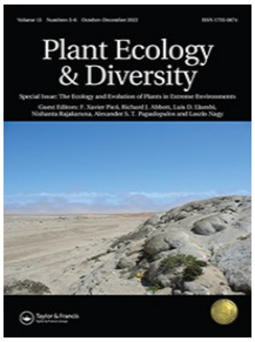

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ARTICLE

Specific leaf area is lower on ultramafic than on neighbouring non-ultramafic soils

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ABSTRACT

Background: Specific leaf area (SLA) is a core trait within the leaf economic spectrum that describes differences in plant performance and productivity. Research on the sources of variation in the leaf economic spectrum and SLA has primarily focused on climate. Much less is known about SLA variation across unusual edaphic environments, such as on ultramafic soils.
Aims: To determine the role of ultramafic soils as a driver of SLA variation.
Methods: We measured SLA for dominant species on paired ultramafic and non-ultramafic soils in five biogeographically distinct regions around the globe and compared mean SLA values to globally reported values.
Results: SLA was lower on ultramafic than on non-ultramafic soils in all regions, except Puerto Rico, and both climate and soil were important drivers of SLA. For three of the five regions, SLA values on ultramafic soils were lower than the global average.
Conclusions: Soils can be a major driver of SLA along with climate. Low SLA on ultramafic soil points to selection for stress resistance strategies. Furthermore, in some bioregions, SLA values on ultramafic soils were among the lowest on the planet and thus represent globally rare phenotypes that should be conserved within these unique edaphic habitats.

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Edaphic; extreme environments; functional trait; leaf economic spectrum; serpentine syndrome; stress resistance syndrome; specific leaf area (SLA)

Introduction

The study of plant form and function across climates was central to the development of ecology. The focus on climate as a primary driver of plant diversity and distribution dates back to at least Theophrastus. Early plant geographers noted that plants in the wet tropics had exceptionally large leaves and early plant ecologists emphasised how leaf morphology and physiology vary with climate (e.g. Schimper 1903). The emphasis on climate led to the use of plant functional traits to explain patterns of plant diversity and distribution across latitudes (e.g. Woodward 1987). In particular, the leaf economic spectrum describes a trade-off between fast and slow rates of resource acquisition and carbon investment. A rapid return on investment (resource-acquisitive strategy) is associated with higher nutrient concentrations and photosynthetic rate per unit mass, and thinner leaves with lower construction costs, while a slower return on investment (resource-conservative strategy) is associated with the opposite suite of traits (Wright et al. 2004). Specific leaf area (SLA) is a central trait within the leaf economic spectrum and species with low SLA tend to be slow-growing and resource-conservative, whereas species with high SLA are fast-growing and resource-acquisitive (Poorter et al. 2009). Variation in the leaf economic spectrum and SLA has largely been attributed to climate. In hot, dry, environments with high light intensity, SLA tends to be lower (Wright et al. 2005), signifying selection for resource-conservative and stress-resistance strategies. While the influence of climate on plant functional trait variation has been well studied, soils have the potential to be an important determinant of plant diversity and function (Gong and Gao 2019;

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Hulshof and Spasojevic 2020), but the effects of soils on plant traits have been less studied.

By mediating water and nutrient availability, and other key environmental factors (e.g. microbial functioning, heavy metal concentrations), soils may be a key driver of functional variation among species. For example, the low water-holding capacity of soils derived from ultramafic rock (also known as serpentine soils) can create a water-limited environment, even when precipitation is plentiful (Kruckeberg 1985). Moreover, across phosphorus gradients associated with substrate age (Laliberté et al. 2013), low SLA values have been found in extremely phosphorus-impoverished soils, supporting the idea that edaphically extreme environments select for resource-conservative and stress-resistant traits (the stress resistance syndrome; Grime 1977; Chapin et al. 1993). Additionally, nitrogen-impoverished soils, such as the white sandy soils found throughout the tropics, result in a unique plant functional composition characterised by resource-conservative strategies (Fine and Baraloto 2016; Samojedny et al. 2022). Finally, soil micronutrient availability is another possible driver of plant trait variation. Both low and high micronutrient availability, such as soils derived from dolomites (magnesium-rich) and metalliferous soils (copper-rich), select for species with low SLA (Molina-Venegas et al. 2016). Considering that approximately half of the world's soils are deficient in micronutrients (Sillanpää 1982), the relationship between SLA and soil fertility has the potential to be significant at regional and global scales.

Ultramafic (serpentine) soils (and the other unusual soils described above) exemplify the notion that soils are an important determinant of plant traits. Ultramafic soils are characterised by having high concentrations of trace and heavy metals (e.g. Fe, Mg, Ni and Cr) and low concentrations of essential plant nutrients (e.g. N, P, K, S, Ca and Mo) (Kruckeberg 1985; Alexander et al. 2007). Because these extreme elemental conditions reduce plant growth rates, ultramafic soils tend to have low organic matter accumulation and cation exchange capacity (Rajakaruna and Boyd 2008). Plants across serpentine habitats tend to possess a set of similar characteristics, known as the 'serpentine syndrome', characterised by xeromorphic foliage, prostrate growth form and dwarfism (Whittaker 1954; Jenny 1980). Ultramafic soils are found in isolated patches worldwide, but with particular abundance in California, Cuba, the Balkan Peninsula, Mediterranean Europe, Indonesia and New Caledonia (Roberts and Proctor 1992; Garnica-Díaz et al. 2022). This global distribution of ultramafic soils creates a model system for understanding the influence of soils on plant traits. Determining leaf trait variation in edaphically extreme environments like ultramafic soils can therefore help us better understand the extent to which soils modulate patterns of variation in functional traits.

Here, we compare specific leaf area (SLA) of plants growing on ultramafic (U) and non-ultramafic (NU) soils in five distinct biogeographical regions. Our objective was to quantify the effect of ultramafic soils on SLA. We expected lower SLA values to occur on ultramafic compared to non-ultramafic soils, reflecting strong selection for resource-conservative strategies regardless of regional climate, which in this study encompasses Mediterranean, tropical and subtropical zones. In addition, because ultramafic soils are considered extreme environments, we expected SLA values for plants growing on ultramafic soil to be on the low end of globally reported SLA values, reflecting extreme resource-conservative strategies and high investment in leaf tissue (Wright et al. 2004; Díaz et al. 2016).

Materials and methods

Data sources and trait collection

We identified sampling sites in five climatically diverse regions: Puerto Rico (tropical wet), Costa Rica (tropical dry), South Africa (subtropical), California and Lesbos (both with Mediterranean climate) (Figure 1a). Ultramafic soils typically occur as islands of low fertility within a comparatively higher-fertility soil matrix. In each region, ultramafic sites were selected on serpentine outcrops and non-ultramafic sites were selected on the surrounding higher-fertility, dominant soil type. In each location, we measured specific leaf area (SLA), calculated as the fresh leaf area (mm^2) divided by dry mass (mg), for the most abundant species on nearby ultramafic (U) and non-ultramafic (NU) soil sites following standardised protocols (Pérez-Harguindeguy et al. 2013). Petioles were included when measuring leaf mass and surface area. We collected fully expanded leaves from 5 to 10 individuals of common species on and off ultramafic soil. While woodiness varied between regions, it was largely consistent within each region across the two soil types. In Puerto Rico and Costa Rica, 100% of the species collected were

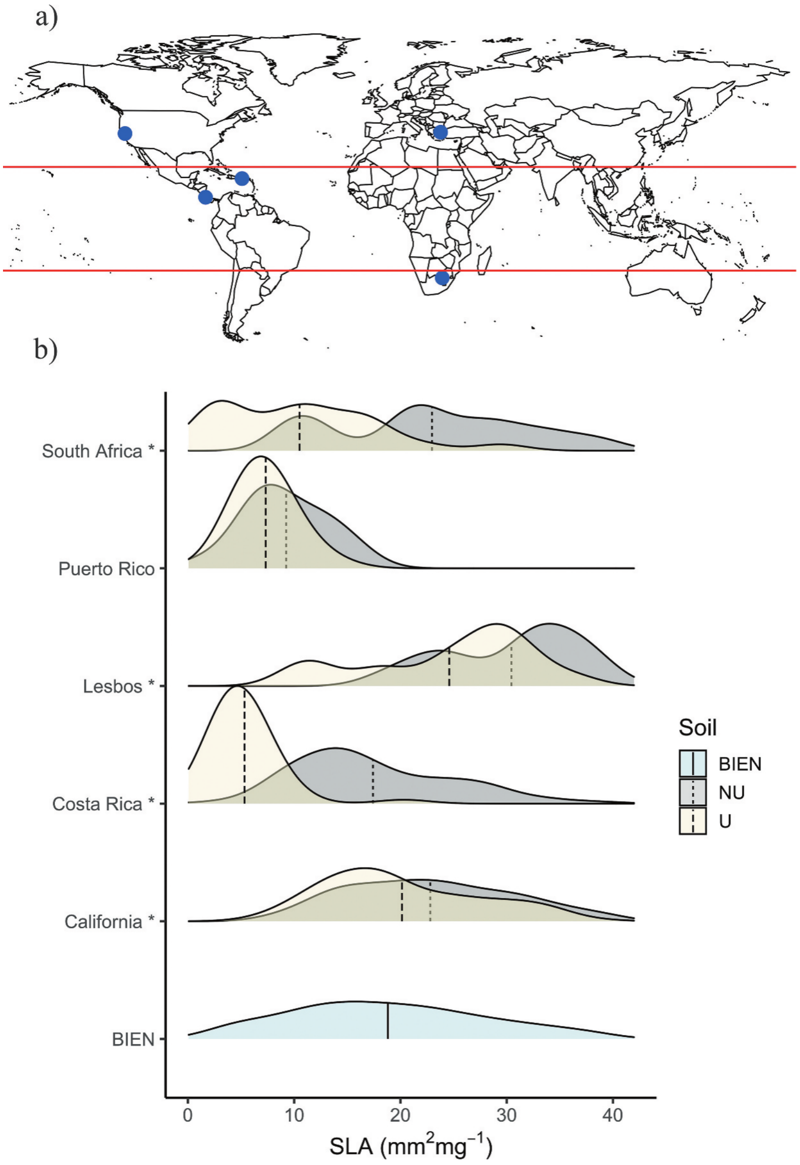

Figure 1. Sampling locations (filled blue circles) where SLA data were obtained (a). Red horizontal lines demarcate the tropics (23.4° North and South). The map was generated using the *map* function of the R *purrr* package (Henry and Wickham 2020). Comparative ridgeline density plots of specific leaf area (SLA) for each region and the global Botanical Information and Ecology Network (BIEN) trait database (b). Grey shapes represent non-ultramafic soil values (NU), yellow represent ultramafic soil values (U) and blue areas indicate the global SLA values obtained from BIEN (n = 44967 species, https://bien.Nceas.ucsb.edu/bien/). Vertical lines represent mean SLA values for plants on each soil type. Asterisks denote a significant difference in means within regions.

woody, while in California and Lesbos, all the species collected were herbaceous. The majority of species collected in South Africa were woody (70.8% of ultramafic and 58.3% of non-ultramafic species; see Siebert et al. 2002 for more information about this region). The taxonomic similarity between U and NU collections varied in each region. South Africa, Puerto Rico and Costa Rica had little species overlap on and off ultramafic soil (<2%), while California had moderate overlap (~35%) of species between U and NU soils (Table 1). In Lesbos, the same 18 widely distributed species were sampled on both U and NU soil. The number of species sampled for each site ranged from 18 in Lesbos to 145 in California (Table 2).

To compare the distribution of ultramafic SLA values to a global distribution, we extracted all SLA values reported in the BIEN database using the *BIEN* package in R (Maitner et al. 2017). To determine the impact of climate on SLA, we extracted mean annual temperature and mean annual precipitation for the years 1970–2000 from the WorldClim 2 database (Fick and Hijmans 2017) at the 1 km^2 scale for each of our sampling sites. We then calculated the mean value across all sites for each region and soil combination. While mean

Table 1. Summary information about the climate (in parentheses) and species composition of each site. Percent species/families shared (taxonomic similarity) between soil types is calculated by dividing the number of species/families sampled on both ultramafic (U) or non-ultramafic (NU) soils by the total number of species/families sampled across both soil types in a region. Site coordinates and full species lists are available in Table S1.

Region (climate)	Soils	Mean annual temperature (ºC)	Mean annual precipitation (mm)	Growth form sampled	Species shared between U and NU (%)	Families shared between U and NU (%)
California	U	13.9	952	Herbaceous	35	80.6
(Mediterranean)	NU	13.9	952	Herbaceous		
Costa Rica	U	24.4	1588	Woody	1.8	28.3
(Tropical dry)	NU	25.8	1662	Woody		
Lesbos	U	15.1	637	Herbaceous	100.0	100.0
(Mediterranean)	NU	15.6	621	Herbaceous		
Puerto Rico	U	23.8	1792	Woody	1.6	31.3
(Tropical wet)	NU	23.9	1902	Woody		
South Africa	U	19.3	699	Woody (70.8%)	0.0	34.6
(Subtropical)	NU	18.9	716	Woody (58.3%)		

Table 2. Specific leaf area (SLA; $mm^2\ mg^{-1}$) for leaves collected on ultramafic (U) and non-ultramafic (NU) soils in five regions: California (CA), South Africa (SA), Lesbos, Greece (L), Puerto Rico (PR) and Costa Rica (CR). Global patterns of SLA across all soils from the BIEN database are also included. Data description includes the number of species sampled (N), average SLA value (Mean), standard deviation (SD), median, first quartile (Q1; 25th percentile), third quartile (Q3; 75th percentile) and minimum (Min) and maximum (Max) values. Main *P*-values for each region represent results from independent contrasts of SLA between U and NU soils within each region. The *P*-values for the BIEN row represent Wilcoxon rank-sum tests (following correction for multiple tests) of SLA on ultramafic soils in each region with the BIEN global average. Significant *P*-values are given in boldface.

Region	Soils	N	Mean	SD	Q1	Median	Q3	Min	Max	*P*-value
California	U	145	20.15	7.36	14.71	18.6	25.24	5.91	39.10	**0.002**
	NU	138	22.81	7.72	16.68	22.42	28.33	8.16	39.91	
Costa Rica	U	39	5.32	3.07	3.51	4.87	6.25	2.03	20.30	**<0.001**
	NU	87	17.41	7.33	12.19	15.57	22.72	2.67	38.72	
Lesbos	U	17	24.58	7.91	18.09	27.27	29.78	10.06	36.40	**0.032**
	NU	18	30.44	6.32	25.20	32.27	35.44	18.40	39.20	
Puerto Rico	U	41	7.33	2.38	5.35	7.07	8.44	3.48	14.40	0.248
	NU	20	9.24	3.75	6.64	8.36	11.75	1.43	15.83	
South Africa	U	24	10.50	7.19	3.21	10.52	15.82	1.87	29.43	**<0.001**
	NU	23	22.96	9.02	16.35	22.50	29.33	9.81	39.35	
BIEN	All	44967	18.82	9.04	12.01	18.17	25.17	1.00	39.99	CA: 0.058 CR: **<0.001** L: **0.014** PR: **<0.001** SA: **<0.001**

climate values varied among regions, they were largely consistent within each region across the two soil types (Table 1) because these were often located in close (<10 km) proximity.

Statistical analyses

We averaged SLA values at the species level for each region by each of the two soil types. However, to ensure the quality of data, we first excluded a few inflated values, likely due to calculation or measurement errors. SLA mean values >40 $mm^2\ mg^{-1}$ were considered outliers as 40 $mm^2\ mg^{-1}$ is near the upper limit of globally observed SLA values for terrestrial vascular plants (Poorter et al. 2009). This resulted in the removal of 18 of 570 values (3.2%). We used the remaining 552 mean species values for all downstream analyses, which were performed in R v.4.1.1 (R Core Team 2021).

To determine whether SLA differs on ultramafic (U) compared to neighbouring non-ultramafic (NU) soil and to assess whether this effect differed among the five regions, we used a two-way analysis of variance on rank-transformed data (*aov* function in the base *stats* package in R). Rank-transformation of SLA was performed to improve normality and homogeneity of variance, as this is a robust approach when model assumptions are not met on untransformed data (Conover and Iman 1981). Soil type, region and their interaction were included as model predictors, treating rank-transformed SLA as the response variable. Given a significant interaction between soil type and region, we used pre-planned independent contrasts to determine whether SLA was significantly different among soil types within each region for a total of five independent contrasts (*glht* function in the R package *multcomp*; Hothorn et al. 2008).

To visually compare the distribution of SLA values on each soil type for each region, and to compare all regions to the BIEN trait database, we created a ridgeline plot using the *geom_density_ridges* function in the R *ggridges* package (Wickham 2016; Wilke 2021). To statistically assess the mean SLA value for ultramafic soils in each region to the BIEN global mean value, we performed individual Wilcoxon rank-sum tests for each region and controlled the family-wise error rate (n = 5) by adjusting the reported P-values using the Holm–Bonferroni method via the *p.adjust* function (base *stats* package in R).

To determine whether SLA was affected by both soil and climate, and to test whether the effect of soil differed depending on climate, we used linear regression on the mean values for each region and soil combination (n = 10; *lm* function in the base *stats* package in R). Climate (average annual precipitation or annual temperature), soil type and their interaction were included as model predictors, while SLA was treated as the response variable. Note that we performed two separate models, one for each climate variable. For both models, the assumption of normality was met (Shapiro-Wilks normality test of residuals, $P > 0.54$), and visual inspection of Q–Q and Scale Location plots revealed minimal skewing of residuals. For each model, we also assessed the relative importance of climate and soil on SLA by calculating the percent variance in SLA explained by each model predictor (*calc.relimp* function in the R package *relaimpo*; Grömping 2006).

Results

Consistent with our overall predictions, we found that, on average, taxa on ultramafic soils had lower SLA than taxa on non-ultramafic soils (Table 3). There was a significant effect of region on SLA (Table 3). Due to the significant interaction between soil and region (Table 3), we performed pre-planned contrasts. We found that in all regions, except Puerto Rico, mean SLA for plants on ultramafic soils was significantly lower than that of non-ultramafic soils (Figure 1b; Table 2). South Africa had the greatest difference in mean SLA values for plants on and off ultramafic (a difference of 12.46 mm^2 mg^{-1}) followed by Costa Rica (a difference of 12.09 mm^2 mg^{-1}). The comparison between the distribution of global SLA values derived from BIEN (mean 18.82 mm^2 mg^{-1}) and our values showed that for three of five regions the mean SLA of taxa on ultramafic soil was significantly lower than the global average (South Africa, Puerto Rico and Costa Rica; Wilcoxon rank-sum tests $P < 0.001$; Table 2). In contrast, ultramafic soils in California and Lesbos had higher SLA than the global average, although only Lesbos was significantly higher after correcting for multiple test comparisons (Lesbos $P = 0.014$, California $P = 0.058$; Wilcoxon rank-sum test).

Table 3. Results of analysis of variance for the effects of soil (ultramafic and non-ultramafic), region (five regions) and their interaction on rank-transformed values of specific leaf area. Sum of squares, degrees of freedom (in parenthesis as a superindex), *F*-values and *P*-values are given. Significant *P*-values are indicated in boldface.

Factor	Sum of squares $^{(df)}$	*F*-value	*P*-value
Soil	1086984$^{(}$**1)**	81.538	**<0.001**
Region	5160418$^{(}$**4)**	96.775	**<0.001**
Soil × Region	807916$^{(}$**4)**	15.151	**<0.001**
Residuals	7225372$^{(}$**542)**		

Table 4. Results of linear regression for the effects of climate (mean annual precipitation and mean annual temperature for model I and II, respectively), soil type (ultramafic and non-ultramafic) and their interaction on specific leaf area. Sum of squares, degrees of freedom (in parenthesis as a superindex), *F*-values, *P*-values and percentage of variance explained (% Var.) are given. Significant *P*-values are indicated in boldface.

	Factor	Sum Squares $^{(df)}$	*F*-value	*P*-value	% Var
Model 1:	Mean annual precipitation	369.35**(1)**	14.051	**0.010**	55.6
	Soil	138.63**(1)**	5.274	0.061	20.1
	Precipitation × Soil	0.32**(4)**	0.012	0.915	0.0
	Residuals	157.72**(6)**			
Model 2:	Mean annual temperature	377.06**(1)**	16.250	**0.007**	56.9
	Soil	137.02**(1)**	5.905	0.051	20.0
	Temperature × Soil	11.12**(4)**	0.479	0.515	1.7
	Residuals	139.22**(6)**			

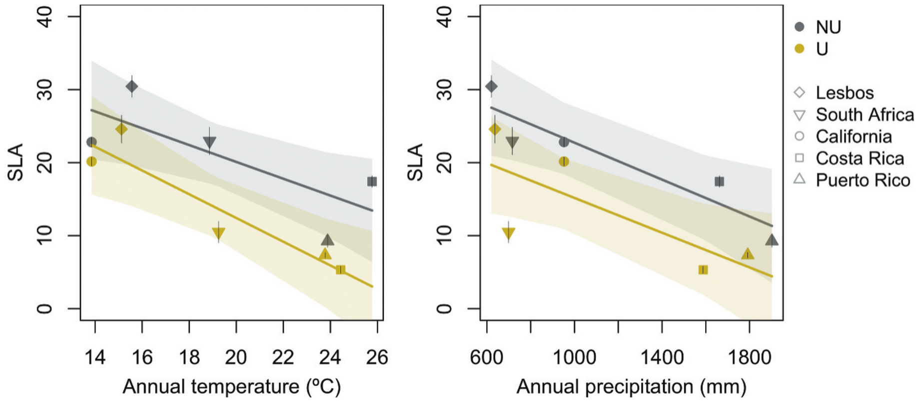

Figure 2. Relationship between mean specific leaf area (SLA) and climate across five regions for ultramafic (U) and non-ultramafic (NU) soils. Vertical lines represent one standard error around the mean. Sloped lines and shaded areas represent the predicted slope and 95% confidence interval from linear regression. See Table 4 for statistical results.

We further found that both climate, and soil to a lower extent, impacted mean SLA across the five regions (Table 4, Figure 2). It must be noted that with only 10 data points this test may be somewhat underpowered and in models excluding the non-significant interaction term, the effect of soil was significant (results not presented). Overall, we found that SLA was lower in regions with higher annual temperatures and higher annual precipitation, and lower on ultramafic soils (Figure 2). The percent variance in SLA explained by climate was more than twice that explained by soil (Table 4), although the effect of climate may be impacted in part by differences in growth form between regions (see discussion below).

Discussion

While many factors are known to influence patterns of functional trait variation that underlie the leaf economic spectrum (Reich et al. 2003; Anacker et al. 2011), most studies focus on climate as the primary driver (e.g. Wright et al. 2005; Moles et al. 2007; Wieczynski et al. 2019). Our study illustrates the importance of soil as a potential determinant of functional trait variation, with SLA being significantly lower on ultramafic than on neighbouring non-ultramafic soils for all study regions except Puerto Rico. Thus, ultramafic-adapted plants within these regions tend to exhibit more conservative resource-use and growth strategies than plants on non-ultramafic soil, despite nearly identical climatic conditions across these neighbouring substrates. This finding is in line with the stress resistance syndrome and the serpentine syndrome (von Wettberg EJ et al. 2014). Furthermore, because the species sampled in Lesbos were identical across both soil types, it appears that serpentine soils not only drive functional trait performance at the community level but at the intraspecies level too (Adamidis et al. 2014a).

In three regions (South Africa, Puerto Rico and Costa Rica), we found that mean SLA values on ultramafic soil fell well below the globally reported average. Furthermore, these ultramafic sites harboured taxa with some of the lowest SLA values on the planet. This suggests that these plant communities contain functionally rare taxa, possibly reflecting extreme edaphic limitations (Hulshof et al. 2020). In contrast, ultramafics in California were not different from the global mean, and in Lesbos, they were significantly higher. The high SLA values in California and Lesbos may be because only herbaceous species were sampled in these regions. The sampling sites in Lesbos and California were dominated by herbaceous vegetation (Adamidis et al. 2014a, 2014b), which generally has higher SLA values than woody species (Garnier et al. 1997) owing to their faster life history strategies (i.e. shorter life spans and faster relative growth rates).

In Puerto Rico, and contrary to our expectations, there was no difference between mean SLA on or off ultramafic soils. Although forest composition and structure differ between ultramafic and non-ultramafic soils in this region (Ewel and Whitmore 1973), our study did not detect differences in SLA. One caveat here could be that sampling in this region occurred across a wider range of topographies and habitat types (Garnica-Díaz 2020), which may have reduced our power to detect mean differences between the two soil types. A more detailed sampling across topography (e.g. Chadwick and Asner 2020) may better capture patterns of trait variation between ultramafic and non-ultramafic soils than reported here. Alternatively, it could be that climatic factors in Puerto Rico, which is warm and humid, may reduce the effect of soil on SLA (whereas Costa Rica has a similarly warm but drier climate and the two soil types there differed in SLA). Again, more detailed sampling across topographies and their associated climatic gradients within Puerto Rico may shed light on this possibility.

The relationship between climate and SLA values across regions departed from our expectations. As mean annual temperature and precipitation increased, SLA tended to decrease. This contrasts with previous studies, where plants in wetter regions, particularly tropical ones, tended to have higher SLA (e.g. Wright et al. 2005; Dwyer et al. 2014). However, there are notable exceptions. Across globallydistributed climbing plants, Gallagher and Leishman (2012) found that low SLA species were associated with higher mean annual temperature and precipitation. In the tropics, across growth form, leaf area is high in lowland forests but decreases with elevation, whereas sclerophylly becomes widespread despite high precipitation (Grubb 1974). This may partially explain low SLA values on ultramafic soils in Puerto Rico and Costa Rica, which occurred in montane areas. In addition, rocky and porous soils, like ultramafic soils, have low water-holding capacity and can create edaphic deserts even in high-rainfall regions (Axelrod 1972). Nutrient leaching of soils in high-rainfall regions may also exacerbate this effect. It is also possible that differences in growth form sampled between regions are driving the relationship between climate and SLA. Tropical sites were dominated by woody species (Costa Rica and Puerto Rico) and woody species tend to have lower SLA (Garnier et al. 1997), as opposed to our sites with cooler and drier climates, which were dominated by herbs (e.g. California and Lesbos). Thus, climate may be having an indirect effect on SLA due to its effect on species' growth form.

Overall, we found that both soil and climate predict SLA globally, which is broadly consistent with other studies. At the global scale, annual precipitation was previously found to be a strong predictor of SLA (Dwyer et al. 2014). Nonetheless, soil pH and soil C:N strongly predicted latitudinal variation in SLA (Gong and Gao 2019) and soil nutrients explained more variance in leaf traits than climate at a global scale (Ordoñez et al. 2009). At a local scale, soil chemistry may account for variation in SLA (e.g. Fortunel et al. 2014; Mori et al. 2021). Furthermore, the shared suite of leaf economic strategies in other unusual or edaphically extreme environments suggests the soil-mediated convergence of conservative plant strategies appears to be a global phenomenon, regardless of climate. For example, on gypsum soils characterised by low soil water and nutrient availability, plants from climatically distinct regions exhibit xerophytic traits such as deep roots and small, succulent leaves (Escudero et al. 2015).

The results shown here, along with those of other studies cited above, indicate that both climate and soil should be considered for understanding geographical variation in functional traits. For example, functional trait values were more different across ultramafic and non-ultramafic substrates in more productive (wetter) areas across a latitudinal gradient in California (Fernandez-Going et al. 2013). However, the opposite was found across elevations in tropical Borneo, with forest structure and diversity being more similar in more productive lowlands (Aiba et al. 2015). Finally, increasing climatic seasonality on granite outcrops resulted in more acquisitive plant traits (Ottaviani and Marcantonio 2020), suggesting that both soil and climate may determine whether selection occurs for resource-conservative strategies. Given the worldwide shifts in climatic regime and its effects on variation in functional trait composition, we expect substantial changes in ecosystem processes such as carbon storage (De Deyn et al. 2008; Hofhansl et al. 2020). Thus, a better comprehension of the degree to which both soil and climate determine trait variation could help identify the consequences of climate and land-use change across biomes and soil types.

Since ultramafic plant communities are characterised by more conservative trait strategies than the non-ultramafic plant communities surrounding them, it is important to consider ultramafic and other edaphically extreme environments as repositories of functionally rare phenotypic and genotypic variants at a global scale. Conservationists have underlined the importance of preserving functionally rare species and communities because of their susceptibility to extinction and their unique ecosystem services (Violle et al. 2017). On nutrient-poor soils like ultramafic soils, low SLA provides species with a competitive advantage because high leaf longevity enhances nutrient residence times in plants (Aerts and Chapin III 2000). However, increased competitive ability comes at the expense of reduced growth rates. Anthropogenic eutrophication disrupts this competitive advantage and invasion subsequently alters the traits of these rare communities as native species become outcompeted (Flinn et al. 2017; Samojedny et al. 2022). Thus, our results underscore the conservation importance of unique edaphic environments like those occurring on ultramafic soils.

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Data availability statement

Data used in this study is, in part, available through TRY (Kattge et al. 2020), BIEN (https://bien.nceas.ucsb.edu/bien/), and Dryad (Hulshof et al. 2021; Spasojevic and Harrison 2022). All code and raw data files are available on the Dryad Digital Repository at https://doi.org/10.5061/dryad.573n5tbbr.

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