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Different Measurement Protocols Impact Specific Leaf Area (SLA) Estimation in Simple Versus Compound Leaves

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ABSTRACT

Aims: Specific leaf area (SLA), the ratio of leaf surface area to dry mass, is a key functional trait widely used to characterize resource allocation to light interception in plants. However, inconsistencies in SLA measurement—particularly whether petiolar tissues (such as petioles and rachises) are included—could lead to discrepancies in SLA estimates, especially in woody plants with compound leaves. This study investigates how two SLA measurement protocols (including vs. excluding the petiolar component) affect SLA estimates in both simple and compound leaves, with the goal of clarifying their implications for ecological studies.

Location: Tropical forests of the Peruvian Amazon.

Methods: Leaf area and dry mass were measured in 2758 individuals representing 1054 woody plant species from three sampling areas. We evaluated differences in the relationship between leaf area and dry mass across leaf types and measurement protocols while controlling for species-level variation and phylogenetic structure. Additionally, a literature review was conducted to evaluate prevailing SLA measurement practices.

Results: Compound leaves exhibited consistently higher SLA than simple leaves of similar size, regardless of the protocol, with differences increasing with leaf size. Excluding the petiolar component amplified the disparity between leaf types, while SLA estimates for simple leaves remained relatively consistent across protocols. SLA declined with increasing leaf area in all cases. The literature review revealed that 46.8% of studies did not specify SLA measurement protocols, and among those that did, 76.2% included the petiolar component.

Conclusions: SLA measurement protocol substantially influences trait estimates, particularly for compound leaves. While the protocol choice should be guided by the specific goals of each study, we argue that a default approach incorporating both laminar and petiolar components is optimal, as it is cost-effective and easy to implement. Clear methodological reporting is essential for ensuring comparability across studies and advancing the use of SLA in plant ecological research.

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1 | Introduction

Through photosynthesis, plants initiate nutrient cycles and energy fluxes that fuel most of the Earth's ecosystems (Fitter and Hay 2002; Lambers et al. 2008). Optimizing light capture for photosynthesis is key to the life cycle of plants. To this end, plants deploy leaves, specialized organs for light interception, whose morpho-physiological properties strongly affect a plant's photosynthetic performance (Givnish 1979; Wright et al. 2004; Niinemets and Sack 2006). Leaf functional traits are used to capture these properties, reflecting how plants interact with their environment and allocate resources (Craine 2009). Exploring how these traits vary across environments is a central focus of trait-based community ecology (McGill et al. 2006; Díaz et al. 2016; Bruelheide et al. 2018), but also in other areas of ecology, such as ecosystem functioning (Lavorel and Garnier 2002), the response to global change (Poorter et al. 2009; Wright et al. 2017), or ecosystem restoration (Laughlin 2014).

The most widely studied set of foliar functional traits in ecological research falls within the leaf economics spectrum (Wright et al. 2004). This set includes specific leaf area (SLA), leaf mass per area (which is the inverse of SLA), leaf lifespan, photosynthetic rate, dark respiration and nitrogen or phosphorus content. Among these, SLA—defined as the ratio of leaf area to dry mass (Pérez-Harguindeguy et al. 2013; Garnier et al. 2016)—is one of the most widely used functional traits. SLA depicts a plant's effective light-capturing surface per unit of carbon investment and can thus be used to characterize foliar resource allocation strategies, which can profoundly influence the plant's photosynthetic capacity (Lambers et al. 2008). SLA correlates with other traits, such as photosynthetic rate and leaf lifespan (Reich et al. 1998; Poorter et al. 2014; Flores-Moreno et al. 2019), making it a valuable proxy in plant functional ecology studies at the species (Poorter and Rozendaal 2008; Shipley and Almeida-Cortez 2003), community (Ackerly et al. 2002; Jung et al. 2010; Rosbakh et al. 2015) and ecosystem levels (Hulshof et al. 2013; He et al. 2018; Bohora Schlickmann et al. 2020).

SLA can differ between leaf types, with compound leaves often exhibiting higher SLA than simple leaves of comparable size. This pattern may reflect greater photosynthetic efficiency per unit biomass, particularly in environments where rapid light capture or efficient water use is advantageous (Givnish 1978). For example, in tropical and arid systems, the modular arrangement of leaflets in compound leaves can reduce self-shading, enhance heat dissipation, and optimize water use, potentially allowing these leaves to maintain higher SLA relative to simple leaves.

In addition, SLA is strongly influenced by foliar structure, as the volume fractions of different tissues vary across leaf parts (Niinemets and Sack 2006; Poorter et al. 2009; John et al. 2017). A whole leaf (WL) usually contains laminar and petiolar components (petioles, petiolules and rachises) (Niinemets and Sack 2006; Bell and Bryan 2008). The laminar component (LC) is mostly comprised of photosynthetic tissue, although it also includes veins, while the petiolar component mainly contains the vascular and mechanical elements (Smith et al. 2004; Lambers et al. 2008). Variations in leaf structure, including the distinction between simple and compound leaves and differences in

leaf size, can significantly alter the biomass allocation to both kinds of tissues (Givnish 1979; Milla and Reich 2007; Milla et al. 2008). As a result, how these components are treated during SLA measurement—whether included or excluded—can lead to substantial disparity in estimated SLA values.

Over the years, various standardized protocols for measuring SLA have been proposed, differing on whether the petiolar component should be included in the measurement (e.g., Cornelissen et al. 2003) or not (e.g., Garnier et al. 2001). These earlier protocols have been revised, refined, and synthesized by more recent guidelines, particularly those outlined by Pérez-Harguindeguy et al. (2013, 2016), which now serve as the prevailing standard for SLA measurement. These authors advocate for the inclusion of the rachis but present a more nuanced perspective on the inclusion of petioles, suggesting that the decision should depend on the specific research question being addressed. Including the petiolar component could have significant implications when measuring SLA in different leaf types, as compound leaves generally have larger total leaf area (including all leaflets) and heavier petiolar tissues compared to simple leaves (Niinemets et al. 2006; Yang et al. 2019). However, to the best of our knowledge, no studies have examined the effects of taking different decisions regarding leaf fractionation on SLA estimations, whether in simple or compound leaves.

This study aims to address this gap by (1) investigating how two different SLA measurement protocols—one that includes both laminar and petiolar components (henceforth whole leaf [WL] protocol), and another that includes only the laminar component (henceforth LC protocol) influence SLA measurements in simple and compound leaves. We analyzed data from 1054 Neotropical woody plant species. Given that compound leaves have heavier petiolar tissues, we hypothesize that considering only the laminar leaf component will result in more similar SLA estimations between simple and compound leaves of comparable sizes. We also expect that, regardless of the measurement protocol, compound leaves may consistently exhibit higher SLA than simple leaves of similar laminar area, with the difference being more pronounced in larger leaves where petiolar mass contributes proportionally less to total leaf biomass. Additionally, we (2) examine the relative contributions of laminar and petiolar components to total leaf area and dry mass in simple and compound leaves to better understand their impact on SLA estimates. Finally, we (3) conduct a systematic review of SLA measurement practices in the literature to assess how protocols, regarding WL versus LC, are reported and applied in ecological studies. The results of this study could help inform the choice of SLA measurement protocol, particularly in ecological studies where both leaf types occur and are measured together.

2 | Methods

2.1 | Study Area and Field Sampling

The study was conducted in the Peruvian Amazon forests, covering a 1200-km latitudinal gradient with an elevation range between 91 m and 528 m a.s.l. Three areas were selected to represent distinct forest types: the Maijuna-Kichwa Regional Conservation Area (Loreto province), the Pacaya-Samiria

National Reserve (Loreto) and the Yanessa Community Reserve (Pasco). These regions correspond to lowland *terra firme* forests, seasonal floodplain and submontane *terra firme* forests, respectively, and experience mean annual temperatures ranging from 24.9°C to 26.8°C and mean annual precipitation between 2271 and 3184 mm (Figure 1). In each area, we established 10 0.1-ha temporary plots and collected for trait measurement, on average, 34.2% (minimum = 14.5%, maximum = 65.4%) of all woody individuals, including trees, lianas, and hemi-epiphytes with a diameter at breast height ≥ 2.5 cm. Leaf samples were collected mostly from the understory, targeting the least shaded locations whenever possible, as the tree canopy often exceeded 25–30 m in height, making it unfeasible to sample outer canopy leaves. Fresh leaves were preserved using the Schweinfurth (alcohol) method (Parnell et al. 2013). Leaves were placed between sheets of newspaper, which were loosely tied together to form a bundle. This bundle was then placed in a large plastic bag and fully immersed in 70% ethanol, with air excluded before sealing the bag with duct tape. To ensure protection, the bundle was further wrapped and sealed in a second airtight plastic bag until transport to the lab. Field sampling and trait measurements were conducted in 2018 and 2019. Further information about

field sampling protocols can be found in Arellano et al. (2016) and Ben Saadi et al. (2022). Floristic data for all plots are available on ForestPlots (plot codes: DPM-11 to DPM-40).

2.2 | Measurement Protocols

We collected an average of 4.89 leaves per individuals (2758 individuals from 1054 species). Rehydration of leaves prior to leaf area (LA) measurement was not possible, as preservation of samples in 70% ethanol irreversibly replaces cellular water and prevents recovery of the original tissue hydration. Each leaf was carefully cleaned to remove any exogenous elements (i.e., fungi, moss, soil) before further measurements. Each leaf sample was divided into laminar and petiolar components: petioles and leaf blades for simple leaves, and rachis, petiolules and leaflets for compound leaves (Figure 2). Winged petioles were manually cut avoiding the blade, while winged rachises were longitudinally cut with scissors, separating the blade from the supportive tissue. Laminal wings were considered as laminal tissues.

LA (cm²) was measured using a CI-202 laser area meter (CID Bio-Science Inc., Camas, USA). For simple leaves, each blade

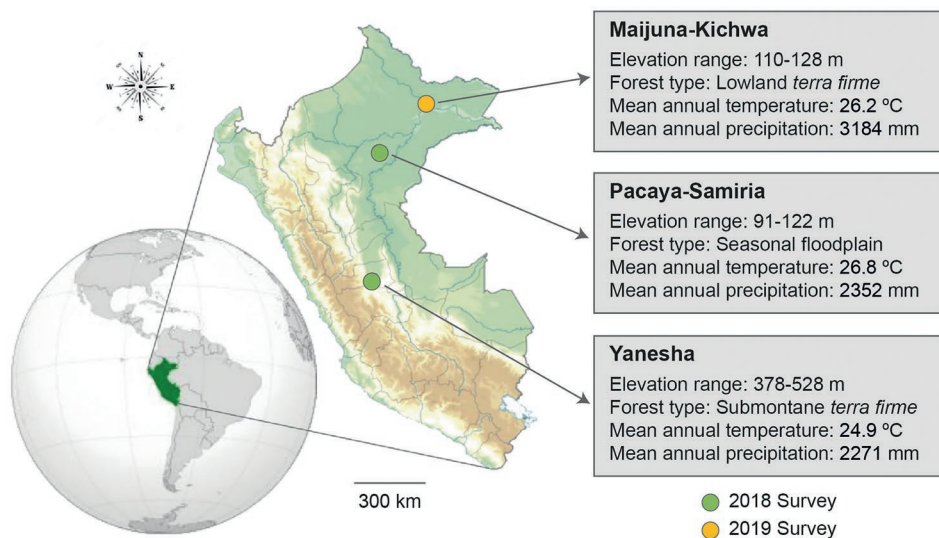


FIGURE 1 | Location and environmental data of the three sampling areas in this study: Majuna-Kichwa Regional Conservation Area, Pacaya-Samiria National Reserve and Yanessa Community Reserve in the Peruvian Amazon. Modified from Ben Saadi et al. (2022).

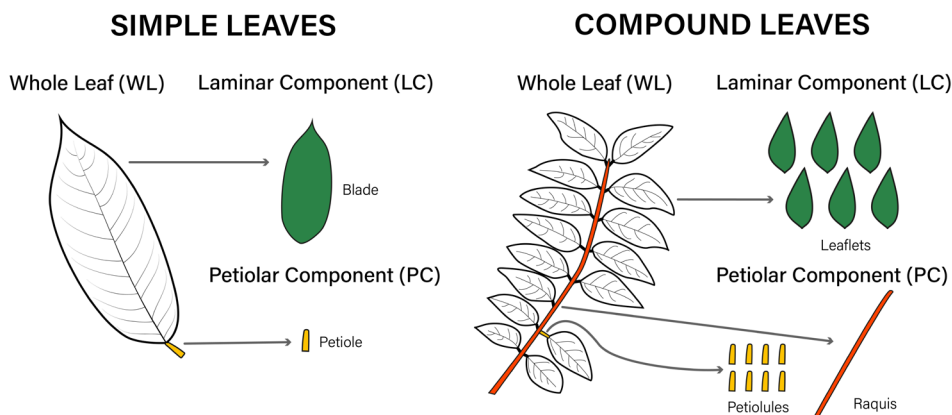


FIGURE 2 | Whole leaf, laminar, and petiolar components in simple and compound leaves.

was scanned individually, while all petioles from the same plant were scanned together to save time and reduce measurement error, as scanning them individually would have increased relative error. For compound leaves, all leaflets from a single leaf were scanned at the same time, and all petiolules were scanned together, while the rachis was scanned individually. The total LA that we considered for the whole leaf (WL) protocol (LA_{WL}) was calculated as the combined area of both laminar and petiolar components (i.e., petioles, petiolules, and rachises), while the LA considered for the laminar component (LC) protocol (LA_{LC}) excluded the petiolar component. The mean LA_{WL} and LA_{LC} per individual plant were obtained by dividing the total leaf areas by the number of sampled leaves per individual.

Following the leaf area measurements, we assessed the dry mass (DM; g) of both laminar and petiolar components. Both kinds of tissues were placed in separate paper bags and oven-dried at 80°C for 48 h. After drying, the samples were immediately weighed to the nearest 0.01 g using an electronic scale. The total DM values that we considered for the WL protocol (DM_{WL}) and the LC protocol (DM_{LC}) were calculated similar to the leaf area measurements, with DM_{WL} including both leaf components and DM_{LC} including only the laminar component. Mean values of both parameters were obtained by dividing the total dry masses by the number of sampled leaves per individual. The resulting dataset is available in Appendix S1.

2.3 | Data Analyses

To explore the contribution of the different leaf components (laminar and petiolar) to LA_{WL} and DM_{WL} in simple versus compound leaves, we calculated the percentage of laminar and petiolar components by dividing their respective area or mass measurements by LA_{WL} or DM_{WL} . We then determined the minimum, maximum, and mean values for each percentage.

We assessed the effects of measurement protocol and leaf type on SLA. For this purpose, we log-transformed the mean LA_{WL} and LA_{LC} as well as the mean DM_{WL} and DM_{LC} . We employed phylogenetic generalized linear mixed models (PGLMMs; Ives and Helmus 2011) to test for differences in the slope and elevation of the relationship between these variables across both leaf types. This approach accounted for the allometric decrease in SLA with increasing LA (Milla and Reich 2007; Niinemets et al. 2007), while avoiding issues of mathematical dependency between SLA and LA. PGLMMs were particularly suitable because, in addition to incorporating phylogenetic relationships among species and the hierarchical structure of the data (multiple observations per species), they also allow the inclusion of additional random effects, which are not readily accommodated by other methods, such as phylogenetic generalized least squares (PGLS) (de Villemereuil and Nakagawa 2014). For each measurement protocol, we fitted five separate models. In all models, $\log(LA)$ was used as the response variable, with fixed effects including all possible combinations of $\log(DM)$ and leaf type: a null model, two single-predictor models, an additive model including both predictors, and a multiplicative model including also the interaction between predictors. Species was included as a random effect in every model to account for intraspecific

variation. All models were fitted using the *pglmm* function of the *phyr* R package (Li et al. 2020). Model selection was based on the Akaike information criterion (AIC), with models differing by more than two AIC units considered substantially less supported and omitted (Burnham and Anderson 2002). To construct the phylogenetic tree for model fitting, we used the *phylo.maker* function from the *V.PhyloMaker2* R package (Jin and Qian 2022). Botanical names were standardized using the Taxonomic Name Resolution Service (Boyle et al. 2013). We then used the default 'GBOTB.extended.TPL' tree, a mega-phylogeny of vascular plants embedded in the package, as the baseline. To better illustrate the results, we used the best-fit models to predict LA and DM values, calculated SLA from these predictions and plotted SLA against LA for each leaf type and measurement protocol. The analysis was initially conducted on the entire dataset and then repeated separately for each of the three sampling regions to assess the robustness of the results. Although our modeling approach avoids potential issues of mathematical dependency between SLA and LA, it introduces another concern: predicted values depend on the variables included in the model. If any relevant factor is missing, this could affect prediction accuracy and lead to different outcomes. To address this, we fitted additional PGLMMs using the entire dataset and observed SLA as the response variable to confirm that the main conclusions were robust and independent of the analytical approach. All analyses were carried out in R 4.4.1 (R Core Team 2024), and all scripts are provided in Appendix S2.

2.4 | Literature Review

To empirically understand how SLA is currently measured in the literature, we conducted a systematic review. On November 11, 2024, we performed an initial search on the Web of Science database using the term "Specific leaf area," which yielded 17,394 results, with 16,170 of these being peer-reviewed articles. Limiting this search to the past 5 years still resulted in 5289 articles, which exceeded the scope of this study. To narrow the focus, we further restricted the review to publications from the past 5 years (2020–2024) appearing in leading journals in ecology and plant science, including *Biotropica*, *Diversity and Distributions*, *Ecography*, *Ecology*, *Ecology and Evolution*, *Ecology Letters*, *Flora*, *Functional Ecology*, *Global Ecology and Biogeography*, *Journal of Biogeography*, *Journal of Ecology*, *Journal of Plant Ecology*, *Journal of Tropical Ecology*, *Journal of Vegetation Science*, *Methods in Ecology and Evolution*, *New Phytologist*, *Oecologia*, *Oikos*, *Perspectives in Plant Ecology*, *Evolution and Systematics*, *Plant Ecology* and *Proceedings of the Royal Society B: Biological Sciences*. After applying this additional filter, the search yielded 502 articles that we specifically reviewed. From each article, we extracted the following information: (1) whether SLA was measured in the study or obtained from external sources; (2) if SLA was measured, whether the article described the measurement protocol in detail beyond the standard definition of SLA as the ratio of leaf area to leaf mass; (3) any references to standardized measurement protocols, if applicable; (4) whether the described protocol aligned with the WL protocol or the LC protocol; and (5) the study's general scope, categorized into four types: (i) community-level studies, (ii) studies focusing on a small number of species, (iii) single-species studies, and (iv) others.

3 | Results

3.1 | Data Overview

This study included 2758 individuals from 1054 woody plant species, with 80.8% of species displaying simple leaves and 19.2% having compound leaves. The proportion of species with simple and compound leaves was similar across regions, with slight variations among Maijuna-Kichwa, Pacaya-Samiria, and Yanesha (Table 1). Most species were trees (85.5%), followed by lianas (13.1%) and hemi-epiphytes (1.4%). Species representation

TABLE 1 | Proportion of species with simple and compound leaves across study regions.

| Region | Forest type | Simple leaves (%) | Compound leaves (%) |
|----------------|-------------------------------|-------------------|---------------------|
| Maijuna-Kichwa | Lowland <i>terra firme</i> | 82.4% | 17.6% |
| Pacaya-Samiria | Seasonal floodplain | 79.2% | 20.8% |
| Yanesha | Submontane <i>terra firme</i> | 75.5% | 24.5% |

ranged from a single individual per species to five or more individuals (Appendix S3).

3.2 | Contribution of Leaf Components to LA and DM in Simple Leaves Versus Compound Leaves

The laminar component accounted for the vast majority of leaf area in both simple (mean=99.3%, range 83.6%–100%) and compound leaves (mean=97.6%, range 90.0%–99.9%) (Figure 3a), whereas the petiolar component contributed only a small fraction (Figure 3b). For DM_{WL} , the contribution of the laminar component ranged from 61.0% to 100% (mean=94.9%) in simple leaves and from 43.9% to 99.3% (mean=79.9%) in compound leaves (Figure 3c), while the contribution of the petiolar component ranged from 0% to 39.0% (mean=5.1%) in simple leaves and from 0.7% to 56.1% (mean=20.1%) in compound leaves (Figure 3d).

3.3 | Effects of Measurement Protocol and Leaf Type on SLA

The model selection approach conducted with the entire dataset for both measurement protocols revealed that, for the WL protocol, two models were equally well supported: one with

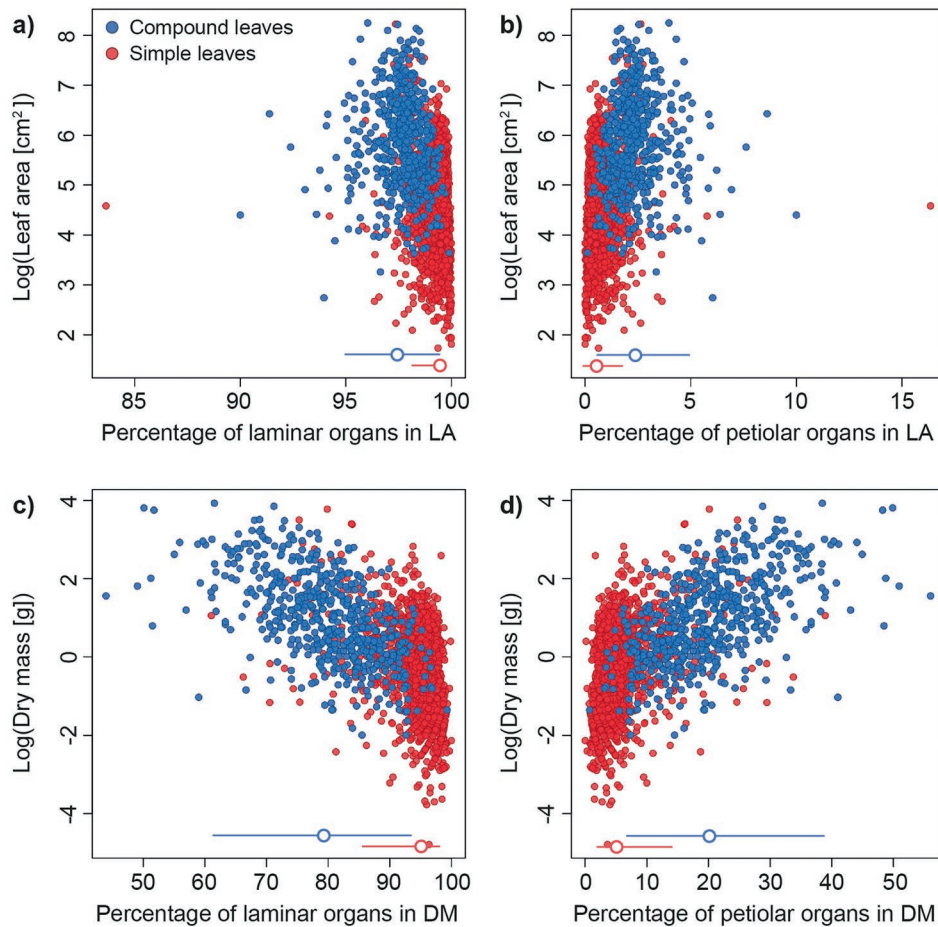


FIGURE 3 | Relationship between the logarithm of leaf area (LA_{WL} , a, b) and dry mass (DM_{WL} , c, d) with the laminar (a, c) and petiolar (b, d) component percentages in simple and compound leaves. The bars at the bottom of each figure indicate the median and the 95% confidence interval of the observed values.

$\log(\text{DM})$ and leaf type (additive terms) and another including also the interaction term (multiplicative terms). For the LC protocol, the best-fit model included both predictors and their interaction (multiplicative terms; Table 2). When we repeated the analyses for each region, the results were similar: In Majuna-Kichwa, the best-fit model for both protocols included multiplicative terms; in Pacaya-Samiria, there were two best-fit models per protocol, one with additive and one with multiplicative terms; and in Yanessa, the LC protocol had two best-fit models (additive and multiplicative), while

TABLE 2 | Akaike information criterion (AIC) values for models explaining variation in $\log(\text{LA})$ based on the whole leaf (WL) and lamina component (LC) measurement protocols in three studied regions of the Peruvian Amazon.

| Model fixed terms | WL protocol | LC protocol |
|---|---------------|---------------|
| $\log(\text{LA}) \sim \log(\text{DM}) * \text{Leaf type}$ | 343.23 | 470.61 |
| $\log(\text{LA}) \sim \log(\text{DM}) + \text{Leaf type}$ | 343.81 | 479.03 |
| $\log(\text{LA}) \sim \log(\text{DM})$ | 362.68 | 524.45 |
| $\log(\text{LA}) \sim \text{Leaf type}$ | 5593.97 | 5598.85 |
| $\log(\text{LA}) \sim 1$ | 5690.97 | 5693.39 |

Note: Boldface indicates the best-fit models, identified by AIC differences of less than two units compared to the model with the lowest AIC.

the WL protocol had only the model with multiplicative terms (Appendix S4).

Model predictions revealed that compound leaves consistently had a greater area than simple leaves for the same leaf mass, resulting in higher SLA, regardless of the measurement protocol used (Figure 4). This difference became more pronounced as leaf mass increased. Additionally, the contrast between simple and compound leaves was less marked in the WL protocol compared to the LC protocol. Interestingly, simple leaves appeared not to be affected by the choice of protocol, showing similar SLA values between both protocols. In addition, we found that an increase in LA led to an overall decrease in SLA across both leaf types and protocols. These patterns were consistent across all three regions (Appendices S5–S7).

Analyses based on observed SLA (Appendices S8–S9) reproduced the same functional relationship with LA found in our main analysis, although with much wider confidence intervals, with both leaf types showing the expected allometric decline of SLA with increasing leaf area. In these analyses, the LC protocol generated a stronger separation between leaf types than WL, as in the main analysis. However, modeling SLA directly changed the vertical offset between leaf types. Under the LC protocol, compound leaves maintained higher SLA values than simple leaves across the entire size range, consistent with the main analyses. In contrast, under the WL protocol, differences between the two leaf types were much smaller, and in larger

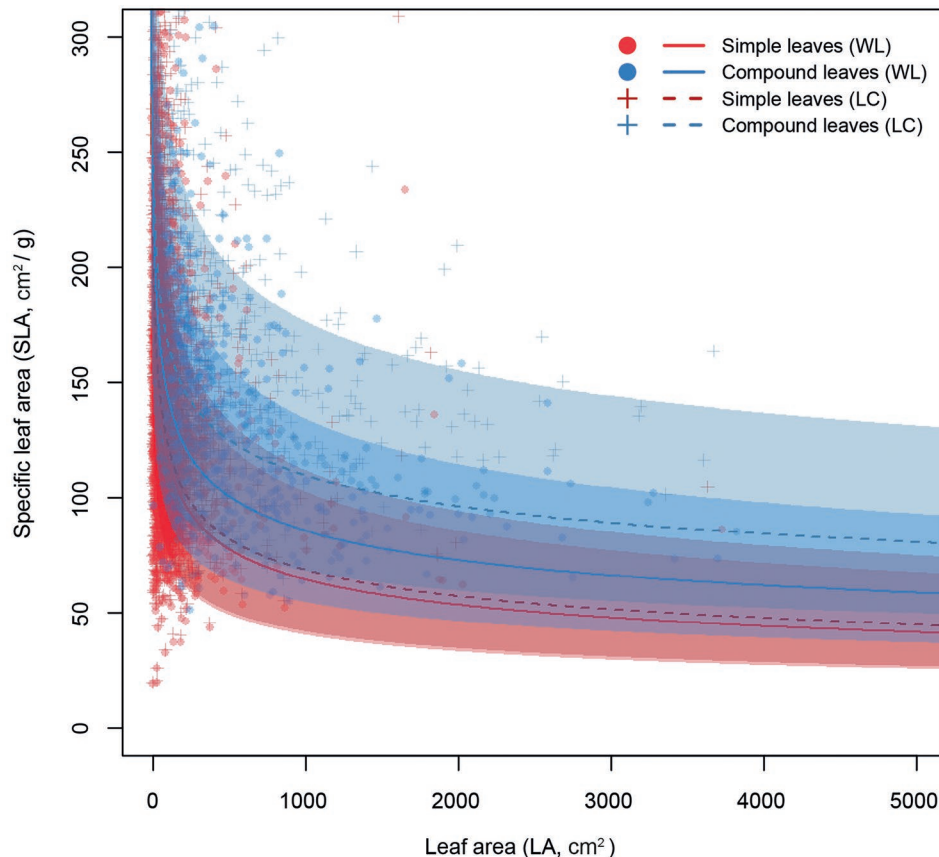


FIGURE 4 | Predictions from the best-fit PGLMM models. The plot illustrates how SLA varies as a function of LA, with predictions separated by leaf type (simple vs. compound) and measurement protocol (lamina component [LC] and whole leaf [WL]). Shaded envelopes represent the 95% confidence intervals.

leaves, the relationship reversed, with simple leaves displaying slightly higher SLA than compound leaves. These shifts in vertical offset also resulted in simple leaves being slightly more sensitive to protocol choice than in the main analysis. Such differences likely reflect the higher noise inherent in observed SLA, and the partial mathematical relationship between SLA and LA. Importantly, these discrepancies do not alter the qualitative conclusions of the study.

3.4 | Literature Review

Of the 502 articles retrieved via the Web of Science search, 308 (61.4%) measured SLA, 92 (18.3%) obtained SLA data from external sources, and 102 (20.3%) did not include this foliar trait at all. Among the 308 articles that measured SLA (Appendix S10), 164 (53.2%) provided detailed measurement protocols beyond the standard definition of SLA as the ratio of leaf area to leaf mass, while 144 (46.8%) did not. The most widely cited references for standardized protocols included the handbook by Pérez-Harguindeguy et al. (2013), along with its corrigendum (Pérez-Harguindeguy et al. 2016), cited 86 times; the handbook by Cornelissen et al. (2003), cited 37 times; and the protocol by Garnier et al. (2001), cited 10 times. Of the 164 articles providing information on measurement protocols, 125 (76.2%) aligned with the WL protocol, while 24 (14.6%) aligned with the LC protocol. Two groups of studies (15, 9.2%) could not be reconciled with either protocol: one involved studies on conifers and the other involved estimating SLA using circular disks of a known area punched from the leaf. Regarding study scope, of the 308 articles measuring SLA, 139 (45.1%) were community-level studies, 101 (32.8%) focused on a small number of species, 61 (19.8%) were single-species studies, and 7 (2.3%) used SLA to predict litter decomposition.

4 | Discussion

SLA is a widely used functional trait in plant ecology. However, the measurement of SLA may vary significantly depending on whether the whole leaf (WL protocol) is considered or only the laminar component (LC protocol). This distinction could be particularly important in compound leaves, where the petiolar component contributes more to dry mass (DM). The results of this study revealed that compound leaves consistently exhibited higher SLA values than simple leaves of the same size, regardless of the protocol used. This difference was particularly pronounced in larger leaves. Interestingly, SLA values for simple leaves remained similar across both protocols, indicating that the protocol choice has minimal impact on SLA measurements for simple leaves. However, the LC protocol resulted in a more pronounced difference in SLA between compound and simple leaves of the same size.

Our results align with the well-documented relationship between SLA and leaf area (LA) reported in the literature. We observed a negative relationship between SLA and LA in both leaf types, consistent with previous studies (Milla and Reich 2007; Niklas et al. 2007; Guo et al. 2021; Li et al. 2022). Species with larger leaves may face diminishing returns on the biomass invested in light capture due to increased support demands

(Niklas et al. 2007). These support demands can be met either by reinforcing the lamina itself or by allocating more investment to sturdier petioles (Milla et al. 2008). Including both laminar and petiolar components in SLA measurements may more accurately reflect these allometric trade-offs, particularly in compound leaves where the petiolar component plays a larger role in structural support (Niinemets et al. 2006).

Simple and compound leaves represent two distinct functional strategies for leaf display, which may lead to differences in traits such as SLA. However, direct comparisons between these two leaf types remain surprisingly scarce in the literature, including studies focused specifically on SLA (Li et al. 2008; Warman et al. 2011; Wang et al. 2017; Yang et al. 2019). To our knowledge, only one study (Wu et al. 2019) has explicitly examined how SLA varies between these two leaf types. This research focused on *Canavalia maritima*, a species in the *Fabaceae* family that can produce both simple and compound leaves. In contrast to our findings, the authors did not observe statistically significant differences in SLA between the simple and compound leaves of this species, though their study was limited by a relatively small sample size. Our study significantly expands on this work by including 211 compound-leaved species across 20 families, and we observed this pattern consistently across the three study regions. This suggests that our findings may be generalizable to a wider range of woody species, at least within tropical biomes, although future research in other biomes will be necessary to fully assess their generality. Additionally, our findings align with those of Yang et al. (2019), who found significant differences in leaf mass per area (the inverse of SLA) between simple and compound leaves across six species of each type. Furthermore, we found that excluding the petiolar component amplified the observed SLA differences, contrary to our hypothesis. These findings may be explained by the tendency of compound-leaved species to allocate a larger proportion of their support mass to the rachis (as suggested by Niinemets et al. 2006), a pattern also observed in our data (Figure 3). This allocation strategy could enable these species to produce leaflets that are broader yet lighter than the lamina of simple leaves. In compound-leaved species, structural support is largely concentrated in the petiolar component, allowing the leaflets to maximize light capture while requiring less investment in laminar tissue, which results in a higher surface area per unit of leaflet mass. While no studies have directly explored this hypothesis, it presents an interesting avenue for future research.

Pérez-Harguindeguy et al. (2013, 2016) adopt a more nuanced stance on whether the petiolar component should be included in SLA measurements compared to earlier standardized protocols (Garnier et al. 2001; Cornelissen et al. 2003). In their “Special cases or extras” section, they emphasize that the decision should be guided by the specific research question but caution that including these tissues can significantly alter the calculated SLA. However, they do not provide empirical data quantifying the effect of including or excluding the petiolar component. Our results fill this gap by demonstrating that (1) the differences between the WL and LC protocols are not uniform but vary with leaf type and size; (2) the inclusion/exclusion of the petiolar component affects compound leaves more than simple leaves, particularly for large leaves; and (3) simple

leaves tend to exhibit relatively stable SLA values across both protocols, which may help researchers make more informed methodological choices. Additionally, Pérez-Harguindeguy et al. (2013, 2016) argue that, while the inclusion of petioles may not always be crucial within a single study, it can introduce substantial systematic error when comparing across studies or even among species within the same site if they differ markedly in leaf structure. Furthermore, variations within the same species across different sites, resulting from inconsistencies in estimates produced by different methods, could be mistakenly interpreted as adaptations to environmental conditions. They, therefore, strongly recommend that researchers specify in their publications whether the petiolar component was included or not. Our literature review indicates that this recommendation has largely gone unheeded, with nearly half of the surveyed studies failing to report whether the petiolar component was included in their SLA measurements. We echo the call of Pérez-Harguindeguy et al. (2013, 2016) for greater methodological transparency, urging researchers to explicitly state their approach and justify their choice in the context of their specific research aims. Given the differences observed between measurement protocols in our study, merely stating that SLA is the ratio of LA to DM is insufficient for ensuring methodological clarity and comparability across studies.

Finally, it is important to acknowledge that, beyond the measurement protocol itself, other sampling choices may likewise influence SLA estimates. For instance, functional trait sampling protocols generally recommend collecting outer canopy leaves in tall woody species (Cornelissen et al. 2003). However, in tropical forests, this is often unfeasible, as canopy leaves are typically located more than 25–30 m above the ground. This limitation becomes especially acute in community ecology studies targeting large numbers of species, where sampling outer canopy leaves is logistically challenging and highly time consuming. Such constraints may nevertheless affect SLA estimates, since shade leaves have been shown to exhibit, on average, 43.3% higher SLA than sun leaves (Paž-Dyderska et al. 2020). Another critical aspect is leaf preservation prior to measurement. Standard protocols emphasize the need to rehydrate leaves if they have been stored for extended periods before area measurement (Cornelissen et al. 2003). In tropical field conditions, however, samples are commonly preserved in 70% ethanol to prevent desiccation and decay during transport. This method precludes proper rehydration, as ethanol irreversibly replaces cellular water and prevents restoration of original tissue hydration. The potential consequences of alcohol preservation on plant morphology, including leaf area, have been explored by Parnell et al. (2013), who reported that alcohol can induce leaf shrinkage relative to fresh material, although the magnitude of this effect varies strongly across species. In our study, all samples were preserved and processed identically. Given the high phylogenetic and functional diversity in our dataset (> 1000 species spanning multiple growth forms, leaf types and sizes), it is possible that alcohol preservation introduced heterogeneous effects on SLA estimates. While all samples were preserved and processed identically, meaning that methodological consistency was maintained, we cannot rule out the possibility that species responses to alcohol storage may have introduced additional variance in our

dataset. Future work should explicitly test whether alcohol preservation biases SLA estimates in ways that covary with species traits or phylogenetic relatedness.

In conclusion, our results demonstrate that the choice of SLA measurement protocol significantly affects outcomes, particularly for compound leaves, which represent between 18% and 25% of individuals in tropical rainforests (Table 1). Given the WL protocol's advantages—cost-effectiveness and ease of implementation—we recommend it as the default method. However, the decision to include or exclude the petiolar component should be guided by the specific goals of the study. In particular, inclusion of the petiolar component may be justified when studies aim to capture total leaf investment, including mechanical support and vascular transport costs, whereas excluding this component may be preferable when the focus is on photosynthetic tissue efficiency alone. We also stress the importance of methodological transparency, urging researchers to clearly report their chosen approach and justify it in relation to their research objectives. Without such clarity, comparing SLA measurements across studies becomes difficult, limiting the broader utility of SLA as a functional trait in ecological research.

Author Contributions

Celina Ben Saadi, Manuel J. Macía, and Luis Cayuela conceived the study and developed the overarching research goals and aims (Conceptualization). Celina Ben Saadi and Julia G. de Aledo conducted the fieldwork (Investigation), and Celina Ben Saadi performed laboratory work (Data curation). Miguel Blázquez, Juliana Cruz Montilla, and Luis Cayuela analyzed the data (Formal analysis). Miguel Blázquez, Juliana Cruz Montilla, Manuel J. Macía, and Luis Cayuela prepared the original draft of the manuscript (writing – original draft). Guillermo Bañares-de-Dios and Rubén Milla contributed ideas during the development of the study and manuscript (conceptualization). All authors critically reviewed and revised the manuscript (writing – review and editing) and approved the final version for publication. Manuel J. Macía and Luis Cayuela managed and coordinated the research activity planning and execution (Project administration) and secured financial support for the project (funding acquisition).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting this study are available in Appendix S1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Dataset supporting the findings of this study. **Appendix S2:** R script used to analyze the data. **Appendix S3:** Species representation by number of individuals. **Appendix S4:** Akaike information criterion (AIC) values for models explaining variation in log(LA) based on the whole leaf (WL) and laminar component-only (LC) measurement protocols for each of the three regions: Maijuna-Kichwa, Pacaya-Samiria, and Yanesha. **Appendix S5:** Predictions from the best-fit PGLMM models in Maijuna-Kichwa (Appendix S4). **Appendix S6:** Predictions from the best-fit PGLMM models in Pacaya-Samiria (Appendix S4). **Appendix S7:** Predictions from the best-fit PGLMM models in Yanesha (Appendix S4). **Appendix S8:** Akaike information criterion (AIC) values for models explaining variation in log(SLA) based on the whole leaf (WL) and laminar component (LC) measurement protocols in three studied regions of the Peruvian Amazon. **Appendix S9:** Predictions from the PGLMM models with multiplicative terms. The plot illustrates how SLA varies

as a function of LA, with predictions separated by leaf type (simple vs. compound) and measurement protocol (laminar component [LC] and whole leaf [WL]). **Appendix S10:** Summary of articles from the literature review in which specific leaf area (SLA) was measured. The table includes the following information: (1) whether the article provided detailed measurement protocols beyond the standard definition of SLA as the ratio of leaf area to leaf mass; (2) references, if any, to standardized measurement protocols; (3) classification of the article's measurement approach as adhering to the whole leaf (WL) protocol, laminar component-only (LC) protocol or other protocols; and (4) the study's general scope, categorized into one of three types: community-level studies, studies focusing on a small number of species or single-species studies.