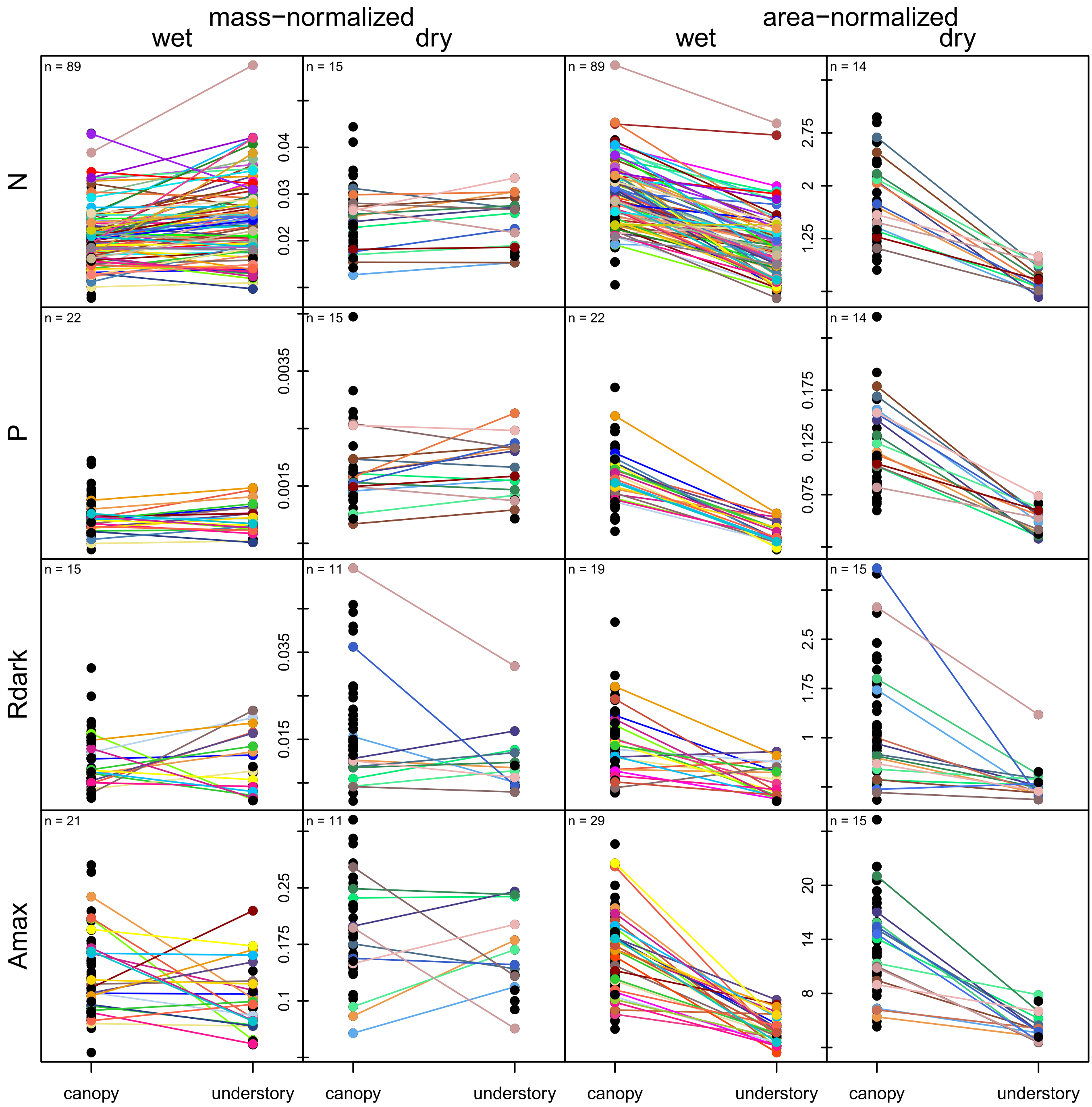

Fig. S4. Mass- and area-normalized values (linear scale) for four traits from wet and dry sites in Panama ($A_{\max}$, maximum net photosynthetic rate; *N*, nitrogen concentration; *P*, phosphorus concentration; R_{dark}, dark respiration rate) and one from Ecuador (*N*; values are combined with *N* from the Panama wet site). Colored points connected by lines represent upper canopy and understory traits for the same species. Black points are for species with observations in only one canopy layer. The figure shows that mass-normalized values do not change systematically across canopy layers, whereas area-normalized values tend to be greater in the canopy than in the understory. Units are $A_{\max}$ and R_{dark}: area-normalized micromoles per second per square meter and mass-normalized micromoles per second per gram; *N* and *P*: area-normalized grams per square meter and mass-normalized grams per gram. Sample sizes (number of species with observations in both the upper canopy and understory) are given in the upper left corner of each panel. For wet site *N*, 67 species are from Ecuador, and 22 are from Panama. Five species appear in more than one subset of the data (two species occur at both wet and dry sites in Panama, and three species occur in both Panama and Ecuador); these instances are treated as separate species in this figure and other analyses.

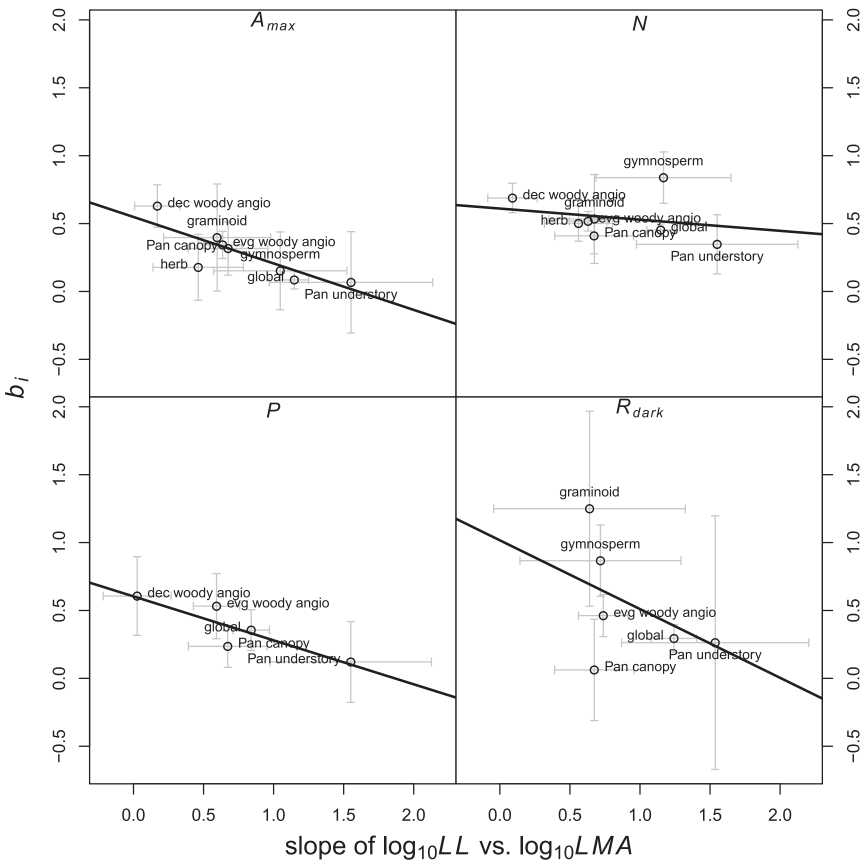

Fig. S5. Interspecific mass proportionality (b_i from Eq. **2**) of traits (clockwise from *Upper Left*: A_{max}, N, R_{dark}, and P) tends to decrease as the strength of the leaf lifespan (*LL*) vs. leaf mass per area (*LMA*) relationship increases (*x* axes are OLS regression slopes). For example, photosynthetic capacity (A_{max}) tends to be area proportional (*y* axis value near zero) in leaf assemblages with strong interspecific relationships between *LL* and *LMA*; in contrast, A_{max} tends toward greater mass proportionality (larger values on *y* axis) in leaf assemblages with weak relationships between *LL* and *LMA*. Each point refers to a Glopnet functional group (the global flora is shown but is not used to calculate the regression line) or to canopy or understory leaves from Panama (wet and dry sites combined). For a given panel (A_{max}, N, R_{dark}, or P), calculations for both *x* and *y* axes were based on the same set of data records, for which the trait (A_{max}, N, R_{dark}, or P), *LL*, and *LMA* were all available. Results for gymnosperms are qualitatively robust to the exclusion of the five deciduous conifers included in Glopnet (*Larix* spp. and *Taxodium distichum*). Error bars are 95% CIs. Sample sizes are in Table S3 for Panama strata and in Table S4 for Glopnet functional groups.

Other Supporting Information Files

Table S1 (DOCX)
Table S2 (DOCX)
Table S3 (DOCX)
Table S4 (DOCX)
Table S5 (DOCX)