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# Divergent drivers of leaf trait variation within species, among species, and among functional groups

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**Understanding variation in leaf functional traits—including rates of photosynthesis and respiration and concentrations of nitrogen and phosphorus—is a fundamental challenge in plant ecophysiology. When expressed per unit leaf area, these traits typically increase with leaf mass per area (*LMA*) within species but are roughly independent of *LMA* across the global flora. *LMA* is determined by mass components with different biological functions, including photosynthetic mass that largely determines metabolic rates and contains most nitrogen and phosphorus, and structural mass that affects toughness and leaf lifespan (*LL*). A possible explanation for the contrasting trait relationships is that most *LMA* variation within species is associated with variation in photosynthetic mass, whereas most *LMA* variation across the global flora is associated with variation in structural mass. This hypothesis leads to the predictions that (i) gas exchange rates and nutrient concentrations per unit leaf area should increase strongly with *LMA* across species assemblages with low *LL* variance but should increase weakly with *LMA* across species assemblages with high *LL* variance and that (ii) controlling for *LL* variation should increase the strength of the above *LMA* relationships. We present analyses of intra- and interspecific trait variation from three tropical forest sites and interspecific analyses within functional groups in a global dataset that are consistent with the above predictions. Our analysis suggests that the qualitatively different trait relationships exhibited by different leaf assemblages can be understood by considering the degree to which photosynthetic and structural mass components contribute to *LMA* variation in a given assemblage.**

functional traits | tropical forests | leaf mass per area | plant functional types | leaf longevity

Leaf traits related to the carbon and nutrient economies of plants represent important aspects of plant functional diversity (1–3). Understanding the drivers of trait variation and relationships among traits is essential for our basic understanding of plant ecology (4, 5) and agricultural production (6, 7) and for accurately representing plant functional diversity in global carbon-climate models (8, 9). Strong correlations among leaf mass per area (*LMA*), leaf lifespan (*LL*), and mass-normalized values of four leaf traits related to photosynthesis and metabolism—light-saturated net photosynthetic rate ( $A_{\max}$ ), dark respiration rate ( $R_{\text{dark}}$ ), nitrogen concentration ( $N$ ), and phosphorus concentration ( $P$ )—have been interpreted as evidence for a mass-based global “leaf economics spectrum” ranging from low-cost (low *LMA*) short-lived leaves with fast photosynthetic returns to high-cost (high *LMA*) long-lived leaves with slow photosynthetic returns (2). However, strong correlations among some pairs of traits may result from mass normalization itself (10), and there is currently no consensus on how to interpret statistical relationships among some leaf traits (11–14).

An important observation that can help clarify the underlying causes of leaf trait relationships is that inter- and intraspecific patterns of trait variation are often fundamentally different (13,

15). For example, in contrast to interspecific global patterns (where area-normalized  $A_{\max}$ ,  $R_{\text{dark}}$ ,  $N$ , and  $P$  are only weakly related to *LMA*) (2, 11), area-normalized  $A_{\max}$ ,  $R_{\text{dark}}$ ,  $N$ , and  $P$  often increase within species as *LMA* increases from shade to sun (15–19). This contrast between interspecific global patterns and intraspecific canopy gradients suggests the presence of multiple biological drivers. Variation in *LMA* integrates variation in the mass per area of multiple tissues and functions, including metabolically active mesophyll cytoplasm that largely determines photosynthetic capacity, as well as structural components (e.g., cellulose) that contribute to leaf toughness (20–23). These different sources of *LMA* variation can lead to divergent trait relationships (Fig. 1) and may help reconcile opposing inter- and intraspecific patterns.

In this paper, we seek a general understanding of the drivers of leaf trait variation across light gradients within species, among species, and among functional groups. In doing so, we present (i) analyses of intra- and interspecific leaf trait variation at three tropical forest sites (wet and dry sites in Panama and a wet site in Ecuador), (ii) analyses of interspecific patterns within functional groups in the Glopnet global leaf traits database (2), and (iii) a conceptual model that explains *LMA* variation in terms of two primary components—photosynthetic capacity and leaf toughness.

## Significance

Leaf traits, such as photosynthetic capacity, nitrogen concentration, and leaf mass per area, strongly affect plant growth and nutrient cycles. Understanding relationships among leaf traits is, therefore, a fundamental challenge in plant biology, crop science, and ecology. Different groups of leaves exhibit distinct relationships among pairs of traits. For example, photosynthetic capacity per unit leaf area increases strongly with leaf mass per area from sun to shade within species, but these same traits are only weakly related across global species. Our analysis suggests that divergent trait relationships can be understood by partitioning leaf mass into photosynthetic and structural support components. Our paper clarifies the causes of relationships among traits and why those relationships differ among different groups of plants.

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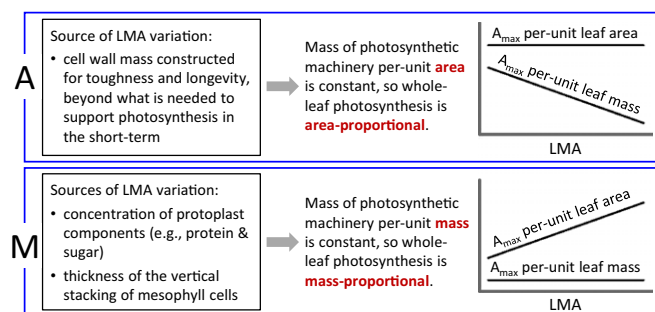
The authors declare no conflict of interest.

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**Fig. 1.** Two extreme cases showing how contrasting sources of variation in leaf mass per area ( $LMA$ ) (20–23) can lead to different relationships between photosynthetic capacity ( $A_{\max}$ ) and  $LMA$ . In case **A** (Upper), the source of  $LMA$  variation affects structural toughness and leaf lifespan but does not directly affect gas exchange (whole-leaf  $A_{\max}$ ). Therefore, whole-leaf  $A_{\max}$  increases with leaf area but not leaf mass. This “area-proportional” trait variation (patterns in Upper Right) is characteristic of the global flora (11). In case **M** (Lower), the sources of  $LMA$  variation directly affect whole-leaf  $A_{\max}$ . Therefore, whole-leaf  $A_{\max}$  increases with leaf mass but not leaf area. This “mass-proportional” trait variation (patterns in Lower Right) is characteristic of intraspecific canopy gradients from sun to shade (15–19). An explanation of trait mass vs. area proportionality is in the text. The linear relationships shown at far right are idealized; real relationships may be nonlinear and would include scatter due to  $LMA$ -independent sources of variation.

The conceptual model—which is introduced in Fig. 1 and is discussed in more detail later in this paper—provides an explanation for divergent patterns in trait variation within species, among species, and among functional groups.

### Mass vs. Area Proportionality of Leaf Traits

A useful starting point for understanding trait relationships is to recognize that the gas exchange rates (e.g.,  $A_{\max}$  or  $R_{\text{dark}}$ ) or nutrient amounts (e.g.,  $N$  or  $P$ ) associated with an entire leaf (the “whole-leaf trait amount”) can depend on leaf mass, leaf area, or some combination of mass and area (11). Leaves with large mass also tend to have large area, but the correlation between mass and area is imperfect due to variation among leaves in lamina thickness and tissue density. The resulting variation in  $LMA$  allows the variance in size-dependent traits (e.g.,  $A_{\max}$ ,  $R_{\text{dark}}$ ,  $N$ , and  $P$ ) to be partitioned into mass- vs. area-proportional fractions (11).

A trait is defined as being purely area proportional in a given assemblage of leaves if the whole-leaf trait amount increases in proportion to leaf area but is uncorrelated with leaf mass after controlling for variation in leaf area. Area-proportional traits are uncorrelated with  $LMA$  when expressed per unit area and are negatively correlated with  $LMA$  when expressed per unit mass (case **A** in Fig. 1). Conversely, a trait is defined as being purely mass proportional if the whole-leaf trait amount increases in proportion to leaf mass but is uncorrelated with leaf area after controlling for variation in leaf mass. Mass-proportional traits are uncorrelated with  $LMA$  when expressed per unit mass and are positively correlated with  $LMA$  when expressed per unit area (case **M** in Fig. 1).

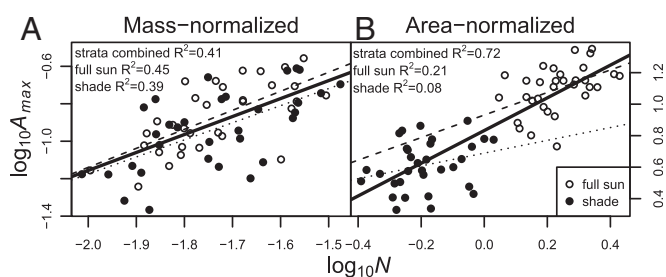
In both area- and mass-proportional cases, normalizing by the variable (mass or area) that controls the whole-leaf trait amount results in normalized trait values that are statistically independent of mass, area, and  $LMA$  (Fig. 1), because in this case, normalization “explains” (or “accounts for”) any size-dependent variation in the trait. In contrast, normalizing by the unrelated variable (i.e., normalizing an area-proportional trait by mass or normalizing a mass-proportional trait by area) results in normalized trait values that are either negatively or positively correlated with  $LMA$  (Fig. 1), because in this case, the whole-leaf trait amount is being divided by an unrelated quantity that is either the numerator (mass) or denominator (area) of  $LMA$ . Here, “unrelated quantity” refers specifically to whole-leaf trait amounts and is not meant to imply that only mass or area is biologically meaningful in a given leaf assemblage (e.g., even in

cases where traits are purely area proportional, leaf mass is still an important quantity related to the economics of investment and return) (14). We use the concepts of mass and area proportionality not to advocate for how traits should be normalized, but rather to provide an analytical framework for quantifying and understanding trait variation in different leaf assemblages.

### Quantifying Trait Mass vs. Area Proportionality Within and Among Tropical Tree Species

Here, we extend a previously developed framework for quantifying mass vs. area proportionality across species (11) to quantify both inter- and intraspecific variation in  $A_{\max}$ ,  $R_{\text{dark}}$ ,  $N$ , and  $P$  at tropical forest sites in Panama and Ecuador. In doing so, we clarify how trait variation differs within vs. among species before discussing our conceptual model (Fig. 1) in greater detail and then using the conceptual model to understand differences in trait variation among functional groups in a global dataset.

Contrasting patterns of trait variation within vs. among species are illustrated by relationships between  $A_{\max}$  and  $N$  for sun and shade leaves of 32 plant species in Panama (Fig. 2 and Table S1). As our analyses below show, interspecific variation in these traits is primarily area proportional (i.e., across species, whole-leaf trait amounts are better predicted by leaf area than mass), whereas intraspecific variation in these traits is primarily mass proportional (i.e., within species, whole-leaf trait amounts are better predicted by leaf mass than area). Following the same logic as described above for relationships between size-dependent traits and  $LMA$ , correlations between two size-dependent traits (e.g., between  $A_{\max}$  and  $N$ ) are stronger when the traits are normalized by the variable (either mass or area) that does not control the whole-leaf trait amount. For example, within species, sun leaves tend to have greater area-normalized  $A_{\max}$  and  $N$  than shade leaves (Fig. 2B), because sun leaves have higher  $LMA$  than shade leaves (Fig. S1) and because intraspecific variation in  $A_{\max}$  and  $N$  is primarily mass proportional (results are shown below). Thus, when  $A_{\max}$  and  $N$  are mass normalized, sun and shade leaves occupy a single envelope of points (Fig. 2A), whereas area normalization results in two separate envelopes and a stronger correlation for the combined sun–shade dataset (Fig. 2B). This strong correlation is simply driven by the separation of sun (high  $LMA$ ) and shade (low  $LMA$ ) leaves. Similarly, among leaves at a given light level, the stronger interspecific correlations obtained from mass normalization (Fig. 2A) compared



**Fig. 2.** Mass-normalized (**A**) and area-normalized (**B**) relationships between maximum net photosynthetic rate ( $A_{\max}$ ) and nitrogen concentration ( $N$ ) for full sun upper canopy (white circles and dashed lines), shaded understory (black circles and dotted lines), and all leaves combined (solid lines). Each point represents 1 of 32 species for which canopy and understory traits were measured in Panama (wet and dry sites yielded similar results and are pooled). Among species within each canopy layer, traits are primarily area proportional (Fig. 3, white bars), and therefore, mass-normalized relationships are stronger (higher  $R^2$  values for sun and shade leaves in **A** compared with **B**). In contrast, within species, traits are primarily mass proportional (Fig. 3, gray bars), and therefore, area-normalized relationships are stronger for the pooled sun–shade dataset (higher  $R^2$  for strata combined in **B** compared with **A**). An explanation of trait mass vs. area proportionality and their effects on trait correlations is in the text.  $A_{\max}$  units are micromoles per second per gram (mass based) and micromoles per second per square meter (area based), and  $N$  units are grams per gram (mass based) and grams per square meter (area based).

with area normalization (Fig. 2B) are also the result of  $LMA$  variation, with high values of  $A_{\max}/\text{mass}$  and  $N/\text{mass}$  corresponding to low  $LMA$  and vice versa (11, 12, 14). The key point here is not to suggest that only one normalizer is valid in a given situation but simply to clarify how mass vs. area proportionality combines with normalization to influence trait relationships.

We now describe our statistical framework for quantifying mass proportionality within and among species. Inferences about mass and area proportionality are interconvertible (e.g., strong mass proportionality implies weak area proportionality and vice versa). Consider the simpler problem of quantifying interspecific mass proportionality, and assume that the whole-leaf amount of trait  $i$  in a species  $j$  leaf ( $X_{ij}$ ) depends on its area ( $\text{Area}_j$ ) and mass ( $\text{Mass}_j$ ) as

$$X_{ij} = a_i \text{Area}_j^{b_{1i}} \text{Mass}_j^{b_{2i}} \varepsilon_{ij},$$

where  $a_i$  is a fitted constant;  $b_{1i}$  and  $b_{2i}$  quantify how trait  $i$  depends on leaf area and mass, respectively, across species; and  $\varepsilon_{ij}$  is a log-normally distributed random variable (assumed to have a median of one in our analysis) that represents both measurement error and interspecific variation that is not explained by leaf area or mass (e.g., variation in photosynthetic capacity due to effects of internal leaf structure on  $\text{CO}_2$  diffusion) (23). The sum of the estimates for  $b_{1i}$  and  $b_{2i}$  is typically close to one (Table S2), and therefore, the above expression can be approximated as

$$X_{ij} = a_i (\text{Area}_j)^{1-b_i} (\text{Mass}_j)^{b_i} \varepsilon_{ij}. \quad [1]$$

Eq. 1 leads to simple expressions for area- and mass-normalized trait values ( $X_{Aij}$  and  $X_{Mij}$ , respectively) that can be analyzed with widely available area- and mass-normalized trait data. The area- and mass-normalized forms, obtained by dividing Eq. 1 by area and mass, respectively, are

$$X_{Aij} = a_i (LMA_j)^{b_i} \varepsilon_{ij} \quad [2]$$

$$X_{Mij} = a_i (LMA_j)^{b_i-1} \varepsilon_{ij}. \quad [3]$$

Eqs. 1–3 yield identical estimates for  $b_i$ , which 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). (Eqs. 1–3 also yield identical estimates for  $a_i$ , the value of  $X_{Aij}$  and  $X_{Mij}$  if  $LMA = 1$ , but we focus our attention on parameter  $b$ , because parameter  $a$  is not relevant to our main questions.) These expressions may be log transformed and analyzed using ordinary least squares (OLS) regression, which yields very similar estimates of mass proportionality as other methods described in ref. 11 (Fig. S2).

To extend Eq. 1 to estimate mass proportionality both within and among species, we assume that the total amount of trait  $i$  in leaf  $k$  of species  $j$  ( $X_{ijk}$ ) depends on species  $j$ 's mean leaf area and mass ( $\overline{\text{Area}}_j$  and  $\overline{\text{Mass}}_j$ , respectively) and also, on leaf-level departures from these means due to intracopy plasticity (24):

$$X_{ijk} = a_i (\overline{\text{Area}}_j)^{1-b_i} (\overline{\text{Mass}}_j)^{b_i} \left( \frac{\text{Area}_{jk}}{\overline{\text{Area}}_j} \right)^{1-w_i} \left( \frac{\text{Mass}_{jk}}{\overline{\text{Mass}}_j} \right)^{w_i} \varepsilon_{ijk}. \quad [4]$$

Parameters  $b_i$  and  $w_i$  quantify mass proportionality of trait  $i$  among and within species, respectively. For example, if trait  $i$  is strongly mass proportional within species ( $w_i$  near one), then intraspecific variation in leaf mass (differences between  $\text{Mass}_{jk}$  and  $\overline{\text{Mass}}_j$ ) would strongly affect the whole-leaf trait amount ( $X_{ijk}$ ), whereas intraspecific variation in leaf area (differences between  $\text{Area}_{jk}$  and  $\overline{\text{Area}}_j$ ) would have little effect on  $X_{ijk}$ .

Because Eq. 4 relies on whole-leaf trait values that are not commonly reported, it is useful to derive alternative forms that can be fit to widely available normalized trait data. Noting that

the mean of  $LMA_{jk}$  across all leaves  $k$  in species  $j$ ,  $\overline{LMA}_j$ , is approximately equal to  $\overline{\text{Mass}}_j/\overline{\text{Area}}_j$ , we can approximate Eq. 4 in area- and mass-normalized forms in terms of interspecific variation in mean  $LMA$  and intraspecific  $LMA$  variation (i.e., differences between  $LMA_{jk}$  and  $\overline{LMA}_j$ ) due to intracopy plasticity (24):

$$X_{Aijk} = a_i (\overline{LMA}_j)^{b_i} \left( \frac{LMA_{jk}}{\overline{LMA}_j} \right)^{w_i} \varepsilon_{ijk} \quad [5]$$

$$X_{Mijk} = a_i (\overline{LMA}_j)^{b_i-1} \left( \frac{LMA_{jk}}{\overline{LMA}_j} \right)^{w_i-1} \varepsilon_{ijk}. \quad [6]$$

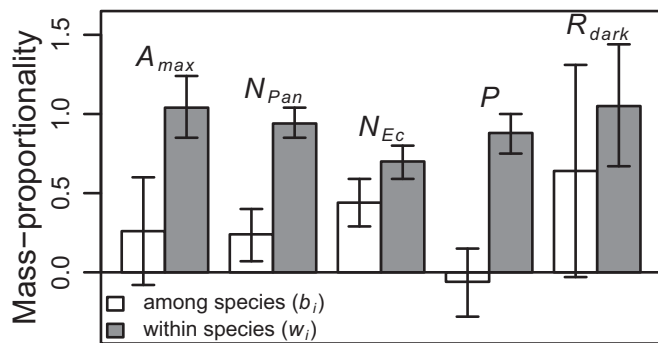
Eqs. 5 and 6 yield identical estimates of inter- and intraspecific mass proportionality ( $b_i$  and  $w_i$ , respectively), and they can be log transformed and analyzed using OLS regression. As in the simpler interspecific model (Eqs. 1–3), the error term ( $\varepsilon_{ijk}$ ) represents not only measurement error but also, trait variation within or among species that is unrelated to  $LMA$  (and therefore, not explained by our model).

We fit Eqs. 5 and 6 to data from Panama (dry and wet sites combined, because both sites yielded similar results), where two values (sun and shade leaves) were available for  $A_{\max}$  (44 species),  $R_{\text{dark}}$  (34 species),  $N$  (32 species), and  $P$  (32 species), and Ecuador, where two values (sun and shade leaves) were available for  $N$  for each of 67 species.

Intraspecific trait variation at the Panama and Ecuador sites was primarily mass proportional ( $w_i > 0.7$  in all cases) (Fig. 3), whereas interspecific trait variation was primarily area proportional ( $b_i < 0.5$  in four of five cases) (Fig. 3). The one exception to interspecific area proportionality ( $b_i = 0.64$  for  $R_{\text{dark}}$ ) has large uncertainty (Fig. 3). Strong interspecific area proportionality for  $A_{\max}$ ,  $N$ , and  $P$  is also apparent across tropical tree species in the Glopnet global database (Table S3) (no estimate for  $R_{\text{dark}}$  due to small sample size). In addition to these results based on Eqs. 5 and 6, strong intraspecific mass proportionality is also implied by an alternative statistical approach (Fig. S3) and by visual inspection of the raw data themselves, because area-normalized trait values tend to be higher for sun leaves (high  $LMA$ ) than shade leaves (low  $LMA$ ), whereas there is no systematic tendency for mass-normalized trait values to increase or decrease across canopy layers (Fig. S4). In summary, strong interspecific area proportionality across tropical plant species emerges from analyses of multiple datasets (Panama, Ecuador, and Glopnet) (Table S3), and strong intraspecific mass proportionality seems to be a robust pattern that does not depend on the particular assumptions used to derive Eqs. 5 and 6.

### Multiple Drivers of Variation in Leaf Mass per Area

Why are traits related to photosynthesis and metabolism ( $A_{\max}$ ,  $R_{\text{dark}}$ ,  $N$ , and  $P$ ) primarily mass proportional within species (Fig. 3, gray bars) but primarily area proportional across tropical species (Fig. 3, white bars and Table S3) and across the global flora (11)? We can gain insight into the causes of these divergent patterns by recognizing that  $LMA$  is a composite trait, with density and volume components for multiple types of tissues and chemical compounds (20). Nearly all  $LMA$  components may be considered to contribute to a leaf's lifetime photosynthesis in some way. However, some structural and chemical components that strongly affect leaf toughness (e.g., cellulose mass per leaf volume) (21, 22)—and thus, the lifespan over which photosynthetic dividends are returned (2, 25)—have little direct effect on photosynthetic capacity and metabolism (Fig. 1). These structural  $LMA$  components may even decrease photosynthetic capacity (e.g., due to the negative effects of cell wall thickness on mesophyll conductance) (26–28). Thus, to understand the causes of covariation between  $A_{\max}$  (as well as  $R_{\text{dark}}$ ,  $N$ , and  $P$ ) and  $LMA$  in a given leaf assemblage, it is important to consider the degree to which  $LMA$  variation is driven by variation in the mass per area of components that directly contribute to photosynthetic capacity (e.g., cytoplasm in palisade mesophyll) vs. those that do not (e.g., cellulose).



**Fig. 3.** Mass proportionality among (white bars) and within (gray bars) species for four leaf traits (maximum net photosynthetic rate is  $A_{max}$ , dark respiration rate is  $R_{dark}$ , nitrogen concentration is  $N$ , and phosphorus concentration is  $P$ ) from Panama (subscript “Pan”: dry and wet sites combined) and one trait ( $N$ ) from Ecuador (subscript “Ec”). Parameters  $b_i$  and  $w_i$  (Eqs. 5 and 6) are zero and one, respectively, for traits that are purely area or mass proportional. Among species, trait variation is primarily area proportional ( $b_i < 0.5$  in most cases). In contrast, within species, trait variation is primarily mass proportional ( $w_i > 0.7$ ). An explanation of trait mass vs. area proportionality is in the text. Error bars are 95% CIs. Sample sizes are in Table S3.

Conceiving of  $LMA$  variation in terms of the mass per area of photosynthetic vs. structural components provides a simple explanation for contrasting intra- and interspecific leaf trait relationships. Shipley et al. (29) used a similar conceptual model to understand interspecific trait covariance in the global flora. We suggest that this conceptual framework also provides a simple explanation for divergent patterns in trait variation within vs. among tropical species (Fig. 3) as well as among different plant functional groups (see below). Our conceptual model posits that variation among leaves in the mass per area of photosynthetic machinery leads to mass proportionality of  $A_{max}$  and related traits (because in this case, variation in  $LMA$  is associated with variation in  $A_{max}$  per area), whereas variation among leaves in the mass per area of structural components that contribute to toughness and  $LL$  but not photosynthetic capacity leads to area proportionality (because in this case, variation in  $LMA$  is independent of variation in  $A_{max}$  per area). The degree of mass vs. area proportionality in a given leaf assemblage should thus reflect the balance between these different drivers of  $LMA$  variation.

Consider the expected contributions of photosynthetic vs. structural leaf mass to  $LMA$  variation in interspecific assemblages with highly variable  $LL$  (e.g., the global flora and tropical forest communities, where  $LL$  often varies by a factor of five or more) (Fig. S1) (21, 30). In these cases, we expect much  $LMA$  variation to be associated with variation in the mass per area of structural and chemical components that contribute to toughness and  $LL$  (20–22, 31, 32). Thus,  $A_{max}$  and related traits should be largely area proportional, because much of the variation in  $LMA$  should be unrelated to the mass of photosynthetic machinery per leaf area (case A in Fig. 1). Mass-normalized values of these area-proportional traits will exhibit strong negative correlations with  $LMA$  and strong positive correlations with each other for reasons described above and in refs. 11 and 12.

In contrast to interspecific assemblages in which  $LL$  increases with  $LMA$ ,  $LL$  often decreases within species as  $LMA$  increases from shade to sun (Fig. S1) (33, 34). This negative intraspecific association between  $LL$  and  $LMA$  may be explained by differences in optimal  $LL$  across light environments [e.g., due to differences in the costs/benefits of deploying new leaves vs. retaining existing ones (35)] and is unlikely to reflect a direct causal relationship between  $LMA$  and  $LL$ . Rather, intraspecific variation in  $LMA$  across light gradients is associated with variation in photosynthetic capacity (16, 19, 20, 36, 37). In this case, we expect  $A_{max}$  and related traits to be strongly mass proportional, because much of  $LMA$  variation is a direct consequence of variation in the mass of photosynthetic machinery per leaf area (case M in Fig. 1).

Unlike the above examples, some other leaf assemblages may resemble neither of the hypothetical cases illustrated in Fig. 1. For example, in temperate deciduous forests with modest (e.g., twofold) variation in  $LL$ , interspecific variation in both photosynthetic capacity and toughness likely contributes to  $LMA$  variation (38) and thus, should exhibit an intermediate degree of mass proportionality.

The above conceptual model of  $LMA$  variation in terms of the mass per area of photosynthetic and structural components has important limitations. First, interpreting  $LMA$  in terms of mass per area components does not explicitly account for leaf anatomy or density (e.g., cellulose mass per volume is a better predictor of leaf toughness and  $LL$  than cellulose mass per area in at least some cases) (21, 22). Second, some  $LMA$  components cannot easily be partitioned into photosynthetic vs. structural functions. For example, thick cell walls enhance leaf toughness and can increase  $LL$  (26), but at least some cell wall mass is required for biomechanical support (e.g., for internal leaf structure and optimal leaf display) and water transport that enable photosynthesis (23, 39, 40). Despite these limitations, interpreting  $LMA$  in terms of photosynthetic and structural components is useful for understanding divergent patterns in trait variation within vs. among tropical species (see above) as well as among different plant functional groups (see below).

### Understanding Differences in Trait Mass Proportionality Among Plant Functional Groups

Conceiving of  $LMA$  variation as arising from variation in photosynthetic and structural components leads to testable predictions regarding patterns of trait variation in different functional groups of species. As explained above and in Fig. 1, interspecific mass proportionality of  $A_{max}$ ,  $R_{dark}$ ,  $N$ , and  $P$  should be relatively low within assemblages in which  $LL$  is highly variable and strongly associated with  $LMA$  variation. In such assemblages, much of the  $LMA$  variation among species should be due to structural leaf mass that contributes little to whole-leaf values of  $A_{max}$ ,  $R_{dark}$ ,  $N$ , and  $P$ ; thus, these whole-leaf trait amounts should be roughly proportional to leaf area rather than mass. Conversely, interspecific mass proportionality should be relatively high within assemblages in which  $LL$  varies little and is weakly associated with  $LMA$ , because in these cases, much of the variation in  $LMA$  should be directly related to the mass of photosynthetic machinery per unit leaf area. The above general predictions can be translated into two quantitative predictions that can be tested by comparing patterns of trait variation across different functional groups: first, the degree of interspecific mass proportionality of  $A_{max}$ ,  $R_{dark}$ ,  $N$ , and  $P$  should increase as the strength of the  $LL$ – $LMA$  relationship decreases; second, statistically controlling for variation in  $LL$  should increase the estimated degree of mass proportionality of  $A_{max}$ ,  $R_{dark}$ ,  $N$ , and  $P$ , because as  $LL$  variation decreases, the fraction of  $LMA$  variation associated with photosynthetic and metabolic traits should increase.

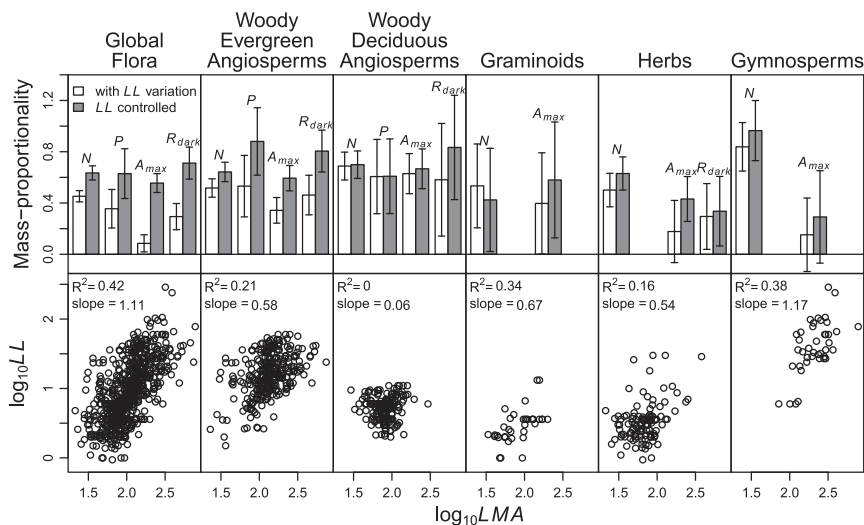
To evaluate the first prediction (interspecific mass proportionality should increase as the strength of the  $LL$ – $LMA$  relationship decreases), we used Eqs. 2 and 3 to estimate interspecific mass proportionality ( $b_i$ ) of  $A_{max}$ ,  $R_{dark}$ ,  $N$ , and  $P$  for different functional groups in the Glopnet global dataset (Fig. 4, white bars and Table S4). Results for  $A_{max}$  strongly support the predicted increase in mass proportionality with decreasing strength of the  $LL$ – $LMA$  relationship (Fig. S5), and results for  $R_{dark}$ ,  $N$ , and  $P$  are also generally supportive, despite the presence of a few outliers and high uncertainty in some estimates (Fig. S5).

To evaluate the second prediction (interspecific mass proportionality should increase after controlling for  $LL$  variation), we modified Eqs. 2 and 3 to statistically control for  $LL$  when estimating interspecific mass proportionality ( $b_i$ ):

$$X_{Aij} = a_i (LMA_j)^{b_i} (LL_j)^{c_i} \epsilon_{ij} \quad [7]$$

$$X_{Mij} = a_i (LMA_j)^{b_i-1} (LL_j)^{c_i} \epsilon_{ij}. \quad [8]$$

Applying Eqs. 7 and 8 (which yield identical results) to Glopnet functional groups suggests that mass proportionality is



**Fig. 4.** (Upper) Mass proportionality among species within Glopnet functional groups tends to be greater when controlling for leaf lifespan ( $LL$ ) variation (Eq. 7) (gray bars) vs. when  $LL$  variation is not accounted for (Eq. 2) (white bars). Error bars are 95% CIs. (Lower)  $LL$  (months) vs. leaf mass per area ( $LMA$ ; grams per square meter).  $R^2$  and slopes are from  $\log_{10}$  regressions. Analyses were restricted to Glopnet records with a reported  $LL$  value, so that both estimates (white and gray bars) use the same set of records. Sample sizes ( $n \geq 25$ ) are in Table S4.

indeed greater among leaves of equal  $LL$  than among leaves of variable  $LL$ . Specifically, Eqs. 7 and 8 yield estimates of  $b_i$  that tend to be greater than those from Eqs. 2 and 3 (Fig. 4, compare gray and white bars and Table S4), particularly for groups with strong  $LL$ – $LMA$  relationships (e.g., the global flora, woody evergreen angiosperms, and gymnosperms).

## Discussion

It is widely recognized that  $LMA$  variation is associated with multiple tissues and functions, including metabolically active mesophyll that determines photosynthetic capacity, as well as structural and chemical components that contribute to leaf toughness (20–23). Here, we have shown that interpreting  $LMA$  variation in terms of photosynthetic and structural components leads to a simple, unified explanation for divergent patterns in trait variation within species, among species, and among functional groups. In leaf assemblages where  $LMA$  variation is driven primarily by structural components that contribute to leaf toughness and leaf lifespan ( $LL$ ) but not photosynthetic capacity, per unit area values of photosynthetic and metabolic traits (e.g.,  $A_{max}$ ,  $R_{dark}$ ,  $N$ , and  $P$ ) should be largely independent of  $LMA$  (case A in Fig. 1). Such cases include the global flora and the functionally diverse tropical forest communities studied here. In contrast, in leaf assemblages where  $LMA$  variation is primarily caused by variation in leaf photosynthetic capacity, per unit area values of  $A_{max}$  and related traits should increase with  $LMA$  (case M in Fig. 1). Such cases include intraspecific sun–shade comparisons (16, 19, 20, 36, 37). Interspecific assemblages with moderate variation in  $LL$  (e.g., temperate deciduous trees) are somewhere between the extreme cases illustrated in Fig. 1.

Observed patterns in trait variation within and among species and functional groups are largely consistent with the above interpretation of  $LMA$  variation in terms of photosynthetic and structural components. This conceptual model also clarifies why whole-leaf trait values (e.g., the rate of gas exchange of an entire leaf or the amount of nutrient in an entire leaf) are better predicted by leaf area than mass in some cases (area proportionality) and better predicted by leaf mass than area in other cases (mass proportionality). Our conceptual model and supporting evidence underscore the futility of advocating for either mass or area normalization of leaf traits as a general principle. Our analyses show that traits are not, as a general rule, either mass or area proportional, and our conceptual model explains why this is so.

Future efforts should focus on moving beyond the conceptual model presented here to provide a more mechanistic framework for representing leaf functional variation in terms of measurable anatomical and chemical traits. Recent efforts to decompose interspecific  $LMA$  variation into anatomical components (41) and to quantify interspecific tradeoffs related to leaf nitrogen

allocation and cell wall thickness (26) could be extended to study intraspecific variation. Simple models based on leaf density and lamina thickness (both of which contribute to  $LMA$  variation within and among the tropical species that we studied) fail to capture the main patterns in the datasets analyzed here (Table S5). Leaf density and cellulose mass per leaf volume are good predictors of leaf toughness and  $LL$  in some previous studies (21, 22, 34) and in some subsets of our data, but they are poor predictors of  $LL$  for sun leaves at the speciose wet Panama site (Table S5). This inconsistency may reflect the variety of factors, including photosynthetic capacity and self-shading, that affect optimal  $LL$  (35, 42). Developing a quantitative, mechanistic model for leaf trait variation within and among species may require integrating optimal  $LL$  theory (35) with anatomical tradeoffs, such as the increase in leaf toughness and the decline in mesophyll conductance (and thus, photosynthetic capacity) as cell wall thickness increases (26–28).

## Materials and Methods

**Trait Data Sources.** The Panama data (Table S1) include leaves sampled at two different canopy positions (“canopy”: full sun at the top of the canopy; and “understory”: well-shaded, sampled within 2 m of the forest floor) from plant species (including trees, treelets, lianas, vines, epiphytes, and hemiepiphytes) within the reach of a canopy crane at two sites: Parque Natural Metropolitano (PNM) and Bosque Protector San Lorenzo (SL). The “dry” PNM site is a semideciduous coastal Pacific forest with a 5-mo dry season from December to April and 1,740 mm of annual rainfall (43). The PNM crane is 40 m tall with a 51-m-long boom. The “wet” SL site is an evergreen Caribbean coastal forest with 3,100 mm of annual rainfall (43). The SL crane is 52 m tall with a 54-m-long boom. Methods for quantifying traits at the Panama sites are described in SI Materials and Methods.

The Ecuador data (44, 45) (SI Materials and Methods) are from the Yasuní Forest Dynamics Plot in a mature terra firme forest in Yasuní National Park and Biosphere Reserve in Amazonian Ecuador, with 3,081 mm of annual rainfall (46). Full sun canopy leaves from Ecuador were collected from sapling and adult trees growing at least partially in forest gaps and clearings with branches that could be clipped from the ground with a pole pruner.

The Glopnet dataset, available from ref. 2, includes ~2,500 records with one or more of the following six traits:  $A_{max}$ ,  $R_{dark}$ ,  $N$ ,  $P$ ,  $LMA$ , and  $LL$ . Eighty-three percent of species in Glopnet are represented by a single record, and therefore, our analyses of Glopnet data primarily represent interspecific variation. Most records are missing data for one or more traits, which restricts the sample size for a given analysis. Analyses of Glopnet tropical trees (Table S3) used records where growth form was reported as “tree” and biome was reported as “tropical rainforest” or “tropical seasonal forest.” Analyses of Glopnet functional groups (Fig. 4 and Fig. S5) used taxonomy, leaf habit (evergreen or deciduous), and growth form data reported in Glopnet to partition species into functional groups: gymnosperms, graminoids (families Poaceae, Cyperaceae, and Juncaceae), herbaceous plants (excluding graminoids), evergreen woody angiosperms (shrubs and trees), and deciduous woody angiosperms (shrubs and trees).

**Analysis.** Results reported in the text are based on OLS regression analysis of  $\log_{10}$ -transformed versions of Eqs. 2, 5, and 7 (area-normalized forms). These analyses are normalization independent, and therefore, fitting Eqs. 3, 6, and 8 (mass-normalized forms) yields equivalent results. Not all analyses could be performed for all datasets. For example, Eq. 7 could not be fit to the Ecuador dataset, which lacks *LL*, and we did not attempt to fit Eq. 5 to Glopnet data, which primarily reports interspecific variation for sun leaves. Additional analyses were performed for comparison with the text OLS analyses as described in *SI Materials and Methods*.

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