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RESEARCH ARTICLE

Global patterns in community-scale leaf mass per area distributions of extant woody non-monocot angiosperms and their utility in the fossil record

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Abstract

Premise: Leaf mass per area (LMA) links leaf economic strategies, community assembly, and climate and can be reconstructed from woody non-monocot angiosperm (WNMA) fossils using the petiole metric (PM; petiole width^2/leaf area). Reliable interpretation of LMA reconstructed from the fossil record is limited by an incomplete understanding of how PM and LMA are correlated at the community scale and what climatic parameters drive variation of both measured and reconstructed LMA of WNMAs globally.

Methods: A modern, global, community-scale data set of in situ WNMA LMA and PM was compiled to test leading hypotheses for environmental drivers of LMA and quantify LMA-PM relationships. Correlations among PM, LMA, climate (Köppen types and continuous data), and leaf habit were assessed and quantified using several uni- and multivariate methods.

Results: Community mean LMA increased under warmer and less seasonal temperatures. Drought-prone communities had the highest LMA variance, likely due to disparity between riparian and non-riparian microhabitats. PM and LMA were correlated for community mean and variance, and their correlations with climate were similar. These patterns indicate that climatic correlatives of modern LMA can inform relative trends in reconstructed fossil LMA. In contrast, matching "absolute" LMA distributions between fossil and modern sites does not allow reliable inference of analogous climate types.

Conclusions: This study furthers our understanding of processes influencing the assembly of WNMA leaf economic strategies in plant communities, highlighting the importance of temperature seasonality and habitat heterogeneity. We also provide a method to reconstruct, and refine the framework to interpret, community-scale LMA in the fossil record.

KEYWORDS

community ecology, functional diversity, functional traits, leaf economic spectrum, leaf mass per area, LMA, paleobotany, paleoclimate, paleoecology

The assembly of plant communities is strongly influenced by the interaction of plant functional traits and the environment (Enquist et al., 2015; Keddy and Laughlin, 2021). Consequently, information gleaned from studies of trait–environment interactions is applicable across communities that share few taxa but a common environment—a point particularly pertinent for describing ancient plant communities comprised of extinct species. A trait that has been widely used

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TABLE 1 Glossary of abbreviations.

Abbreviation	Meaning
General terms	
LMA	Leaf dry mass per area (g/m^2)
PM	Petiole metric
LES	Leaf economic spectrum
WNMA	Woody non-monocot angiosperm
Percent evergreen	Percentage of evergreen species in a community
Climate variables	
MAT	Mean annual temperature (°C)
TS	Temperature seasonality
MART	Mean annual range of temperature (°C)
T warm Q	Temperature of the warm quarter (°C)
T cold Q	Temperature of the cold quarter (°C)
MAP	Mean annual precipitation (cm/year)
P wet Q	Precipitation of the wet quarter (cm)
P dry Q	Precipitation of the dry quarter (cm)
P wet M	Precipitation of the wettest month (cm)
P dry M	Precipitation of the driest month (cm)
PS	Precipitation seasonality
AI	Aridity index
PET	Potential evapotranspiration (mm)

to describe the prevalence and diversity of ecological strategies in both modern and ancient plant communities is leaf dry mass per area (LMA; abbreviations listed in Table 1) (Royer et al., 2010; Blonder et al. 2014; Enquist et al., 2015; Peppe et al., 2018).

Leaf mass per area is a constituent of the leaf economics spectrum (LES; Wright et al., 2004; Reich, 2014), which describes physiologically constrained trade-offs. At one end of the LES, plants emphasize low density and nitrogen-rich photosynthetic enzymes and invest less in structural compounds, resulting in leaves that are "cheaper" to construct and have lower LMA and higher within-leaf CO_2 diffusion rates. Thus, plants with low-LMA leaves typically acquire resources more rapidly and employ a "fast" LES strategy (Poorter et al., 2009; Reich, 2014; Onoda et al., 2017). On the other hand, low-LMA leaves often have less structural integrity, less defense against herbivores (Azevedo-Schmidt and Currano, 2023), and therefore short leaf life spans (Wright et al., 2004). In economic terms, fast LES strategies (e.g., deciduous plants) offset a short payback time (short leaf life span) with a higher payback (assimilation) rate and a lower total expenditure (low LMA). At the other end, slow LES strategies (e.g., evergreen plants) with higher expenditure (high LMA) and a slower payback (assimilation) rate require longer payback times (long leaf life span), which they achieve by being more robust and with better herbivore defenses (Poorter et al., 2009). Additionally, beyond carbon economics, the LES reflects energetic processes that influence thermoregulation (Vogel, 2009; Michaletz et al., 2016).

Several proxies have been developed to reconstruct LMA from fossil plants (Royer et al., 2007; Peppe et al., 2014; Soh et al., 2017; Cheesman et al., 2020) and used to reconstruct plant ecological strategies during extreme environmental change (e.g., Blonder et al., 2014; Butrim and Royer, 2020, 2022; Carvalho et al., 2021) and to document the functional composition of fossil floras (e.g., Wing et al., 2009; Lowe et al., 2018; Peppe et al., 2018; Flynn and Peppe, 2019; Wagner et al., 2019; Allen et al., 2020; Baumgartner and Peppe, 2021; West et al., 2021; Reichgelt et al., 2022). The most widely applied proxy utilizes a species-scale relationship between LMA and the petiole metric (PM = petiole width^2/leaf area) within woody non-monocot angiosperms (WNMAs; Royer et al., 2007, 2010; Cheesman et al., 2020; Lowe et al. 2024). The relationship is thought to result from biomechanical constraints, whereby a leaf with greater mass requires a petiole with a larger cross-sectional area (approximated by petiole width^2) for support (Niklas, 1994; Royer et al., 2007).

Given the demonstrated relationship between LMA and ecological strategy, the distribution of LMA across entire plant communities should reflect fundamental properties of an environment (Enquist et al., 2015). Using this logic, paleoecological studies have inferred paleoenvironments from fossil assemblages by visually comparing its reconstructed LMA distribution to measured LMA distributions of modern sites to identify a best match and, by extension, an analogous environment (i.e., distribution matching; Royer et al., 2010; Lowe et al., 2018; Peppe et al., 2018; Flynn and Peppe, 2019; Wagner et al., 2019; Allen et al., 2020; Baumgartner and Peppe, 2021; West et al., 2021). However, several assumptions underpinning this distribution-matching approach remain untested. For example, reconstructed LMA (from PM) is assumed to be correlated with measured LMA at the community scale. Royer et al. (2007) showed a significant PM–LMA correlation for community mean using a limited data set of 25 sites, but correlations for other community central moments (e.g., variance and kurtosis) have not been explored.

The most central set of assumptions in matching LMA distributions is that their position (e.g., mean), influenced by the most prevalent phenotype/LES strategy, and shape (e.g., variance and kurtosis), influenced by LES diversity, vary uniformly and distinctly across abiotic gradients (Swenson et al., 2012; Enquist et al., 2015; Wieczynski et al., 2019; Maitner et al., 2023). Several hypotheses invoking different ecological processes have been posed to explain variation across climatic gradients. The abiotic filtering hypothesis posits that harsh climates limit available niche space and thus LES diversity (Weiher et al., 1998; Swenson et al., 2012; Wieczynski et al., 2019). The favorability hypothesis posits that climates more favorable to plant metabolism and growth (e.g., wetter and warmer) increase the prevalence of fast LES strategies due to their competitive edge in acquiring resources. When resources are scarce, high rates of resource acquisition are not possible, favoring slow LES strategies (Poorter et al., 2009; Reich, 2014). In contrast, the seasonality hypothesis states that warm environments with low temperature seasonality promote slow LES strategies with evergreen, instead of deciduous, leaf habits (e.g., Adams et al., 2008). The favorability hypothesis emphasizes the importance of payback rate (potential rates of resource acquisition) and predicts a negative LMA–temperature relationship, while the seasonality hypothesis emphasizes the importance of potential payback time (growing season length) and predicts a positive LMA–temperature relationship.

The abiotic filtering hypothesis has received support in several cases (e.g., Swenson et al., 2012; Wieczynski et al., 2019), but could be dependent on the extent to which heterogenous habitats are sampled, for example, along the strong abiotic gradients that characterize certain harsh arid environments (Lammerant et al., 2023). Similarly, the relative importance of the favorability and seasonality hypotheses along temperature gradients is generally unresolved. Increased temperature can increase plant physiological rates (e.g., respiration, photosynthesis; Gillooly et al., 2001; Michaletz and Garen, 2024) and favor fast LES strategies, but it is often associated with decreased temperature seasonality which favors slow LES strategies in WNMAs (Adams et al., 2008). Empirical studies, which included plant groups beyond WNMAs, have found conflicting results, reporting positive species-scale relationships between LMA and mean annual temperature (MAT; Niinemets, 2001; Wright et al., 2005; Moles et al., 2014), negative relationships (Swenson et al., 2012; Šímová et al., 2018; Maynard et al., 2022), or no relationship (Ordoñez et al., 2009; Pinho et al., 2021). Community-scale studies show weak negative (Simpson et al., 2016; Bruelheide et al., 2018; Wieczynski et al., 2019) relationships with MAT.

Conflicting results in LMA–MAT relationships may in part be influenced by difficulties in comparing studies with varying inclusion of different plant groups with contrasting stress responses (e.g., stress-tolerant evergreen conifers and stress-avoidant deciduous WNMAs coexisting in cold climates) and growth forms (e.g., angiosperm herbs vs. WNMAs; Šímová et al., 2018). Thus, focusing on WNMAs might facilitate comparisons among plant communities and provide more reliable perspectives on leaf economic strategies that are also more applicable to the fossil record. Lastly, many of these studies aggregated trait values across broad spatial scales and aligned them with taxonomic lists generated in local vegetation census efforts (e.g., Bruelheide et al., 2018). Instead, locally measured (i.e., in situ) LMA provides a more accurate characterization of the realized traits of local plant communities (Enquist et al., 2015; Maitner et al., 2023).

Here, we employed a global and community-scale data set of modern in situ LMA and PM data to document patterns and hypothesized drivers of LMA distributions in plant communities and used the results to refine the use of LMA within paleoecology. We focused on WNMAs because they are the dominant plant group within paleoecological LMA studies. First, we tested the favorability and seasonality hypotheses by quantifying relationships among community LMA mean, climatic variables, and the percentage of evergreen species, and the abiotic filtering hypothesis by quantifying relationships of community LMA variance and kurtosis with climatic variables. Because we focused on climatic drivers, we did not incorporate soil data despite its known influence on LMA (e.g., Joswig et al., 2021). Second, we hypothesized that reconstructed LMA (from PM) can be reliably related to measured LMA at the community scale by testing for (1) correlations of LMA and PM for community mean, variance, and kurtosis; (2) similar correlations of both the reconstructed and the measured LMA to climate and leaf habit; and (3) distinctiveness of LMA distributions among modern climate types (such that they can be matched reliably with fossil LMA distributions). Our study provides new insights into fundamental plant trait–environment relationships within WNMAs by showing the importance of temperature seasonality and habitat heterogeneity and contributes to more robust, quantitative approaches in paleoecology.

MATERIALS AND METHODS

Sites and leaf sampling

We compiled a global set of community-scale LMA and PM data for WNMAs using criteria to make them roughly comparable with Late Cretaceous and Cenozoic fossil leaf assemblages (see below). All sites and species assignments are derived from prior work (Figure 1; Peppe et al., 2011; Su et al., 2010, 2013; Wieczynski et al., 2019; Kattge et al., 2020), totaling 281 sites and 8409 site–species pairs. Criteria for including sites in this compilation were that (1) leaf trait data represent leaves sampled in situ, (2) WNMA species of each community were completely or mostly sampled, (3) sites had minimal human influence (e.g., planting) or disturbance, (4) leaf sampling was done, at least in part, from the exposed outer canopy of trees, with no tree saplings sampled, and that (5) species were sampled across a spatial scale that could reasonably be represented in a fossil leaf assemblage (0.1–300 ha). Sites sampled for the development of leaf physiognomy-based paleoclimate proxies fit these criteria well (Peppe et al., 2011; Su et al., 2010, 2013), but other sites were carefully filtered. For example, to ensure the WNMA component of each in situ site from the study by Wieczynski et al. (2019) was well represented, we included only sites with ≥3 WMNA species and ≥50% of WNMA species with reported LMA, resulting in the inclusion of 26 of their 66 in situ sites. Additionally, sites from the TRY Plant Trait Database (Kattge et al., 2012, 2020) were only used if they clearly met the above criteria by referencing original data publications (Appendices S1–S3). However, some variation in sampling methodology could not be avoided. For example, some sites included in the data set exclusively sampled leaves from trees above a defined DBH (i.e., 2–5 cm) whereas others sampled prominent lianas, shrubs, and trees

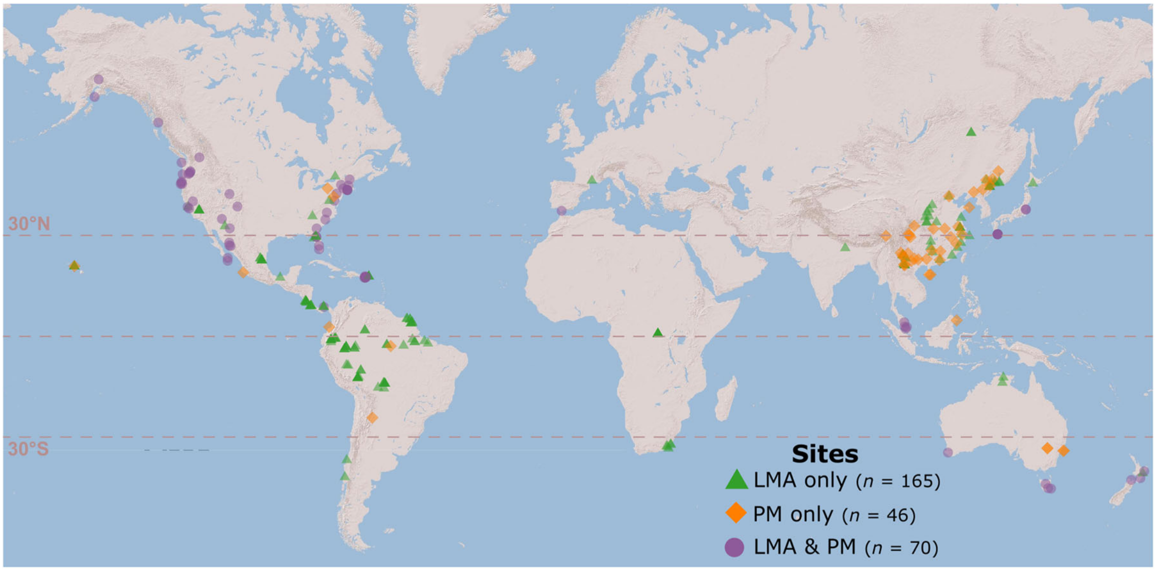


FIGURE 1 Site map. Some sites are represented by leaf dry mass per area data (LMA; green triangles), some by petiole metric data (PM; orange diamonds), and some by both (purple circles). Sites include both novel and previously published data (see Appendix S1). n = number of sites.

(e.g., CLAMP sites of Peppe et al., 2011). Some sites sampled exclusively riparian (e.g., Kowalski and Dilcher 2003 sites of Peppe et al. 2011) or non-riparian vegetation, whereas others sampled a mix of both. Two sites contributing PM data, but not LMA data, included leaves sampled from forest floor litter rather than, or in addition to, standing vegetation (i.e., sites Gorgona and Allegheny National Forest, Pennsylvania, USA).

Leaf trait data

Data for LMA and PM were compiled from the sites, with some sites having only LMA or PM data. All LMA data in our study were acquired from previous work (Royer et al., 2007, 2012; Wieczynski et al., 2019; Kattge et al., 2011, 2020) and some unpublished or updated data (Appendices S1, S2). The PM data for 32 sites of Peppe et al. (2011) were compiled from reports by Royer et al. (2007, 2012), and of those, 26 sites were updated to reflect new morphotype designations and/or to include more taxa. These were supplemented with new PM data at 53 sites of Peppe et al. (2011). In addition, new measurements used to calculate PM were made at 32 of the 50 sites of Su et al. (2010, 2013), which span a gradient from tropical to cold temperate climates in China (Figure 1).

Leaflets of compound leaves were treated as leaves. Digital images of the leaves were measured using the program ImageJ (Schneider et al., 2012) to calculate LMA and PM (petiole width^2/leaf area); petiole width was measured at the junction of the petiole and the leaf lamina, and leaf area was the summed area of the leaf petiole and blade following the method of Royer et al. (2007) and Lowe et al. (2024) (but see Appendix S4 for special cases). Leaf area and petiole width used to calculate LMA and PM were measured on either fresh or dry leaves. Area measured on dry leaves did not appear to bias results toward greater LMA or PM due to shrinkage (Appendix S5).

To apply the filtering criteria detailed above, we updated taxonomic names (species or subspecies level) to correct for misspellings and synonymy using the R packages Taxonstand (Cayuela et al., 2021), taxize (Chamberlain and Szocs, 2013), and WorldFlora (Kindt, 2020). Taxa included in the Peppe et al. (2011) and Su et al. (2010) studies were already restricted to WNMA taxa, but those from Wieczynski et al. (2019) and from most sites included from the TRY database were not. To filter for WNMA taxa only, we ascribed growth form using data from Olson et al. (2020) and the TRY - Categorical Traits Dataset (Kattge et al., 2012), and major taxonomic group was assigned by referencing online resources.

To test whether LMA relationships are influenced by patterns of leaf habit, we ascribed habit type (i.e., evergreen, semi-evergreen, or deciduous) to each taxon using the TRY - Categorical Traits Dataset (Kattge et al., 2012) and by searching online databases. The percentage of evergreen species in a community was calculated for each site by assigning evergreen species a 1, semievergreen/semideciduous 0.5, and deciduous 0, and then calculating community average from these scores and converting to percentage. To ensure that leaf habit was accurately described for community-scale sites, only those sites where leaf habit was available for ≥50% of the WNMA species were included in community-scale leaf habit analyses (214 sites for measured LMA and 72 sites for PM; Appendix S1).

Climate data

Continuous (univariate) and categorical (defined using multiple variables) climate data were obtained for each site to determine the most important climatic variables driving LMA variation (Appendix S3). Continuous climate data were obtained through WorldCLIM 30-second bioclimatic variables (Fick and Hijmans, 2017) and 30-second gridded aridity index and potential evapotranspiration maps (Zomer et al., 2022). For sites from the TRY database, mean annual temperature and precipitation reported in TRY were preferentially used over the gridded climatic data. For categorical data, each site was assigned a Köppen climate type using distribution maps of Beck et al. (2018). Only the first two Köppen hierarchies were considered to reduce the total number of categories for greater ease of interpretation (Table 2).

Analyses

All statistical analyses were performed using R (version 4.1.1; R Core Team, 2013).

Abiotic filtering, favorability, and seasonality hypotheses

To relate LMA with climatic variables, we first transformed continuous climate data using the bestNormalize package (Peterson, 2021), which determines and applies the most appropriate transformation (among ordered quantile, arcsinh, Box-Cox, square-root, and Yeo-Johnson transformations) to force normality in data to permit subsequent parametric statistical tests.

To calculate central moments, we calculated species averages for PM and LMA data, which were then used to calculate community mean, variance, and kurtosis, with each species carrying equal weight (i.e., species-weighted). Data typically used to weight central moments by species abundance (e.g., total stem basal area) were not readily available for many of the sites included in this study; in addition, comparable abundance data are difficult to obtain from the fossil record (Burnham et al., 1992). Therefore, modern sites with abundance data (i.e., Wieczynski et al., 2019) were still treated in a consistent manner using species-weighted calculations. Across sites, LMA and PM exhibited right-skewed distributions, so the mean, variance, and kurtosis for each site were $\log_{10}$-transformed. Log_{10} transformation was applied after the calculation of central moments, rather than before (on species averages), because it produced more normal distributions of central moment values across sites, and in one case, resulted in increased predictive power (Appendix S6).

We applied ANOVA to test for differences in LMA central moments across categorical climate types, using the aov function (R Core Team, 2013). To test for linear relationships between central moments of LMA and continuous climatic data, and between species and LES diversity, we created linear models using the lm function (R Core Team, 2013). For continuous climate data, we included only a subset of bioclimatic variables (i.e., see Table 1). In assessing the influence of the changing abundance of leaf habit types on trait–climate relationships, the percentage of evergreen species was transformed to force normality by ordered quantile (as determined by the bestNormalize package, Peterson, 2021) because it exhibited a bimodal distribution across sites.

Paleoecological hypotheses

For determining whether LMA can be reliably inferred from the fossil record at the community scale, relationships in modern sites between PM and measured LMA central moments were tested and defined using linear models created with $\log_{10}$-transformed values (as described above) using the lm function (R Core Team, 2013). Given that LMA and PM share leaf area as a denominator, the extent of spurious correlation (X/Z vs. Y/Z type; Jackson and Somers, 1991; Brett, 2004) was determined using the bootstrapping approach of Brett (2004) (Appendix S7). To test

TABLE 2 Terminology used in this study in reference to Köppen climate type abbreviations (Beck et al., 2018).

Major climate class	Climate type	Abbreviation	Köppen abbreviations
Tropical	Tropical everwet	TE	Af
Tropical	Tropical seasonally dry	TSD	Am
Tropical	Tropical seasonally very dry	TSVD	Aw
Arid	Arid	A	BWh, BWk, BSh, BSk
Temperate	Warm temperate dry summer	WTDS	Csa, Csb, Csc
Temperate	Warm temperate dry winter	WTDW	Cwa, Cwb, Cwc
Temperate	Warm temperate everwet	WTE	Cfa, Cfb, Cfc
Temperate	Cool temperate dry summer	CTDS	Dsa, Dsb, Dsc, Dsd
Temperate	Cool temperate dry winter	CTDW	Dwa, Dwb, Dwc, Dwd
Temperate	Cool temperate everwet	CTE	Dfa, Dfb, Dfc, Dfd

whether climatic drivers of variation in the measured LMA similarly drive variation in the reconstructed LMA, each modern site with PM data was treated to simulate a fossil assemblage. To do so, LMA central moments were reconstructed from PM using the PM–LMA relationships defined in this study, and the reconstructed LMA was subsequently treated in the same manner described for LMA above: $\log_{10}$-transformed and compared to categorical and continuous climate and leaf habit data.

A quantitative version of distribution matching was developed to test whether reconstructed LMA of fossil leaf assemblages can be matched to measured LMA distributions of modern sites across distinct climates. Each modern site with PM data was converted into a simulated fossil assemblage ($\mathrm{rLMA}_{[\mathrm{site}]}$) by reconstructing LMA at the species-scale using an expansion of the Royer et al. (2007) data set (Appendix S8). Rather than using the LMA distribution of a single site to represent an entire environment type, as done in previous work (e.g., Royer et al., 2010; Lowe et al., 2018), we compiled a climate-type distribution for each climate type ($\mathrm{LMA}_{[\mathrm{climate\ type}]}$), which represents a single probability density function containing all species-averaged LMA data within a given climate type. Each site was then compared to each climate-type distribution ($\mathrm{rLMA}_{[\mathrm{site}]}$ vs. $\mathrm{LMA}_{[\mathrm{climate\ type}]}$), with the site in question excluded from the calculation of its own $\mathrm{LMA}_{[\mathrm{climate\ type}]}$ to avoid circularity. Similarities of distributions were quantified using the Kolmogorov–Smirnov (K-S) test, via the ks.test function (R Core Team, 2013). The K-S test produces a test statistic (D) describing the similarity of two cumulative probability distributions in position and shape (example in Figure 7B), offering an improvement to the visual comparisons done in previous studies. For each climate type, we calculated (1) the correct match rate, that is, the percentage of sites that best matched their true climate type and (2) a false match rate, that is, the percentage of sites that best matched a climate type different from their own. To consider whether distributions of LMA were more distinct for coarser groupings of temperate climate types, we created four binned climate types: cool temperate with wet summers (i.e., everwet and dry winter climates), warm temperate with wet summers, warm temperate with dry summers, and arid.

Lastly, we tested whether directly comparing PM, instead of reconstructed LMA, would produce better ability to match fossil vs. modern assemblages by avoiding errors introduced when reconstructing LMA from PM (Appendix S8). Thus, in addition to $\mathrm{rLMA}_{[\mathrm{site}]}$ vs. $\mathrm{LMA}_{[\mathrm{climate\ type}]}$ comparisons, we also made and quantified $\mathrm{PM}_{[\mathrm{site}]}$ vs. $\mathrm{PM}_{[\mathrm{climate\ type}]}$ comparisons in the same manner to assess which method results in more accurate matching between a site and its true climate type.

RESULTS

Table 3 provides an overview of the hypotheses of this study and their key results.

Measured community LMA: correlations with climate and leaf habit

Categorical climate types

Community mean and variance of LMA differed between categorical (Köppen) climate types (ANOVA; $P < 0.001$, adj-$R^2 = 0.35$ and 0.22, respectively; Figure 2), but not community kurtosis (ANOVA; $P = 0.63$). However, there was large variability between sites within the same climate type (Figure 2; Appendix S9).

Temperate climates

With regard to temperature, cool climates had lower LMA mean than warm climate types, so long as there was sufficient growing season precipitation (i.e., everwet and dry winter types; Figure 2A). Cool temperate dry winter sites (i.e., monsoonal sites in northern China) had the lowest LMA mean of all climate types, overlapping with cool temperate everwet sites only (Figure 2A). The three highest LMA values for warm temperate everwet sites included two sites from Tasmania (Mt. Read and Frodsham) and one from New Zealand (Gouland Downs). In addition, the seven warm temperate everwet sites from Australia, Tasmania, and New Zealand were among the 12 highest LMA sites of their climate type.

With regard to precipitation, warm temperate sites with wet summers (everwet and dry winter sites) did not differ significantly in LMA mean from warm temperate dry summer and arid sites (Figure 2A). Within warm temperate dry summer sites, a southwest Australian site (Margaret River) occurred as a high LMA outlier. No significant differences existed between other temperate climate types (Figure 2A). The highest median of LMA variance was found in relatively unfavorable arid and warm temperate dry summer sites, significantly higher than cool temperate sites (Figure 2C). There was statistical overlap of LMA variance within all other warm temperate and cool temperate climate types.

Tropical climates

With regard to precipitation, tropical everwet sites had significantly higher LMA mean than seasonally dry sites but overlapped with seasonally very dry sites (Figure 2A). All tropical climate types had significantly higher LMA mean than cool temperate climate types, except that tropical seasonally dry overlapped with cool temperate everwet. Compared to warm temperate sites, the only statistical difference was that tropical everwet sites had higher LMA mean than warm temperate dry winter sites. There were no significant differences in LMA variance between any tropical climate types (Figure 2C). Tropical everwet and seasonally dry sites had significantly lower LMA variance than arid sites (Figure 2C).

Continuous climate variables

Combining all climate types together in linear models resulted in significant correlations for community LMA mean and

TABLE 3 A summary of hypotheses tested in this study and their predictions, key results, and interpretation. LES, leaf economics spectrum; LMA, leaf mass per area; PM, petiole metric.

Hypotheses	Prediction	Key results	Interpretation
Prevalence of LES strategies			
Favorability	Fast LES strategies more prevalent in favorable (warm, wet) climates	Measured LMA mean is higher in warmer and less seasonal climates, following a trend of increasing percentage of evergreen species	Seasonality hypothesis better supported, particularly in temperate climates
Seasonality	Slow LES strategies more prevalent in warmer, less seasonal environments		
Diversity of LES strategies			
Abiotic filtering	Low LES diversity in harsh (cold, dry) climates	Measured LMA variance highest in arid and warm temperate dry summer and lowest in cool temperate dry winter sites	Partially supported, habitat disparity in dry climates also important
Reconstructed LMA relates to measured LMA at community-scale			
PM–LMA correlation	LMA and PM correlate for community mean, variance, and kurtosis	Correlations are significant for mean and variance, weaker for the latter, and nonsignificant for kurtosis	Partially supported
Similar variables influence variation in reconstructed and measured LMA	Reconstructed and measured LMA have similar relationships to climatic and leaf habit variables	The trends across climate, and correlations with leaf habit, were similar between reconstructed and measured LMA	Supported
LMA distribution matching can be used to infer paleoclimates	Sites correctly match their LMA distribution to that of their true climate type at a high rate	In general, sites matched poorly with their true climate type	Not supported

variance with many climatic variables (Figure 3), but not for community kurtosis, which had nonsignificant or very weak correlations with climate (all adj-$R^2 < 0.07$). Relationships were stronger for LMA mean than variance. LMA mean was most strongly correlated with temperature parameters, particularly those relating to temperature seasonality (Figure 3A).

Temperate climates

Relationships between LMA and temperature were stronger when temperate climate types were considered independently, rather than at the global scale. In temperate climates, mean LMA decreased as temperature seasonality increased and winters got colder. The variance of LMA was most strongly, and negatively, correlated with temperature seasonality variables, and weaker and positively correlated with precipitation and vapor pressure variables (Figure 3B).

Tropical climates

Relationships of LMA mean and variance with climatic variables within tropical climate types were weak. Precipitation variables were those most correlated (i.e., have the highest R^2) to LMA mean, though weakly (adj-$R^2 < 0.06$; Figure 3A). Variance of LMA correlated most strongly with temperature seasonality, precipitation, and vapor pressure variables, although also weakly (adj-$R^2 < 0.09$; Figure 3B).

Leaf habit

When all climate types are combined, the percentage of evergreen species in the community (percent evergreen hereafter) correlated positively with LMA mean (adj-$R^2 = 0.30$). As with continuous climatic variables, the relationship of LMA and percent evergreen was stronger for temperate climate types when they are considered independently (adj-$R^2 = 0.46$; Figure 4A). For tropical climate types, there was no significant correlation between LMA mean and percent evergreen (Figure 4A). Across all climate types, communities dominated by deciduous WNMAs (i.e., >50% deciduous species) had significantly lower measured LMA mean compared to communities dominated by evergreen WNMAs (Figure 4B).

Because temperature seasonality was the climate variable explaining the greatest proportion of variation in LMA mean in temperate climates, we explored whether increasing LMA mean with decreasing temperature seasonality was mediated by increases in percent evergreen, by increases in the LMA within deciduous and evergreen leaf types, or both. Percent evergreen in temperate climates was most strongly and negatively correlated with measures of temperature seasonality (adj-$R^2 = 0.50$ with MART; Appendix S10). Temperate evergreen species had significantly

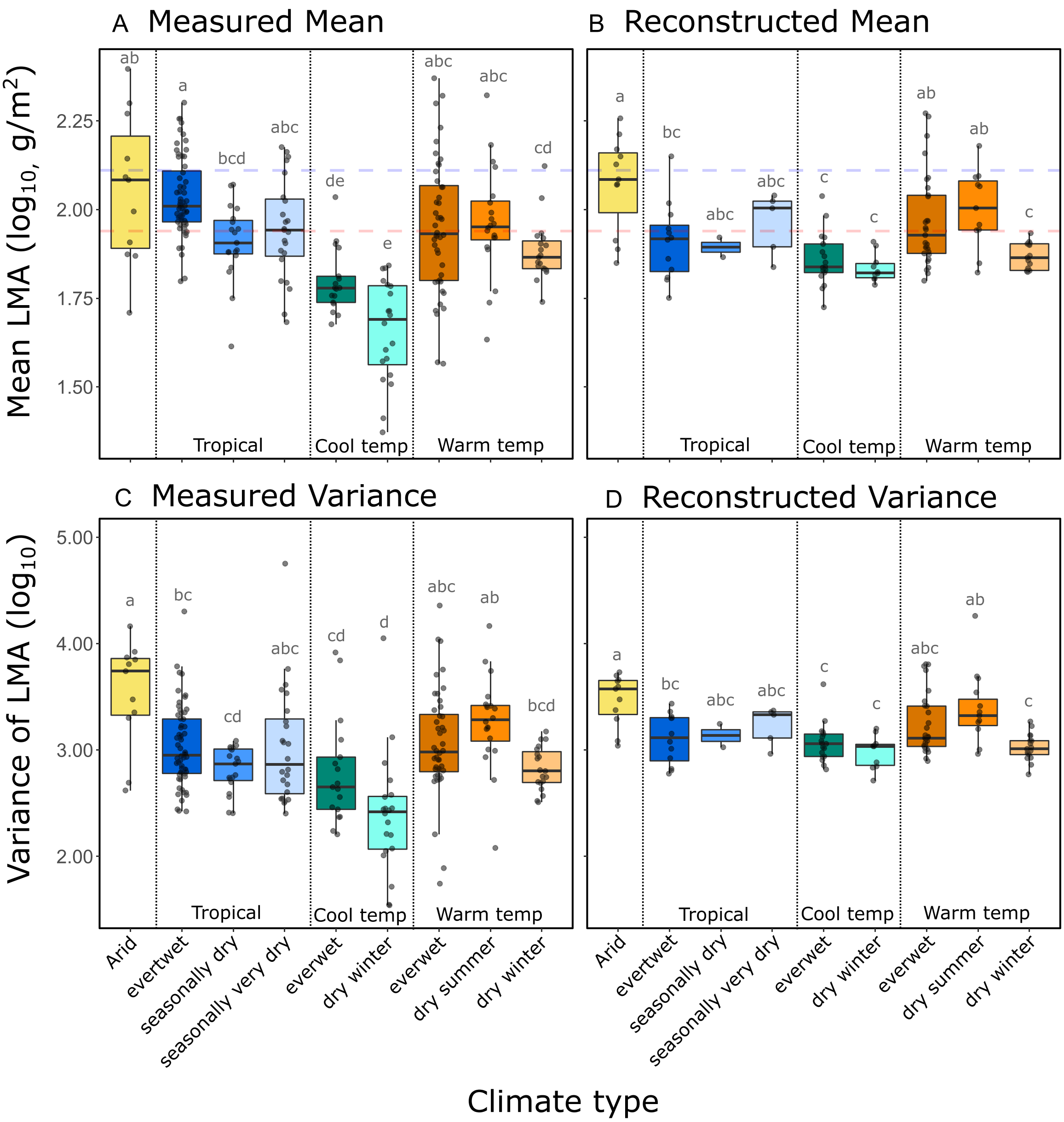
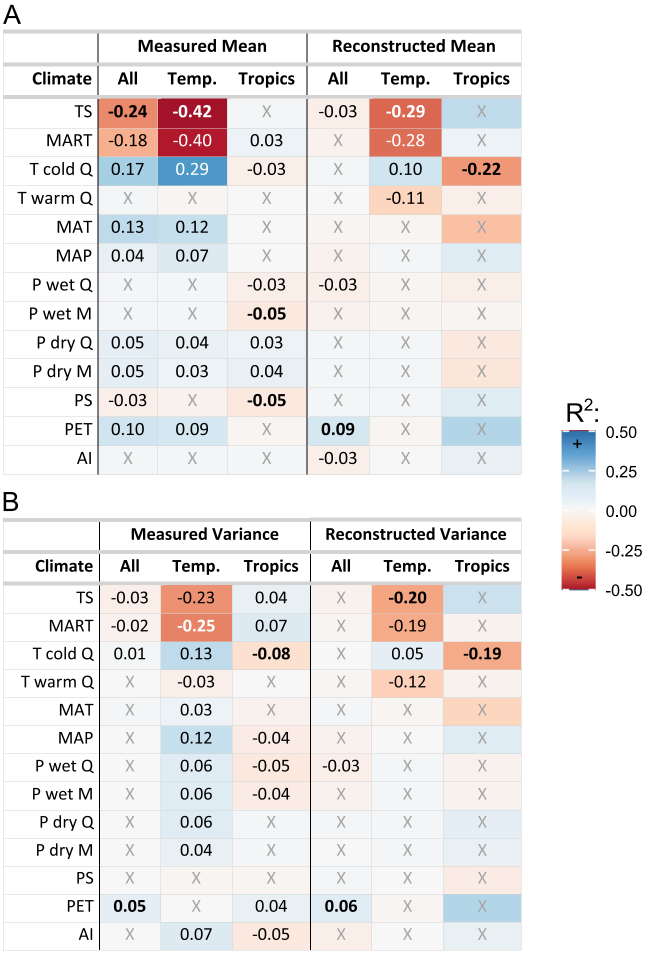


FIGURE 2 Leaf dry mass per area (LMA) central moments among differing climate types. No shared letters between climate types indicates statistical significance in the difference of LMA; (A, B) Horizontal dotted lines represent cutoffs suggested by Royer et al. (2007), whereby leaves with leaf life spans of >1 or <1 year generally have species averaged LMA of >129 g/m^2 (blue) and <~87 g/m^2 (red), respectively. (A) Measured LMA mean (g/m^2). (B) Reconstructed LMA mean. (C) Measured LMA variance [(g/m^2)^2]. (D) Reconstructed LMA variance.

higher LMA than temperate deciduous species (Figure 5). In addition, there was a modest decrease in LMA within evergreen species with increasing temperature seasonality (adj-$R^2 = 0.14$, $P = 0.017$), but no significant relationship between LMA and temperature seasonality among deciduous taxa ($P = 0.992$; Figure 5). Within tropical climates, the strongest relationship with percent evergreen was its negative correlation with temperature seasonality, positive correlation with the aridity index, and negative correlation with potential evapotranspiration, although all relationships were weaker than in temperate climates (all adj-$R^2 < 0.20$; Appendix S10).

Relationship of community-scale LMA and PM

Central moments of WNMA PM distributions were correlated with those of measured LMA for mean and variance (adj-$R^2 = 0.57$ and 0.29, respectively; Figure 6A, B), but not for kurtosis (Figure 6C), for the 70 sites that had both data types. Table 4 provides parameters necessary to calculate 95% prediction intervals using the presented linear models for LMA mean and variance. In contrast, the PM vs. LMA relationship for mean and variance was not significant when considering spurious correlation; that is, the observed correlation coefficient was not higher than those produced by



A

Climate	Measured Mean All	Measured Mean Temp.	Measured Mean Tropics	Reconstructed Mean All	Reconstructed Mean Temp.	Reconstructed Mean Tropics
TS	**-0.24**	**-0.42**	X	-0.03	**-0.29**	X
MART	-0.18	-0.40	0.03	X	-0.28	X
T cold Q	0.17	0.29	-0.03	X	0.10	**-0.22**
T warm Q	X	X	X	X	-0.11	X
MAT	0.13	0.12	X	X	X	X
MAP	0.04	0.07	X	X	X	X
P wet Q	X	X	-0.03	-0.03	X	X
P wet M	X	X	**-0.05**	X	X	X
P dry Q	0.05	0.04	0.03	X	X	X
P dry M	0.05	0.03	0.04	X	X	X
PS	-0.03	X	**-0.05**	X	X	X
PET	0.10	0.09	X	**0.09**	X	X
AI	X	X	X	-0.03	X	X

B

Climate	Measured Variance All	Measured Variance Temp.	Measured Variance Tropics	Reconstructed Variance All	Reconstructed Variance Temp.	Reconstructed Variance Tropics
TS	-0.03	-0.23	0.04	X	**-0.20**	X
MART	-0.02	**-0.25**	0.07	X	-0.19	X
T cold Q	0.01	0.13	**-0.08**	X	0.05	**-0.19**
T warm Q	X	-0.03	X	X	-0.12	X
MAT	X	0.03	X	X	X	X
MAP	X	0.12	-0.04	X	X	X
P wet Q	X	0.06	-0.05	-0.03	X	X
P wet M	X	0.06	-0.04	X	X	X
P dry Q	X	0.06	X	X	X	X
P dry M	X	0.04	X	X	X	X
PS	X	X	X	X	X	X
PET	**0.05**	X	0.04	**0.06**	X	X
AI	X	0.07	-0.05	X	X	X

FIGURE 3 Strength of relationships between leaf dry mass per area (LMA) central moments and continuous climatic variables, expressed as R^2 values, for all, temperate, and tropical climate types. Negative R^2 values and warm colors designate negative relationships; positive values and cool colors designate positive relationships. Grey X's mark nonsignificant relationships. Climate variables include temperature seasonality (TS), mean annual range of temperature (MART = maximum temperature of the warmest month − minimum temperature of the coldest month), temperature of the cold quarter (T cold Q), temperature of the warm quarter (T warm Q), mean annual temperature (MAT), mean annual precipitation (MAP), precipitation of the wet quarter (P wet Q), precipitation of the wet month (P wet M), precipitation of the dry quarter (P dry Q), precipitation of the dry month (P dry M), precipitation seasonality (PS), aridity index (AI), and potential evapotranspiration (PET). (A) Measured and reconstructed LMA mean; (B) Measured and reconstructed LMA variance.

randomized data (Appendix S7). Thus, the PM–LMA relationships presented in this study offer a means of prediction but do not provide evidence that there is a biological significance between the association of LMA and PM (Brett, 2004)—significance that can instead be inferred from additional lines of evidence such as biomechanical principles (see further discussion in Appendix S7).

Reconstructed LMA mean did not consistently over- or underestimate measured LMA mean (Appendix S11), with a median offset of 0.22 g/m^2 (interquartile range [IQR] = 28.0). However, sites in tropical everwet and tropical seasonally very dry climates were all underestimated, and cool temperate everwet sites were consistently, although only slightly, overestimated (range: −6.1 to 31.2 g/m^2; Appendix S11). There was no consistent over- or underestimation of variance, with a median offset of 23.1 [(g/m^2)^2; IQR = 2006.4], and there was no strong pattern of offset in different climate types (Appendix S11).

Reconstructed LMA: correlations with climate and leaf habit

Relationships of LMA to climatic variables and leaf habit were similar when LMA was reconstructed indirectly via PM as when LMA was measured directly (see above). For example, similar trends were seen across temperature regimes in temperate summer wet climates because cool sites had significantly lower reconstructed mean LMA than warm sites (Figure 2B). In addition, similar trends were seen across precipitation regimes in temperate climates because warm temperate summer dry and arid sites overlapped with warm temperate summer wet sites. There were no statistical differences among tropical climate types (Figure 2B). Although differences in LMA variance between climate types were less pronounced for reconstructed LMA, compared to measured LMA, arid sites had the highest median variance (Figure 2D) for both.

Similarities existed for relationships with continuous climate variables as well. Measures of temperature seasonality most strongly and negatively correlated with mean and variance of reconstructed LMA in temperate climates, although the correlations were weaker and less apparent at the global scale (Figure 3). Percent evergreen similarly correlated with reconstructed LMA mean across temperate sites only (adj-R^2 = 0.53; Figure 4C).

LMA distribution matching

Community-scale measured LMA distributions varied substantially in position and shape within climate types (Appendix S9). An example of variation within a climate type is provided by warm temperate everwet (Figure 7A), highlighting the site Pee Dee, SC, which was used in previous publications to typify this climate type (e.g., Royer et al., 2010; Lowe et al., 2018; Flynn and Peppe, 2019; Allen et al., 2020; West et al., 2021), for which the LMA distribution was similar to the climate-type distribution.

When considering all climate categories, reconstructed LMA community distributions in general matched poorly with the measured distribution of the climate type they belonged to, because only 19% of sites best matched with their true climate type (Figure 7C). Although cool temperate everwet and warm temperate

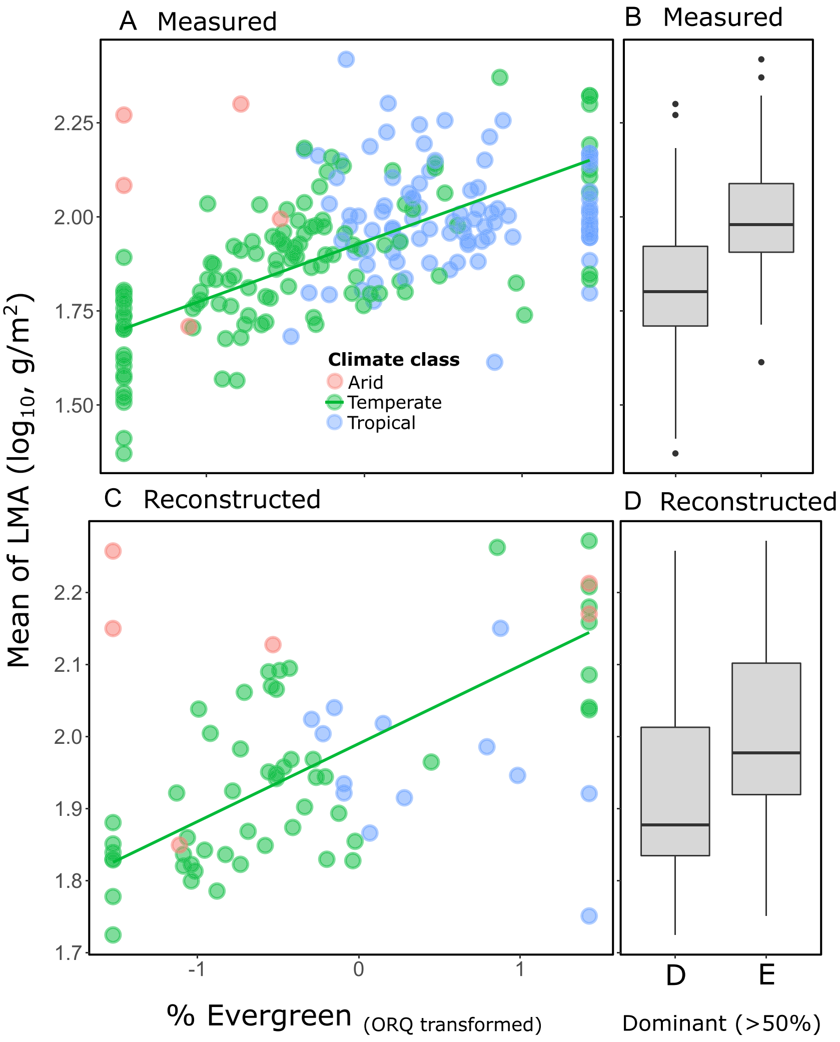


FIGURE 4 Relationship between the percentage of evergreen species in a community and the mean leaf dry mass per area (LMA) of that community, separated by major climate class. A linear model was fitted to only temperate sites as relationships within arid and tropical climates were nonsignificant. (A) Measured LMA mean and percentage evergreen. (B) Difference of measured LMA mean between communities that are deciduous (D) and evergreen (E) dominated (i.e., >50% of species). (C) Reconstructed LMA mean and percentage evergreen. (D) Difference of reconstructed LMA mean between communities that are deciduous (D) and evergreen (E) dominated (i.e., >50% of species).

dry winter sites had higher rates of correct matches, they also had high rates of false matches. There was an overall better correct match rate when $PM_{[site]}$ vs. $PM_{[climate\ type]}$ comparisons were made, with 26% of sites having a correct match (Figure 7E). The PM distributions of both arid and cool temperate dry winter sites showed some distinctness because the former had a long tail of high PM values and the latter lacked a tail with the distribution confined to lower PM values (Appendix S8). Coarser groupings of temperate climate types allowed higher correct-match rates, with 29% for reconstructed $LMA_{[site]}$ vs. measured $LMA_{[climate\ type]}$ comparisons (Figure 7D), and 52% for $PM_{[site]}$ vs. $PM_{[climate\ type]}$ comparisons (Figure 7F). However, false matches were consistently high across climate types. For example, although 78% of sites in cool wet summer climates best matched with their climate type ($PM_{[site]}$ vs. $PM_{[climate\ type]}$), 43% of all sites that best matched with the cool wet summer distribution belonged to other climate types (Figure 7F).

DISCUSSION

This study showed, using a global and community-scale data set of modern in situ LMA data, that climate imparts significant controls on the prevalence and diversity of WNMA LES strategies within plant communities, particularly in temperate climates, which can be explained by leaf economics, trait filtering, and habitat disparity. In addition, we provided evidence and guidelines for how information gleaned from global patterns in the modern world can be applied in a robust framework to interpret reconstructions of community-scale LMA from PM measurements of fossil leaf assemblages.

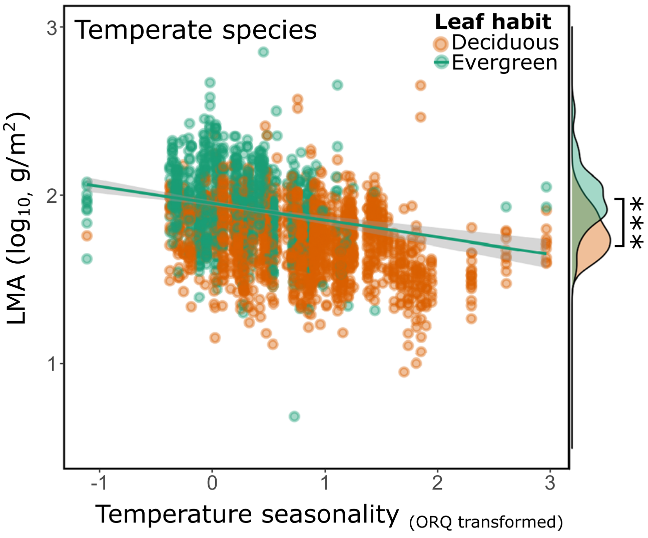


FIGURE 5 Relationship of site-specific species averaged leaf dry mass per area (LMA; *y*-axis) and the temperature seasonality (*x*-axis) for deciduous (orange; $P = 0.992$), and evergreen (green; adj-$R^2 = 0.14$, $P = 0.017$) species. In addition, kernel density plots of site-specific species averaged LMA compared between deciduous and evergreen species. Only species from temperate climate types are included. ***$P < 0.001$ (*t*-test).

Global patterns in the modern world

The prevalence of LES strategies

Overall, correlations between LMA community central moments and climate were stronger for mean than variance, consistent with previous work (Figure 3; Bruelheide et al., 2018; Šímová et al., 2018; Wieczynski et al., 2019; Butrim et al. 2024). We found that as temperatures get warmer and less seasonal, LMA mean increases, reflecting an increased prevalence of slow LES strategies for WNMA components of plant communities (Figure 3A), supporting the seasonality hypothesis. This result is inconsistent with the favorability hypothesis in terms of climate, which instead predicts that increased temperature favors fast LES strategies by creating more favorable conditions for plant metabolism and growth. The increase in LMA with lower temperature seasonality was mediated by both relatively more evergreen WNMA species assembled in plant communities (Figure 4A; Adams et al., 2008), which had higher LMA than deciduous species, and a modest increase in the LMA of evergreen species (Figure 5). These results suggest that at the global scale, factors such as growing season length that influence potential "payback time" can have more significant influence on the dynamics of LES strategies in WNMA communities than potential resource acquisition rates (i.e., "payback rates").

LMA–climate relationships were generally stronger than those seen in previous studies (e.g., Bruelheide et al., 2018; Wieczynski et al., 2019; Maynard et al., 2022). Stronger relationships likely reflect the importance of in situ data for characterizing plant community trait distributions (e.g., Maitner et al., 2023) and our focus on WNMAs, which minimizes discordant patterns across plant groups. For example, as the growing season shortened with higher temperature seasonality, WNMA components became increasingly deciduous (lower LMA; Figure 4A), employing a stress-avoidance strategy, alongside an increased contribution of evergreen conifers (higher LMA; Brodribb et al., 2012), that have characteristic traits and physiological mechanisms that confer a stress-tolerance strategy (e.g., vessel-less wood, accumulation of soluble sugars, and synthesis of cold-hardy proteins; Chabot and Hicks, 1982; Chang et al., 2021). Herbaceous and woody plants also show discordant trends across gradients of temperature seasonality (Šímová et al., 2018). Thus, combining these plant groups in analyses may obscure patterns relevant for understanding leaf economics within plant groups.

The varying prevalence of LES strategies in tropical climates was poorly explained by the percentage of evergreen species (Figure 4A) and the climatic variables analyzed in this study (Figures 2A, 3A). Nonsignificant percent-evergreen–LMA relationships are likely influenced by a weaker dichotomy between evergreen and deciduous habits in the tropics compared to temperate climates and the fact that deciduous species often occur in seasonally dry climates where low soil water availability may also favor high LMA (Reich, 1995; Kikuzawa et al., 2013; Russo and Kitajima, 2016; Chakrabarty et al., 2021). Weak LMA–climate relationships were also found in a study across nine neotropical lowland biogeographic regions, where traits conferring leaf hydraulic efficiency were suggested as being more critical (Pinho et al., 2021)—traits that may be unrelated to LMA (Sack et al., 2005; Maréchaux et al., 2020). On the other hand, stronger LMA–climate relationships consistent with the favorability hypothesis have been found across smaller local and regional scales in the tropics, with LMA increasing with increasing elevation and decreasing temperature (e.g., van de Weg et al., 2009; Asner et al., 2016; Neyret et al., 2016; Enquist et al., 2017; Martin et al., 2020), and increasing water table depth (Lourenço et al., 2020).

The diversity of LES strategies

We found significant relationships of climate with variance (Figures 2C, 3B), but nonsignificant or very weak correlations with kurtosis. Maitner et al. (2023) found that calculations of kurtosis of community-scale trait distributions are generally more inaccurate (i.e., have weaker correlations with "true" distributions where all individuals were sampled) than lower central moments such as mean and variance and that inaccuracy is worse when not accounting for intraspecific variation (see further discussion in Unexplained variance in LMA–climate relationships). Thus, LMA variance is used in this study, and not kurtosis, to characterize the diversity of LES strategies in plant communities.

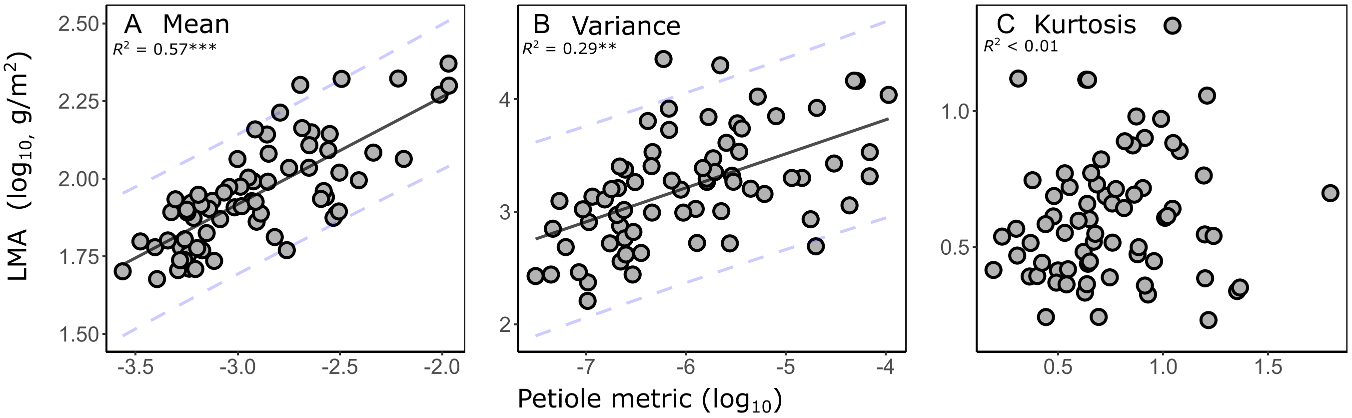


FIGURE 6 Scaling relationship between community-scale central moments of petiole metric (PM) and leaf dry mass per area (LMA) on a $\log_{10}$-$\log_{10}$ scale measured from leaves of woody non-monocot angiosperms. (A) Community mean; the linear regression is $\log_{10}\mathrm{LMA} = 2.954 + 0.345(\log_{10}\mathrm{PM})$. (B) Community variance; the linear regression is $\log_{10}\mathrm{LMA} = 5.028 + 0.302(\log_{10}\mathrm{PM})$. (C) Community kurtosis; a linear regression is not provided because the relationship was not significant.

TABLE 4 Variables required to calculate 95% prediction intervals for estimates of community mean and variance of leaf mass per area (LMA) using the formula for "predicting mean of $\bar{Y}_i$ of k items for a given value X_i" presented by Sokal and Rohlf (2012 p. 489):

$\log_{10}\mathrm{PI} = \log_{10}\mathrm{rLMA} \pm \sqrt{s^2{}_{YX}\left[\frac{1}{k} + \frac{1}{n} + \frac{(X_i - \bar{X})^2}{\Sigma x^2}\right]} \times t_{0.05(n-2)}$, where PI = prediction interval, rLMA = reconstructed leaf mass per area central moment, $s^2{}_{YX}$ = unexplained mean square or mean square error, $\bar{X}$ = mean $\log_{10}$ PM of calibration data, X_i = site $\log_{10}$ PM central moment, Σx^2 = sum of squares regression, $t_{0.05[n-2]}$ = critical value of Student's distribution for two-tailed significance level of 0.05 and (n − 2) degrees of freedom. n = the number of sites; PM = petiole metric.

Central moment	$S^2{}_{YX}$	n	$\bar{X}$	Σx^2	$t_{0.05(n-2)}$
Mean	0.01212861	70	−2.902972	1.154691	1.995469
Variance	0.1713672	70	−5.97104	5.085184	1.995469

We found mixed support for the abiotic filtering hypothesis in explaining variation in the diversity of LES strategies for WNMAs. The LMA variance was highest in arid and warm temperate dry summer environments (Figure 2C), inconsistent with the abiotic filtering hypothesis that instead predicts that arid climates impart strong filtering resulting in low diversity of LES strategies. This result indicates that high habitat disparity across microhabitats (e.g., riparian and non-riparian environments) in water-limiting climates influences high diversity when diverse microhabitats are considered (Lammerant et al., 2023). However, in support of the abiotic filtering hypothesis, LES diversity in temperate climates was most strongly, and negatively, correlated with temperature seasonality (Figure 3B), such that short yet productive growing seasons (e.g., cool temperate dry winter; Figure 2C) led to an apparent selection of consistently fast LES strategies (e.g., deciduous taxa) at the exclusion of slow LES strategies (e.g., evergreen taxa) in WNMAs. Wieczynski et al. (2019) also found community species-weighted LMA variance to be most strongly, and negatively, correlated with measures of temperature seasonality.

We did not find any differences in LES diversity between tropical climate types (Figure 2C). Previous work has shown significant, though conflicting trends, with functional diversity being either higher (Swenson et al., 2012) or lower (Aguirre-Gutiérrez et al., 2022) in drier tropical forests. These contradicting results suggest that several additional factors (e.g., soil characteristics, biotic interactions) complicate diversity–climate relationships in the tropics (e.g., Fyllas et al., 2009; Asner et al., 2016) (see below).

Unexplained variance in LMA–climate relationships

Although climate imparts important influence on the prevalence and diversity of WNMA LES strategies, each climate type hosted a range of LMA distribution shapes (Figures 2, 7A), consistent with the results of Butrim et al. (2024). In addition, all climatic variables explained less than 50% of the variation in LMA central moments. Several potential factors may contribute to this unexplained variance including confounding correlation between climatic variables, variation in the spatial scale (0.1–300 ha) and incorporation of microhabitats at different sites, differences in whether shrubs and lianas were sampled at sites (Reich et al., 2007; Poorter et al., 2009), regional fire and disturbance regimes (Carreño-Rocabado et al., 2012; Archibald et al., 2018; Fonseca et al., 2018), biotic factors such as competition and herbivory (Poorter et al., 2009; HilleRisLambers et al., 2012), and soil characteristics (Fyllas et al., 2009; Ordoñez et al., 2009; Maire et al., 2015; Asner et al., 2016; Joswig et al., 2021). For example, low soil fertility likely explains the relatively high LMA mean in Australian and New Zealand sites within warm temperate

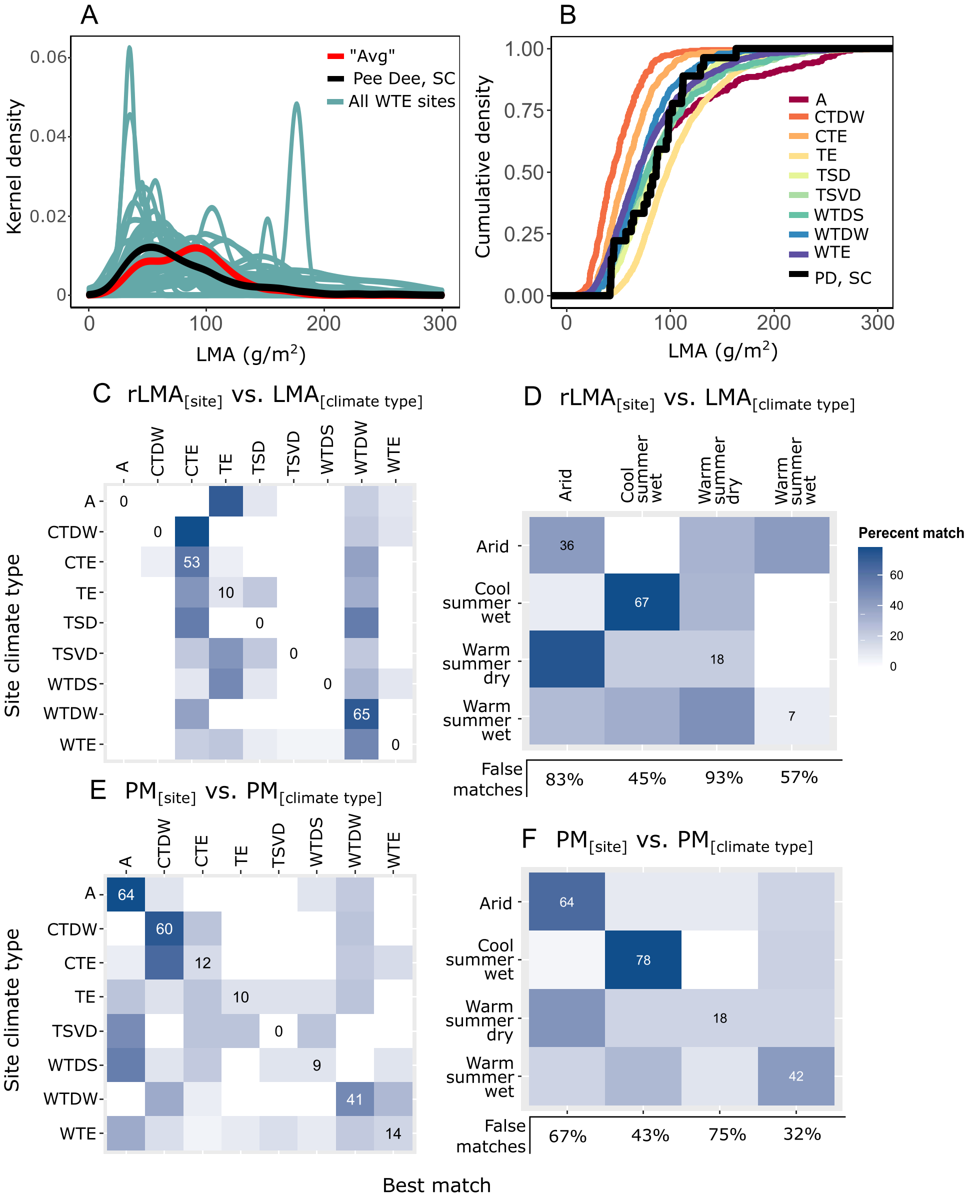


FIGURE 7 Determining the distinctiveness of leaf dry mass per area (LMA) distributions across climate types to test whether LMA distributions from fossil sites can be reliably matched to a modern climate type to infer an analogous paleoclimate. Abbreviations are defined in Table 2. (A) Example to showcase the amount of variability observed within climate types. LMA distributions are plotted for all sites in WTE climates (green), an example used in previous work to typify this climate type (Pee Dee, SC; black), and the "climate type distribution" provides a single characteristic distribution for this climate type. (B) To simulate how fossil leaf assemblages would be quantitatively matched to a (Avg; red), LMA was reconstructed at the species level using PM, and the similarity of its reconstructed LMA cumulative density distribution (Pee Dee, SC [PD, SC] as an example) to each climate type distribution is shown, and was quantified using the Kolmogorov–Smirnov test statistic. (C–F) Confusion matrices, where each row represents all sites belonging to a given climate type and the columns along that row representing the climate type that best matched each site. A darker blue corresponds to a higher percentage of matches. The diagonal cells represent the correct match rate expressed as a percentage. (C) All climate types with reconstructed LMA ($\mathrm{rLMA}_{[\mathrm{site}]}$) compared to measured $\mathrm{LMA}_{[\mathrm{climate\ type}]}$. (D) Coarser groupings of temperate climate types with $\mathrm{rLMA}_{[\mathrm{site}]}$ compared to measured $\mathrm{LMA}_{[\mathrm{climate\ type}]}$. (E) All climate types with petiole metric ($\mathrm{PM}_{[\mathrm{site}]}$) compared to $\mathrm{PM}_{[\mathrm{climate\ type}]}$. (F) Coarser groupings of temperate climate types, with $\mathrm{PM}_{[\mathrm{site}]}$ compared to $\mathrm{PM}_{[\mathrm{climate\ type}]}$.

everwet climates because nutrient-poor soils are common in those regions (Beadle, 1966; McGlone et al., 2004).

In addition, incorporating intraspecific variation into the calculation of community-scale central moments via bootstrapping and weighting those calculations by species abundance, improves how accurately they reflect the "true" trait distribution of a community (i.e., if all individuals were sampled; Violle et al., 2012; Enquist et al., 2015; Wieczynski et al., 2019; Maitner et al., 2023). Neither approach was taken in this study due to limitations in sampling strategies at most sites and may contribute additional unexplained variance. However, there was a strong correlation between species- and abundance-weighted LMA mean (adj-$R^2 = 0.85$) for a subset of sites of this study where data on stem basal area were available (Appendix S12), and trait means are unaffected by whether intraspecific variation is incorporated by bootstrapping (Maitner et al., 2023). In contrast, there was no significant correlation between species- and abundance-weighted LMA variance (Appendix S12), and calculations of trait variance are more accurate when intraspecific variation is incorporated (Maitner et al., 2023). We suggest that confounding effects of intraspecific variation and species abundance may be minimal for calculations of mean but more pronounced for variance; thus, scaling results of species-weighted variance of LMA to ecosystems should be done cautiously.

Application to paleoecology

Reconstructing community-scale LMA from fossil leaf assemblages

We found significant correlations between measured LMA and PM for community mean and variance (Figure 6); therefore, the prevalence and diversity of LES strategies in ancient plant communities can be inferred via LMA reconstructions from fossil leaves. Reconstructing mean and variance with PM at the site level using the linear regressions presented in this study (Figure 6), as opposed to reconstructing LMA at the species level and subsequently calculating mean and variance, allows for a simpler estimation of uncertainty. Accurate LMA reconstructions in the paleontological record also rely on minimizing time averaging and habitat mixing to make sure that fossil leaf assemblages approximate plant communities. Minimizing time averaging and habitat mixing are best achieved when fossils are pooled across a narrow stratigraphic height and from a single locality (e.g., Lowe et al., 2018).

Although the mean and variance of LMA and PM show a clear correspondence, the community kurtosis of LMA and PM did not (Figure 6C). We suggest calculating reconstructed LMA variance and associated uncertainty (from PM variance) using the equations of this study (Figure 6, Table 4), instead of simply assessing the shape of distributions visually, because visually distinguishing between variance (i.e., spread of values from their mean; Sokal and Rohlf, 2012) and kurtosis (i.e., "tailedness" of a distribution; Balanda and MacGillivray, 1988; Westfall, 2014) may be difficult.

Interpreting reconstructed LMA mean and variance

Reconstructed LMA from fossil leaf assemblages can be assessed using two main approaches: (1) comparing absolute values of reconstructed LMA to modern measured LMA to identify analogous environments, vegetation, or climates or (2) assessing relative trends of reconstructed LMA across fossil assemblages spanning gradients of time and/or space. Below we discuss the utility and reliability of both approaches.

Comparisons of absolute values between fossil and modern assemblages

In previous work, paleoenvironmental types were inferred by comparing reconstructed LMA distributions to measured LMA distributions of modern sites to find a best match and analogous environment type (Royer et al., 2010; Lowe et al., 2018; Peppe et al., 2018; Flynn and Peppe, 2019; Wagner et al., 2019; Allen et al., 2020; Baumgartner and Peppe, 2021; West et al., 2021). Here, we found that the reconstructed LMA distribution of sites matched poorly with the LMA distribution of their true climate type, owing to substantial variation within and overlap across climate types (Figure 7). Substantial overlap of LMA distributions between sites in differing biomes was also found by Butrim et al. (2024). Higher match rates were achieved for $\mathrm{PM}_{[\mathrm{site}]}$ vs. $\mathrm{PM}_{[\mathrm{climate\ type}]}$ comparisons, rather than reconstructed $\mathrm{LMA}_{[\mathrm{site}]}$ vs. measured $\mathrm{LMA}_{[\mathrm{climate\ type}]}$, reflecting the error introduced through LMA reconstruction. The best match rate occurred when comparing coarser groupings of temperate climate types for cool wet summer and arid sites, with the former sharing a lack of tail over higher LMA values (>125 g/m^2), and the latter tending to have a low peak and exaggerated tail over high LMA values. However, sites of other temperate climate types had considerable false match rates with these climate types. This pattern corroborates the results of Butrim et al. (2024) and demonstrates that reconstructed LMA or PM distributions from fossil leaf assemblages cannot be reliably matched with modern community distributions to infer analogous (Köppen) climate types.

In contrast, we did find support for the use of absolute values community mean in some cases. Absolute values of reconstructed LMA have been used in prior work to infer leaf habit (i.e., deciduous vs. evergreen) of fossil species (Royer et al., 2007, 2010). Similarly, we briefly consider if absolute values of reconstructed LMA can be used to distinguish deciduous and evergreen dominated communities. Here, we found that reconstructions of LMA mean <80 g/m^2 had a high probability of being deciduous dominated (i.e., 75% of sites were deciduous dominated below the cutoff), >140 g/m^2 had a high probability of being evergreen dominated (i.e., 80% of sites were evergreen dominated above the cutoff), and values between those were indiscriminate (Appendix S13).

Relative trends of reconstructed LMA across time and space

Most relative trends in measured LMA mean and variance among climate types were mirrored in reconstructed LMA (Figures 2–4); hence, relative trends reconstructed from the fossil record can be interpreted in terms of climatic factors in a similar way as with measured LMA today. That said, we argue that the fundamental interpretation of reconstructed

LMA mean and variance should be done at the level of LES strategies rather than climate (further discussed by Butrim et al., 2024). Nevertheless, paleoecological investigations often aim to provide paleoenvironmental context to plant community dynamics. Our study highlights the importance of habitat disparity in driving high LMA variance. For example, higher LMA variance can be expected to characterize well-sampled fossil assemblages that represent riparian and non-riparian taxa in water-limiting paleoenvironments (e.g., Allen et al., 2020). Within temperate climates, increases in WNMA LMA mean were often associated with increases in the percentage of evergreen species (Figure 4) and decreases in temperature seasonality (Figure 3), which was highlighted by differences between the cool temperate and the warm temperate climate types (Figure 2). In contrast, in tropical climates, we found that climate and the percentage of evergreen species poorly explain variation in the prevalence and diversity of LES strategies (Figures 2–4). Paleoecological studies reconstructing community-scale LMA in tropical paleoclimates will benefit from considering additional biotic and abiotic factors influencing LMA (e.g., Fyllas et al., 2009; Asner et al., 2016) and identifying applicable studies addressing LMA–climate relationships across more regional gradients (e.g., van de Weg et al., 2009; Asner et al., 2016; Neyret et al., 2016; Enquist et al., 2017; Martin et al., 2020).

In general, it is important to consider additional abiotic and biotic factors beyond climate when interpreting relative trends in reconstructed LMA of fossil assemblages. For example, it is best to consider likely soil characteristics when possible because they have important influence on LMA distributions by, for example, integrating information about potential nutrient-rich volcanic inputs (e.g., Lowe et al., 2018), paleosol chemical weathering proxies (e.g., Beverly et al., 2018), regional bedrock and landscape history (e.g., Carvalho et al., 2021), or taxonomic inferences of taxa with particular soil requirements (e.g., Wing et al., 2012). It is also important to recognize that an understanding of WNMA leaf economic strategies may be an incomplete perspective on plant communities when herbaceous angiosperms or conifers are also prevalent, with potential to bias interpretations of assembly and interactions across communities and ecosystems. For example, if a fossil assemblage is interpreted as conifer-dominated, WNMAs may occupy a niche space of fast LES strategies, while most of the community biomass is held in conifers with slower LES strategies, and thus community LMA mean and variance may be underestimated (Becker, 2000; Brodribb et al., 2012).

CONCLUSIONS

We tested different hypotheses for the distribution of leaf economic strategies within WNMA members of plant communities and found that the favorability hypothesis, which predicts climatic conditions more favorable to plant growth will have a greater prevalence of fast LES strategies, was not supported by this study. Instead, variables describing temperature seasonality and growing season length were more important for explaining the prevalence of LES strategies within communities, in support of the seasonality hypothesis. For example, colder and more seasonal climates have a greater prevalence of fast and deciduous LES strategies and evergreen species with lower LMA. The abiotic filtering hypothesis, which predicts low LES diversity in harsh climates, was partially supported. Cool temperate wet summer sites had the lowest LES diversity, where high temperature seasonality leads to consistently fast LES strategies. In contrast, arid and warm temperate dry summer sites have the highest LES diversity, where high environmental disparity between riparian and non-riparian environments exists. Climatic variables and the percentage of evergreen species poorly explained variation in LES strategies across tropical climate types, highlighting the importance of additional biotic and abiotic factors.

This study also assessed the extent to which LMA reconstructed from the fossil record reliably reflects measured LMA. We found that the prevalence and diversity of WNMA leaf economic strategies can be assessed in ancient plant communities using fossil leaf assemblages through the correlation of LMA and PM for community-scale mean and variance. However, fossil LMA reconstructions generally cannot be reliably interpreted through direct comparisons with modern assemblages. Instead, we propose that relative differences of reconstructed LMA of fossil assemblages separated in time or space can be explained by potential variation in climatic conditions and the percentage of evergreen vs. deciduous species, particularly in temperate climates. Further, noise in the PM and LMA relationships and in the LMA and climate relationships demonstrates the importance of incorporating independent lines of evidence when drawing strong interpretations from reconstructed LMA distributions. This study thus furthers our understanding of patterns and processes driving the assembly of WNMAs in plant communities and refines our ability to gain important perspectives on community assembly from the geologic past.

AUTHOR CONTRIBUTIONS

A.J.L., C.A.E.S., D.J.P., D.L.R., D.J.W., T.R., and B.J.E. developed the project; A.J.L., D.J.P., D.L.R., D.J.W., B.J.E., S.T.M., and A.J.K. contributed LMA and PM measurements of modern leaves; M.J.B. acquired and filtered data from TRY; A.J.L. led the analyses and statistical tests. All authors contributed to data interpretation and writing and editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors confirm that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data incorporated in this study are available in Appendices S1–S3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Community/site-level central moments and their data sources.

Appendix S2. References for mentions of data sources in Appendix S1.

Appendix S3. Modern site metadata.

Appendix S4. Special cases in the protocol for measuring petiole width.

Appendix S5. Leaf mass per area (LMA) when leaf area is measured from fresh vs dried leaves.

Appendix S6. Differing $\log_{10}$-transformation approaches.

Appendix S7. Spurious correlations in LMA and PM relationships.

Appendix S8. Species-scale relationship between LMA and PM.

Appendix S9. Probability density function within and between climate types.

Appendix S10. Relationship between percentage evergreen and continuous climatic variables.

Appendix S11. Offset between measured and reconstrued LMA.

Appendix S12. Abundance- vs. species-weighted measured of LMA mean and variance.

Appendix S13. Potential cutoffs to distinguish evergreen- from deciduous-dominated communities.

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