



Multidimensional structure of grass functional traits among species and assemblages

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Keywords

Functional trait; Grass; Height; Poaceae; Seed mass; Specific leaf area; Trait co-variation; Trait–environment correlation

Abbreviations

CulmMax = Maximum culm length; WidthMax = Maximum leaf width; LengthMax = Maximum leaf length; LDMC = Leaf dry matter content; RootDepth = Maximum rooting depth; SLA = Specific leaf area; SRL = Specific root length; N_{mass} , N_{area} , P_{mass} , P_{area} = Leaf nitrogen or phosphorous per unit mass or area; MAT, MAP = Mean annual temperature or precipitation; LHS = Leaf–Height–Seed; Biodiversity Information Standards = TDWG.

Nomenclature

Clayton et al. (2006 onwards)

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Abstract

Questions: Research efforts have sought to understand trait–trait relationships among species and trait–environment relationships. However, connections between these two approaches are rare, despite the fact that species-level trait–trait correlations constrain the possible trait–environment correlations. We ask how functional traits of grasses are related to each other and to environmental variation.

Location: Global, with particular focus on the continental United States.

Methods: We compiled distribution data for grasses with three spatial grains – TDWG Level 3 ‘botanical countries’, US counties and vegetation plots within the US. We combined these data with trait data compiled from published sources for 14 traits describing physical and chemical features of the leaves, seeds, roots and entire plant. Trait–trait relationships were explored using correlations and PCA, and trait–environment relationships using regression. Finally, we implemented a null model to predict trait–trait correlations at the assemblage level from those at the species level.

Results: The functional trait composition of grass species varied strongly along environmental gradients. At the species level, there were two main clusters of related traits – one describing general plant size (including height, seed mass, leaf size and rooting depth), and one describing the leaf economics spectrum (including specific leaf area, N_{mass} and P_{mass}). Most trait–trait correlations at the assemblage level did not differ significantly from that predicted from the species level, suggesting that the former are strongly constrained by the latter. Trait–trait and trait–environment relationships in grasses were broadly similar to those observed for other groups, with some exceptions related to the particular growth form, physiology and ecology of grass species.

Conclusions: The unique evolutionary history and ecological role of grasses has led to some unusual trait–climate relationships in the group. Co-variation among traits at the species level is an important template upon which environmental filters act to determine assemblage trait composition.

Introduction

Plants differ in their strategies along a number of axes, including those related to resource capture, allocation, reproduction and stress tolerance (Grime 1977, 2001). These differences are often related to structural or chemical traits, leading to plant strategy classification schemes based on such functional traits (Westoby 1998). Understanding the coordination and co-variation of traits among species can help reveal evolutionary constraints on basic plant

function (e.g. Suding et al. 2003; Wright et al. 2004). Further, because optimal strategies are expected to depend upon the abiotic environment (e.g. da Silveira Pontes et al. 2015), examining trait–environment relationships can elucidate the drivers of plant adaptation. Thus, understanding spatial variation in functional traits of assemblages (*sensu* Fauth et al. 1996) has become a major undertaking in ecology and biogeography, with important applications in climate and vegetation models, among other areas (Violle et al. 2014).

Plant strategies are multidimensional (Laughlin 2014), and a given functional trait can be directly related to multiple strategy axes. For example, plant height may relate to both a species' light competition and herbivory avoidance strategies (da Silveira Pontes et al. 2015). Further, traits may show indirect relationships with strategy axes, via physiological or genetic trade-offs with other traits. For example, a species that allocates resources to tall stature has fewer resources remaining to allocate to producing large seeds (e.g. Jakobsson & Eriksson 2000). Thus, understanding trait variation with respect to environmental variation may often require a multivariate approach, and further depends on understanding both primary trade-offs among traits in non-limiting conditions and the emergent secondary trade-offs that arise along environmental gradients (Suding et al. 2003). One promising approach is the simultaneous consideration of species-level trait–trait correlations and assemblage-level trait–trait correlations (i.e. correlation between community-weighted mean trait values of assemblages; Ackerly et al. 2002; Cornwell & Ackerly 2007).

In general, trait–trait correlations among species are thought to result from physiological constraints or trade-offs (Reich et al. 1999; Reich 2014). For example, a very small plant species cannot produce very large seeds, while a species with a high allocation to leaf biomass requires lower allocation to other organs. Similarly, among grasses, there is a trade-off between root nitrate and ammonium uptake capacities (Maire et al. 2009). As species sort along environmental gradients, the trait composition of the assemblage is expected to change (e.g. Cornwell & Ackerly 2009) but the kinds of changes that are possible are constrained by primary correlations among species trait values (Suding et al. 2003; Gross et al. 2007; Maire et al. 2009). Environmental gradients that cause changes in the trait composition of assemblages may lead to stronger trait–trait correlations (e.g. Ackerly et al. 2002) if positively correlated traits respond in similar ways to the environment. On the other hand, even well-correlated traits could respond oppositely to an environmental gradient, leading to a weakening (or even reversal) of a species-level trait correlation (Fig. 1; Cornwell & Ackerly 2007). While trait–trait correlations among species have received extensive study, trait correlations among assemblages have received relatively little attention (despite many studies on trait composition of assemblages). This limits our capacity to understand trait–environment relationships, particularly because we have limited ability to ascribe variation in trait composition to a direct influence of a gradient, or to an indirect effect via another trait.

Studies of plant functional traits need to begin with a sound basis for focusing on certain traits, including an

understanding of the links between traits and plant strategies (da Silveira Pontes et al. 2015). Westoby (1998) highlighted three major axes of plant strategy differentiation, represented by three easily measurable traits. These axes describe a species' resource acquisition, competitive and reproductive strategies. Specific leaf area (SLA, leaf area per unit mass) relates to a species' position on the leaf economics spectrum, with thin, high-SLA leaves producing rapid return on investments and low SLA corresponding with more conservative strategies (Wright et al. 2004). Plant height relates to the trade-off between being a strong competitor for light and allocating more resources to reproduction, roots or leaves. Finally, seed mass represents a species' reproductive strategy along the trade-off between high investment in few offspring and low investment in many offspring (Diaz et al. 2016). Because it is based on leaf, height and seed traits, this is called the LHS scheme (Westoby 1998).

It can be valuable to consider additional traits as well (Weiher et al. 1999). For example, leaf chemistry and root characteristics can have important influences on species distributions and effects on the environment (e.g. Canadell et al. 1996; Cornwell et al. 2008; Liu et al. 2010) and, while often correlated with SLA, they are not perfectly so. Of the leaf chemistry traits, nitrogen and phosphorus concentrations (per unit area or per unit mass) are often thought to be particularly important (Reich & Oleksyn 2004). Two key root traits are maximum rooting depth and specific root length (SRL, root length per mass investment; Canadell et al. 1996; Hill et al. 2006; Ostonen et al. 2007), reflecting a species' water competition strategy and position along a 'root economics spectrum', analogous to the leaf economics spectrum (Mommer & Weemstra 2012; Reich 2014; Roumet et al. 2016).

Geographic variation with respect to climate has been studied for a number of traits, especially for measures of mean temperature and annual precipitation. Globally, SLA tends to decrease with temperature and increase with precipitation (Wright et al. 2004, 2005), although trees alone tend to show increases with both temperature and precipitation (Swenson et al. 2012; Šímová et al. 2015). Seed mass increases with net primary productivity (Moles et al. 2007) and precipitation (Sandel et al. 2010), and within trees, increases with both temperature and precipitation (Swenson et al. 2012; Šímová et al. 2015). Plant height increases with precipitation, both in general and for trees (Moles et al. 2009; Swenson & Weiser 2010; Šímová et al. 2015). Results for tree height along temperature gradients are somewhat mixed, with both weak negative (Swenson et al. 2012) and positive (Swenson & Weiser 2010; Šímová et al. 2015) relationships appearing. These differences could be due to differences in study extent, with Swenson

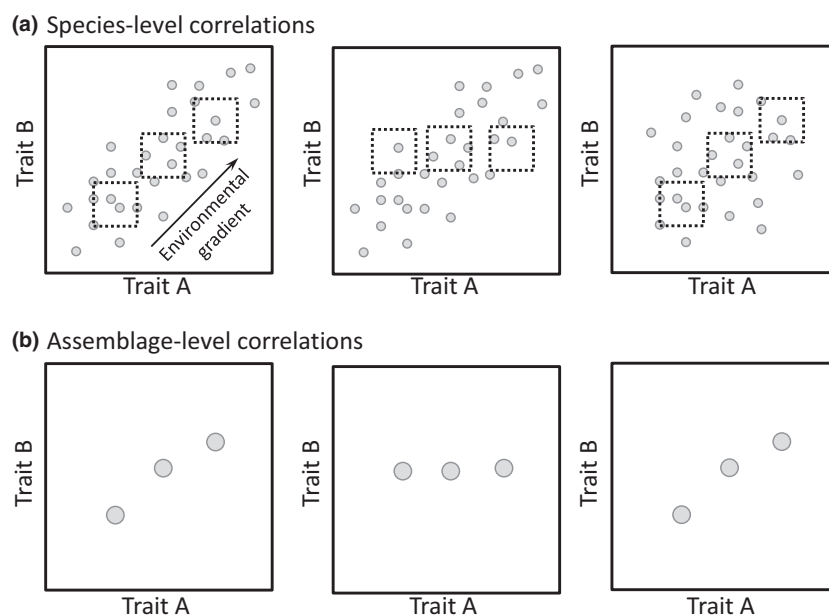


Fig. 1. Correlations at the species and assemblage level. Environmental conditions vary across space, imposing a varying filter (dashed boxes) that selects species with certain trait states. This may strengthen a species-level correlation (first column), weaken it (second column), or produce a correlation at the assemblage level when none exists at the species level, depending on whether the two traits do or do not share responses to the gradient.

et al. (2012) considering the entire New World and the other studies limited to North America. With regard to leaf chemistry, on a per area basis, P tends to decline with temperature (Ordoñez et al. 2009) while N increases with temperature and decreases with precipitation (Wright et al. 2005). On a mass basis, P decreases with temperature (Reich & Oleksyn 2004; Ordoñez et al. 2009) and, within trees, with precipitation (Swenson et al. 2012). The relationship between N_{mass} and temperature has variously been shown to be increasing (Ordoñez et al. 2009; Swenson et al. 2012), hump-shaped (Reich & Oleksyn 2004) or decreasing (Swenson & Weiser 2010).

Here, we focus on the grass family (Poaceae). It is a species-rich group with great economic and ecological importance (da Silveira Pontes et al. 2015). In many ways, Poaceae is an ideal model group for macroecological studies, with globally distributed diversity (Visser et al. 2014) and abundant data available on species distributions, functional traits and phylogenetic relationships (e.g. Clayton et al. 2006 onwards; Edwards et al. 2010; Kellogg 2015; Soreng et al. 2015). Indeed, a number of important macroecological or macroevolutionary studies have focused on the evolution and distribution of the C_4 photosynthetic pathway in grasses (Hattersley 1983; Ehleringer et al. 1997; Collatz et al. 1998; Edwards et al. 2010; Grass Phylogeny Working Group II 2012; Pau et al. 2013). However, beyond this well-studied feature of the family and an analysis of global diversity patterns (Visser et al. 2014), many basic aspects of grass distribution remain relatively

little explored (Oyarzabal et al. 2008). In fact, relatively few studies have focused explicitly on geographic trait variation in any herbaceous group (but see Schmidt et al. 2011; Sandel & Dangremond 2012). Nevertheless, many ecosystems are naturally dominated by herbaceous species (Parr et al. 2014), and where herbaceous and tree species co-occur, they often experience very different microhabitat conditions. Thus, geographic patterns in herbaceous species functional traits may differ from those observed for trees.

Here, we examine geographic patterns in a large suite of traits across a range of spatial grain sizes (vegetation plots, United States counties and TDWG Level 3 botanical countries). We seek to understand the relationships among functional traits of grass species, and how these relationships translate to trait–trait correlations of abundance-weighted means of assemblages. In particular, we ask whether the multivariate structure of traits changes, and whether trait–trait correlations at the assemblage level generally reflect correlations at the species level. Alternatively, they may be influenced by environmental selection on individual traits, which may either strengthen or weaken this relationship. Finally, answering the call for better focus on constrained species groups (Poorter et al. 2014), we compare trait–trait and trait–environment relationship in grasses to those observed in other groups to investigate the generality of these relationships in a large, morphologically and phylogenetically distinct, largely herbaceous, group.

Methods

Distribution

We considered three kinds of species distribution information. At the coarsest grain, we used grass species lists from TDWG Level 3 units (Brummitt 2001; hereafter 'botanical countries' or 'countries'), which correspond with countries or sub-national units for large countries (e.g. states in the United States, provinces in Canada). These species lists were obtained from GrassBase (Clayton et al. 2006 onwards), a compilation of all species and genera in the Poaceae including taxonomic data, synonymy, distributions for TDWG level 3 botanical countries, and species descriptions from floras and taxonomic literature standardized using the DELTA format (Dallwitz 1993 onwards). Distribution data were from a global survey of published floras and checklists, but do not include herbarium records or online databases (Vorontsova et al. 2015).

Within the United States, we obtained county-level species lists from the USDA Plants database (USDA NRCS 2014). Finally, we used vegetation plots from VegBank (Peet et al. 2013). In total, we obtained records for 369 countries, 3060 counties in the contiguous United States (no records were available from Maryland), and 70 627 vegetation plots in the contiguous United States.

Vegetation plots were, however, concentrated mainly in the western states (Fig. 2). Plots in VegBank are contributed by individual researchers or groups, and use various sampling designs. They range widely in size from nine to 50 000 m², but 66% of the plots with known area are 400 m². We used GrassBase (Clayton et al. 2006 onwards) species list as a taxonomic backbone, and matched other names to it using the GrassBase synonymy table.

Traits

We considered the following traits for each species: lifespan (annual or perennial, abbreviated *Lifespan*), photosynthetic pathway (C₃ or C₄, abbreviated C4), maximum culm length (CulmMax), maximum leaf length (LengthMax), maximum leaf width (WidthMax), seed mass (Seed), SLA, leaf dry matter content (LDMC), leaf N per area (N_{area}), leaf N per mass (N_{mass}), leaf P per area (P_{area}), leaf P per mass (P_{mass}), maximum rooting depth (RootDepth) and SRL. Trait data were compiled from a large number of sources. Particularly notable sources include GrassBase (Clayton et al. 2006 onwards), with data for lifespan, culm length, leaf width and leaf length; the Kew Gardens Seed Information Database (Royal Botanic Gardens Kew 2014), with seed mass data; the C₃/C₄ database of Osborne et al. (2014) and the global plant trait database, TRY (Kattge

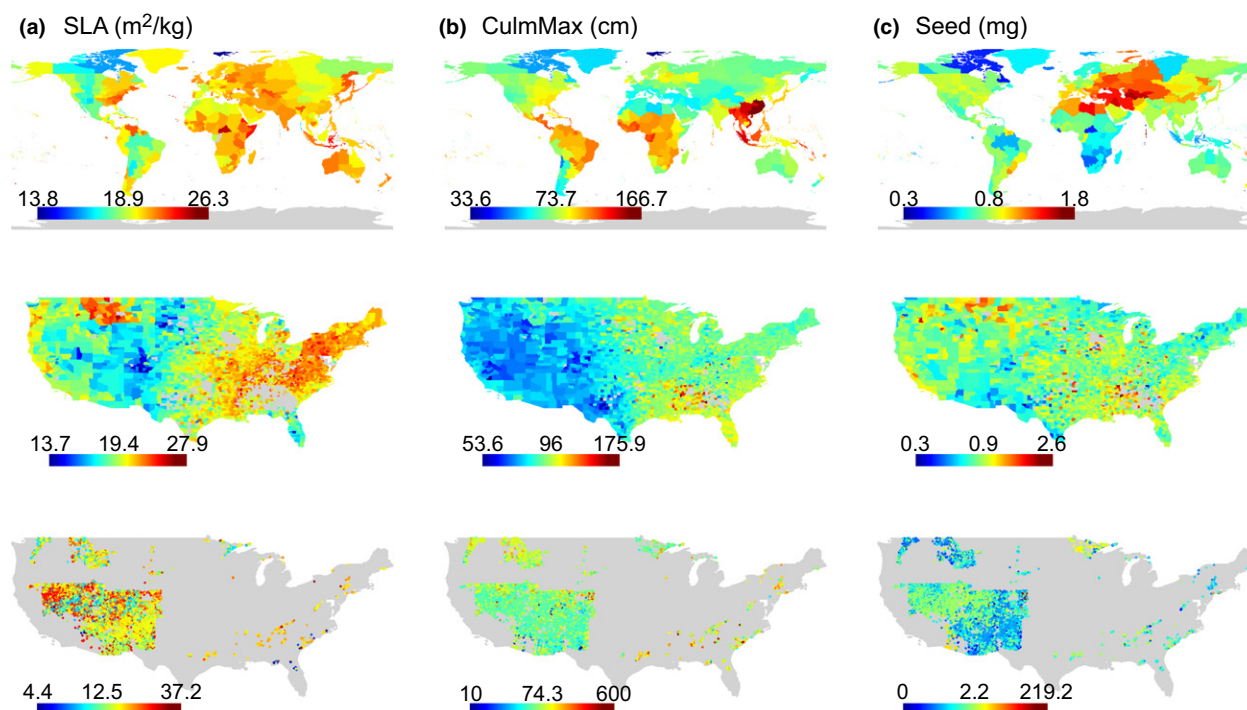


Fig. 2. Geographic variation in assemblage mean specific leaf area (SLA, **a**), maximum culm length (CulmMax, **b**) and seed mass (Seed, **c**) of grasses. Means are shown for countries (top rows), counties (middle row) and vegetation plots (bottom row).

et al. 2011; see supporting information for full references to all TRY data sources). PyDelta was used to extract trait data from the DELTA component of GrassBase. Measurements from GrassBase are from taxonomic literature and represent healthy adult individuals from the geographic range of the source publication only (e.g. the description of *Hordeum jubatum* is from The Grasses of Texas [Gould 1975] so the measurements reflect adult size in Texas only, not including size variation in Europe and South America). In addition, we performed an extensive literature review to compile additional data from published sources (full references in Appendix S11). All quantitative traits showed positively skewed distributions (Appendix S1), so we log-transformed all trait values prior to analysis, including calculating averages for assemblages (see below). Log-transformed traits showed only weak skew (between -0.87 and 0.71).

Among 11 313 grass species recognized in GrassBase, trait coverage ranged from $>85\%$ (lifespan, C4, CulmMax, WidthMax) to $<1\%$ (RootDepth). Of these, 1201 species occurred in the United States county distribution data, and trait coverage was better for these species (for example, Seed coverage increased from 14% to 57% and SLA from 4% to 23%). Widespread and abundant species were more likely to have measured trait values, leading to much better trait coverage at the country, county and plot levels (Appendix S2). For example, in the vegetation plots, we had at least 35% coverage for all 14 traits, and $>60\%$ coverage for 12 traits.

Climate

We used 30-yr normals of precipitation and maximum monthly temperatures as simple descriptions of climate. These were obtained from the PRISM climate group (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 27 Aug 2013). We calculated mean values of these two rasters within each county and country, and extracted the values at the spatial coordinates of each individual vegetation plot. We call these mean annual temperature (MAT) and mean annual precipitation (MAP).

Analysis

Within each distribution unit (country, county or vegetation plot), we calculated the mean value of each trait across all grass species within that unit (in the case of vegetation plots, weighted by the abundance of each species, otherwise the unweighted mean). For the categorical traits Lifespan and C4, this was accomplished by treating perennial or C₄ as the value 1, and annual or C₃ as the value 0. To enable a direct comparison of the county and

vegetation plot means, we also aggregated the vegetation plot means to the county level by calculating the mean value across all plots within the county, weighted by the trait coverage in those plots. For the analysis that followed, we used data for a particular trait from a country or county only if we had values for at least ten of the species in the country or county, and a vegetation plot only if we had trait values for at least 50% of the grass abundance in the plot.

We began by considering the correlations among traits at the species, vegetation plot, county and country level using Pearson's correlation coefficient. We also calculated pair-wise Spearman's correlation coefficients in each case, which were typically quite similar to the Pearson coefficients [median absolute difference of 0.02, 0.08, 0.03 and 0.03 at the species, plot, county and country levels, respectively, with the two magnitudes of the two coefficients themselves being correlated strongly ($r > 0.94$)]. We then performed PCAs to describe the multivariate structure of the trait data at the country, county, plot and species levels (in this case, using all countries, counties or plots regardless of trait coverage). Because the PCA requires a full matrix, we limited the species analysis to six traits (SLA, CulmMax, WidthMax, Seed, N_{mass}, P_{mass}) in order to maintain a reasonable number of species in the analysis (141) and repeated county and plot-level PCAs using this reduced trait set. PCA is most informative when applied to data with primarily linear internal relationships, so we also visually checked for linear relationships among traits (Appendix S8–S10).

To assess the dependence of county-level trait–trait correlations on species-level trait–trait correlations (Fig. 1), we implemented a simple null model. We shuffled the species names in the trait matrix and recalculated trait means at the country and county level using this randomized matrix. This maintains trait–trait correlations among species, but eliminates any environmental gradients that would strengthen or weaken those correlations among assemblages. We repeated this process 1000 times, and compared the observed county-level correlation to this distribution. This procedure uses the species-level trait correlation structure to predict the county-level correlation structure that would be expected if environmental filters do not act separately on the two traits. If the observed correlation falls near the middle of the null distribution, it is plausible to attribute the geographic co-variation of the two traits to species-level constraints and trade-offs alone. On the other hand, if the correlation is stronger or weaker than that predicted from the species-level correlation, this suggests some degree of separate filtering on the two traits. The approach is similar to that advocated by Dray et al. (2014), but the focus is on trait–trait correlations rather than trait–environment relationships.

Finally, we fit linear models to explain variation in trait means as a function of temperature and precipitation, including quadratic terms and an interaction if appropriate. In each case, we considered all subsets of a full model ($\text{MAT} + \text{MAP} + \text{MAT}^2 + \text{MAP}^2 + \text{MAT}:\text{MAP}$), but excluding models where (1) the quadratic term was present without its main effect, or (2) the interaction was present without both main effects. In total, this produced 12 possible models, and we selected the model with the best AIC. MAP was square root-transformed prior to analysis.

All analysis was performed in R 3.1.0 (R Foundation for Statistical Computing, Vienna, AT), using the raster, maptools and vegan packages.

Results

Spatial patterns

Most traits showed marked geographic variation, with many showing strong east–west gradients across the United States (Fig. 2 and Appendix S4). Eastern species

tended to be large (high CulmMax, WidthMax and LengthMax), with high SLA and SRL. Globally, South-east Asia contains many tall-growing species (e.g. bamboos), while the largest-seeded species are concentrated in the Middle East and Eastern Europe. Saharan Africa contains the highest concentration of annual grass species.

Trait correlations

At the species level, there were two particularly marked sets of correlated traits. The first included measures of plant size: WidthMax, CulmMax, LengthMax and RootDepth (Appendix S3, Fig. 3). The second was a cluster of leaf traits including SLA, LDMC, N_{area} , N_{mass} , P_{area} and P_{mass} . Neither SRL nor Seed were strongly correlated with any other trait, although there were moderate correlations between Seed and the size measures (around 0.3; Appendix S3). Some traits (particular RootDepth and SRL) had very low coverage, so correlations involving these traits must be interpreted with caution.

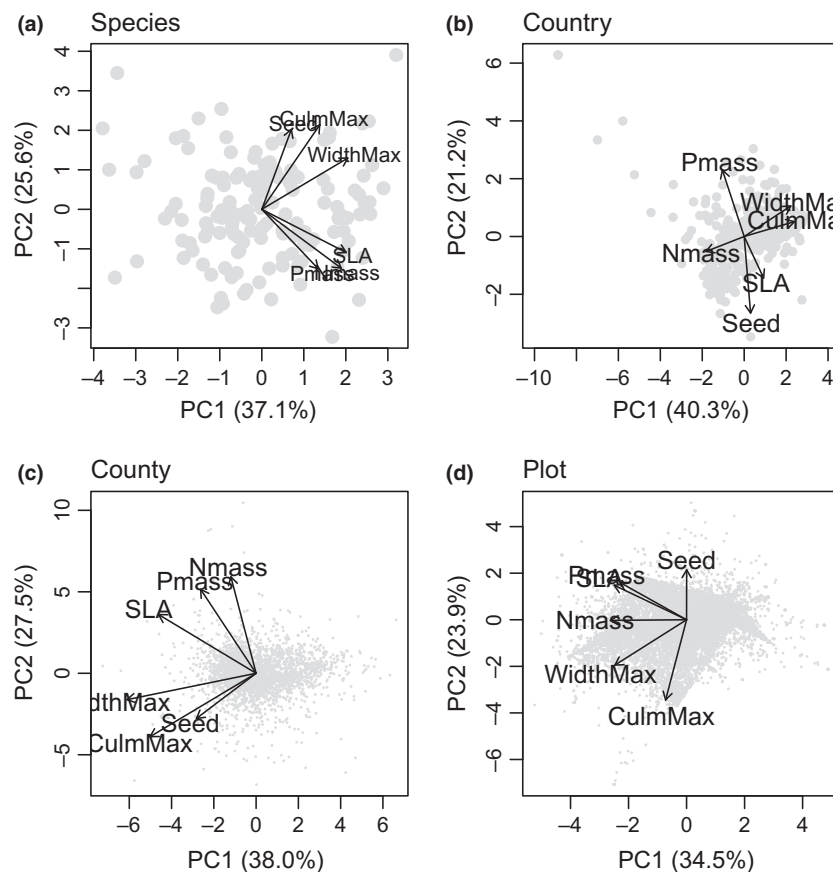


Fig. 3. Principal components analysis of trait relationships at the species (a), country (b), county (c) and plot (d) level. The top row shows an analysis of six well-represented traits (SLA, CulmMax, WidthMax, Seed, N_{mass} , P_{mass}), while the bottom row shows the relationships across all 14 traits. The contour lines describe variation in MAP.

The trait correlation structure changed somewhat at the assemblage level, and depended as well on the grain of the assemblage. Among plots, for example, strong correlations appeared between Seed and SRL and LDMC and P_{mass} ($r < -0.5$), while a strong species-level correlation between WidthMax and RootDepth ($r = 0.49$) disappeared. At the county level, correlations between SLA and SRL and SLA and WidthMax appeared ($r > 0.5$), and among countries strong negative correlations between CulmMax and Narea and N_{mass} ($r < -0.46$; Fig. 4). As such, the major axes of variation in traits across these levels (as identified by PCA) varied substantially (Fig. 3 and Appendix S5).

Considering multivariate relationships among six well-represented traits (SLA, CulmMax, Seed, WidthMax, N_{mass}, P_{mass}), the PCA explained 62.7% of the variation among 141 species (Fig. 3). It revealed two largely orthogonal axes of variation – one describing

plant size (including WidthMax, CulmMax and Seed) and one characterizing leaf economic traits (SLA, N_{mass} and P_{mass}). At the country level, the first two PCA axes explained 61.4% of the variance, at the county level 65.5%, and at the plot level 58.4%. The strong association of leaf economic traits at the species level broke down somewhat at the plot and county levels, as did the general ‘plant size’ axis, with Seed becoming weakly correlated with CulmMax and WidthMax at the country level and negatively correlated at the plot level.

Considering all 14 traits at the country, county and plot levels, the first PC axis separated wet countries with large individuals from dry countries with high N concentrations and wet counties with large individuals and many C₄ species from dry counties with high N_{area} (Appendix S4). There was a strong separation of plots according to precipitation, with dry plots containing many C₄ species with

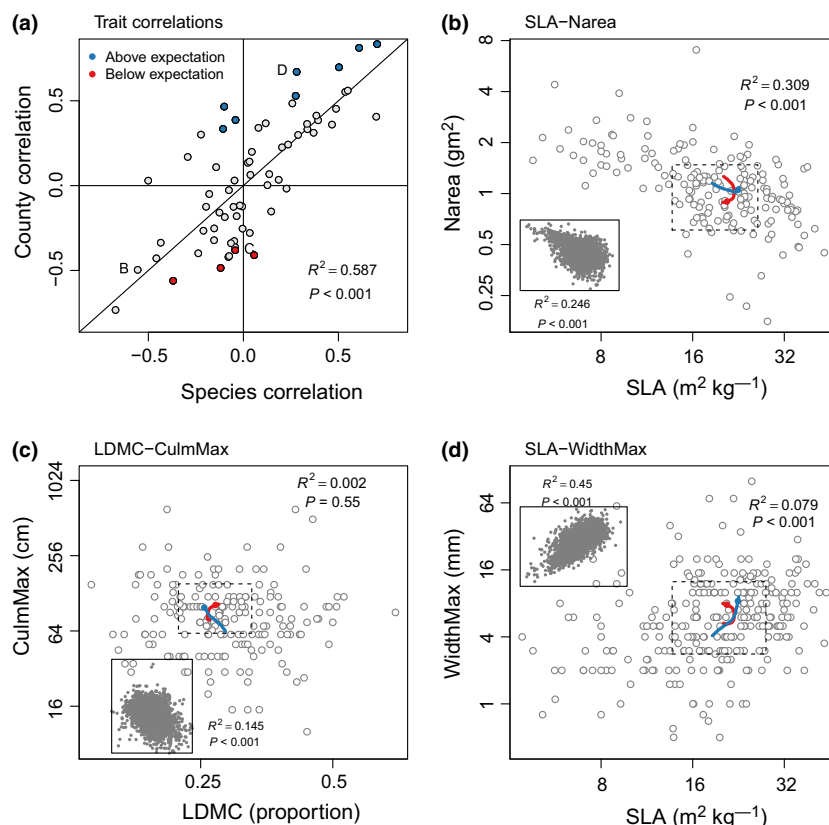


Fig. 4. The relationship between trait–trait correlations at the species and county level. Across all trait pairs (a), there is a fairly strong relationship between correlations at the two levels. A null model test revealed that some pairs show more positive correlation at the county level than is expected given the species correlation (blue points), while others were more negative (red points). The b, c and d labels refer to particular pairs that are illustrated in the corresponding panels. In each panel, the main plot shows the relationship across species, while the inset shows the relationship across counties. The dotted box shows the extent of values illustrated in the inset. The red arrow indicates the effect of increasing precipitation on the environmental filters in each bivariate trait space, while the blue arrow indicates the effect of increasing temperature. For example, SLA and WidthMax are moderately positively correlated at the species level (d). Large R^2 and P -values in panels b–d refer to the species-level relationship, while the smaller values near the inset panel refer to the county-level relationship.

high RootDepth and SRL, and wet plots favouring large individuals, high seed mass and high N_{mass} (Appendix S4).

Trait–trait correlations among assemblages differed in some cases from those expected from the species-level trait correlations, for 12 or 15 of 66 trait pairs for counties (Fig. 4) and countries (Appendix S6), respectively. For example, SLA and WidthMax were weakly positively correlated at the species level, but similar responses of SLA and WidthMax to precipitation gradients led to a relatively strong county-level correlation between the two (Fig. 4). Three trait pairs showed stronger negative correlations among counties than is expected given correlations among species ($P < 0.05$), including LDMC–CulmMax, LDMC–WidthMax and Narea–WidthMax. Five positive relationships became stronger at the assemblage level: WidthMax–SLA, WidthMax–CulmMax, LengthMax–CulmMax, SLA–WidthMax, CulmMax–WidthMax. Finally, CulmMax–SLA, LengthMax–SLA and WidthMax–SRL were weakly negatively correlated among species, but moderately positively correlated ($r = 0.33\text{--}0.47$) among counties. It was rare for a trait to become significantly more weakly correlated at the assemblage level than at the species level – rather environmental filters primarily strengthened existing species trait–trait correlations.

Relationships with climate

Models using MAT and MAP to explain trait variation explained an average of 38, 31, 27 and 11% of the variation in country means, county means, plot means aggregated to counties and plot means, respectively (Table 1). Of the LHS traits at the country level, CulmMax was best explained ($R^2 = 0.583$), followed by Seed ($R^2 = 0.197$) and SLA ($R^2 = 0.140$; Fig. 5, Table 1). SLA was hump-shaped with respect to both MAT and MAP, CulmMax increased with both, and Seed was hump-shaped with respect to MAT and decreased with MAP. At the county level, SLA was best explained ($R^2 = 0.457$), CulmMax followed ($R^2 = 0.379$), and very little variation was explained for Seed ($R^2 = 0.147$). SLA was hump-shaped with respect to temperature and increased with precipitation. CulmMax was weakly related to MAT, but increased with MAP (Fig. 5). Other notable patterns at the country level included a strong decrease in lifespan and increase in C_4 with MAT, and a strong decline of N_{area} with both MAT and MAP. At the county level, the major relationships included a similar increase in C_4 species with MAT, a decline in LDMC with MAP, a decline in N_{area} with MAT and an increase in SRL with MAP (Table 1, Appendix S4 and S7).

At the vegetation plot level, relationships with climate were generally weaker (Fig. 5 and Appendix S7), likely reflecting the influence of many other factors that

influence local community composition. Aggregating to the county level clarified the climate signal, and in most cases where there was a strong relationship at the county level, there was a relatively similar relationship in the plot data aggregated to counties. The relationships between MAP and SRL and LDMC are two exceptions, with the county-from-plot patterns showing hump-shaped and increasing relationships, respectively.

Discussion

In this study, we set out to elucidate the geographic structure of grass functional traits and understand the role of climate and trait correlations transferred across organization scales in generating these patterns.

Among grass species, there were two main axes of trait variation, one describing general size (height, leaf size and seed size) and one describing variation along the leaf economics spectrum (SLA, N_{mass} and P_{mass}). This agrees closely with a recent result from a global analysis across all vascular plants (Diaz et al. 2016). Nevertheless, species-level trait correlation structure for grasses differed in some important ways from other well-studied groups. For example, among Neotropical tree species, leaf size is hardly related to SLA, height or seed mass (Wright et al. 2007), while among grasses, leaf size is moderately to strongly correlated with all three. On the other hand, Neotropical tree height and SLA are negatively correlated, but hardly correlated among grasses (see also Gross et al. 2007). In general, there is evidence for an unusually strong general 'size' axis among grasses, including traits describing leaf size, seed mass, height and rooting depth. This likely reflects the relatively constrained gross morphology of grasses. Relationships between SLA and leaf N and P concentrations, which are important components of the leaf economics spectrum, tended to be somewhat weaker for grasses than have been reported from all plants, both within C_3 and C_4 grasses and for all grasses together (Wright et al. 2004), particularly when N and P were expressed on a per mass basis. N and P concentrations are well correlated across all plants, but relatively weakly correlated among grasses (but see He et al. 2008 for a relatively stronger relationship between leaf N and P within some Chinese grasses).

In general, trait correlations at the species and county level were similar. Thus, trade-offs and constraints at the species level are an important template upon which assemblage-level correlations are built. This has important implications for understanding trait–environment relationships, as any particular pair-wise relationship could in fact reflect environmental filtering on another correlated trait (Suding et al. 2003). This may prove to be a general explanation for differences in trait–climate relationships among clades.

Table 1. Standardized regression coefficients from linear models explaining trait means from countries, counties, counties-from-plots or plots. A missing entry indicates that a variable was not included in the best model. Note that MAP was square root-transformed prior to analysis. Particular coefficients and models as a whole had $P < 0.01$, unless noted otherwise ($[] P > 0.05$, $() P > 0.01$).

	MAT	MAT ²	sqrt (MAP)	MAP	MAT:MAP	R ²
Lifespan Country	−0.407	0.071	0.217	−0.029	0.059	0.523
Lifespan County	−0.107	0.138	0.052	0.003		0.114
Lifespan Plot-County	−0.361	0.583	0.613	−0.141	−0.309	0.148
Lifespan Plot	−0.955	0.649	1.117	−0.118	−0.657	0.137
C4 Country	1.570	0.257	0.017	−0.166		0.809
C4 County	0.788	−0.007	−0.432	−0.170		0.612
C4 Plot-County	1.613	−0.480	−0.559	−0.249	−0.373	0.404
C4 Plot	2.253	−0.346	−0.192	−0.524	−0.185	0.399
SLA Country	[−0.005]		0.033	[−0.005]	−0.038	0.229
SLA County	[0.002]	−0.021	0.051	−0.011	−0.013	0.457
SLA Plot-County	0.053	−0.078	(0.046)	(−0.038)	(−0.045)	0.134
SLA Plot	0.015	[0.003]	−0.055	0.007	0.016	0.030
Seed Country	−0.065	−0.109	−0.109	(0.028)	0.088	0.239
Seed County	0.056	−0.044	[0.000]		0.069	0.147
Seed Plot-County	0.222	[−0.069]	−0.139		0.234	0.144
Seed Plot	[−0.015]	0.022	−0.439	0.129	0.126	0.091
CulmMax Country	0.122	0.024	0.105	−0.038	[0.024]	0.587
CulmMax County	0.009	[−0.004]	0.060	−0.019	0.032	0.379
CulmMax Plot-County	[0.03]	0.046	0.157	−0.072	0.056	0.321
CulmMax Plot	−0.091	0.030	0.073	−0.021	0.081	0.155
WidthMax Country	0.169	0.043	0.194		[0.021]	0.701
WidthMax County	0.023	−0.029	0.122	−0.036	0.037	0.496
WidthMax Plot-County	0.132	[0.000]	0.213	−0.115	(0.079)	0.255
WidthMax Plot	[−0.002]	0.034	0.121		0.107	0.095
LengthMax Country	0.058	(0.016)	0.062	−0.023	[0.001]	0.360
LengthMax County	0.027		0.030	−0.022	0.023	0.276
LengthMax Plot-County	(0.042)		0.151	−0.128	0.125	0.388
LengthMax Plot	[0.005]	−0.028	0.106	−0.014	0.053	0.037
LDMC Country	0.011		−0.025	−0.010	0.014	0.154
LDMC County	0.009	0.011	−0.030	0.005	−0.004	0.354
LDMC Plot-County	0.098	0.031	(0.031)	−0.054	(0.029)	0.385
LDMC Plot	0.045	0.007	0.131	−0.028	−0.009	0.145
Narea Country	−0.120	−0.012	−0.017	0.024	[−0.009]	0.717
Narea County	−0.083	0.017	−0.012	0.019	[−0.002]	0.505
Narea Plot-County	−0.204	0.048	[0.018]	[0.023]	−0.067	0.396
Narea Plot	−0.059	0.014	0.064	−0.009	−0.061	0.122
Nmass Country	−0.064	(−0.012)	0.019	(0.01)	−0.033	0.254
Nmass County	−0.017	0.011	0.024	0.013	−0.017	0.081
Nmass Plot-County	−0.044	−0.022	[0.003]		[−0.018]	0.207
Nmass Plot	−0.032	0.006	−0.039	0.014	−0.031	0.069
Parea Country	0.032	[0.011]	[−0.002]	(−0.017)	[0.012]	(0.05)
Parea County	−0.017	0.016	−0.018	0.010	0.009	0.139
Parea Plot-County	−0.122	0.057	−0.106	0.050	−0.056	0.281
Parea Plot	−0.018	(0.004)	−0.037		−0.046	0.032
Pmass Country	−0.023		0.051		−0.028	0.155
Pmass County	−0.009	−0.012	0.033	−0.006	[−0.003]	0.185
Pmass Plot-County	−0.053	(0.026)	(−0.046)	0.053	−0.069	0.141
Pmass Plot	−0.015	0.008	−0.086	0.008	−0.021	0.050
RootDepth Country	[−0.028]	0.049	0.104		(0.047)	0.309
RootDepth County	−0.041		0.028	−0.055	0.017	0.234
RootDepth Plot-County	0.196	(−0.07)	0.210	(−0.087)	[−0.053]	0.240
RootDepth Plot	0.112	−0.011	0.086	−0.031	−0.012	0.106
SRL Country	−0.086	−0.039	0.073	(0.023)	(−0.039)	0.193
SRL County	0.006	−0.025	0.060	−0.010	−0.010	0.406

Table 1. (Continued)

	MAT	MAT ²	sqrt (MAP)	MAP	MAT:MAP	R ²
SRL Plot-County	−0.069	0.066	[−0.001]	−0.064	[−0.019]	0.265
SRL Plot	−0.034	0.032	0.066	−0.032	−0.020	0.084

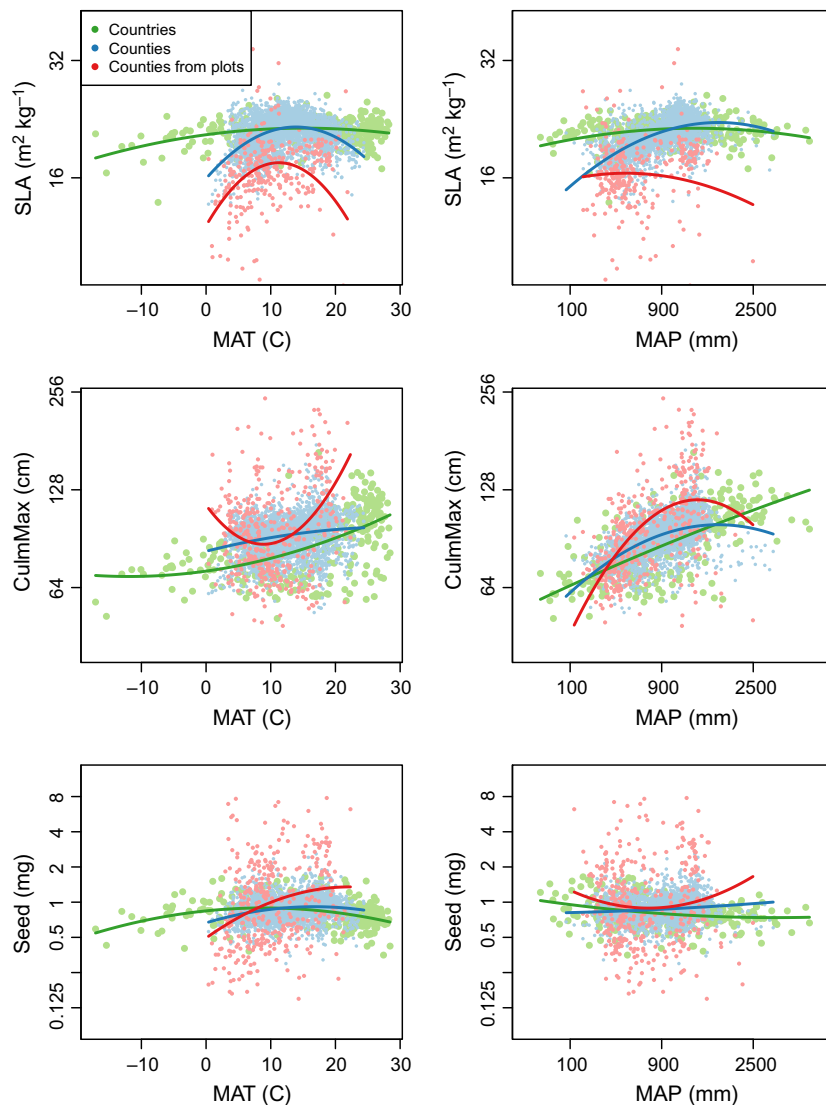


Fig. 5. Trait–climate relationships for LHS traits, derived from trait means for three kinds of assemblages: botanical countries, US counties and vegetation plots aggregated to the county level (Counties from plots). The fitted curves represent quadratic regressions.

If clades vary in their species-level trait–trait correlation structure, certain trait–environment relationships are likely to change as well.

On the other hand, this analysis showed that even well-correlated traits can be subject to independent environmental filtering, with neither trait simply ‘riding’ the patterns caused by a correlated trait. In roughly 20% of cases, trait–trait correlations at the assemblage level

differed from that expected from the correlation among species. In these cases, the correlation among assemblages was generally stronger than that among species, suggesting that environmental filtering acts on both traits, but in the same direction as the species correlation. For example, SLA and SRL were only weakly correlated among species, suggesting that there is no primary physiological constraint on this relationship. However, among counties, a strong

positive correlation appeared between them, suggesting that they respond similarly to environmental gradients, with high values of both favoured under high precipitation (Fort et al. 2013). While it is theoretically possible for traits that are strongly correlated among species to become significantly more weakly correlated among assemblages, we did not find empirical evidence for this among the grasses.

Some of the major relationships between climate and trait means that have appeared in other cases were apparent for the grasses, but there were some important differences as well. Consistent with previous work, the measures of individual size (CulmMax, WidthMax and LengthMax) were most consistently and positively associated with precipitation (Oyarzabal et al. 2008; Moles et al. 2009; Swenson & Weiser 2010; Šímová et al. 2015). And, as other studies have found, SLA tended to increase with precipitation, except in the wettest countries (Wright et al. 2004, 2005; Oyarzabal et al. 2008). However, we found here a hump-shaped relationship between temperature and SLA, which seems not to have been seen in other plant groups (but see Rosbakh et al. 2015 for some evidence of a similar non-linear relationship). Seed mass is also an interesting exception, with almost no variance explained by the climate variables except at the country level. This stands in contrast to previous studies in all plants that have found major latitudinal gradients in seed mass (Moles et al. 2007) and strong relationships with precipitation (Sandel et al. 2010). The relationships of grass leaf chemistry and climate also differed from those for other plant groups in some important ways. N_{area} has previously been shown to increase with temperature and decrease with precipitation (Wright et al. 2005), while we found a strong decrease with temperature and a weak response to precipitation. Various relationships between temperature and N_{mass} have been reported in the past (Reich & Oleksyn 2004; Ordoñez et al. 2009; Swenson & Weiser 2010; Swenson et al. 2012). Grasses show a negative relationship, consistent with Swenson & Weiser's (2010) results for trees.

The unusual responses of grass seed mass and N_{area} to climate gradients might be explained by changes in grass habitats along climate gradients and particular trait correlations in the grasses. In explaining the latitudinal decline in seed mass, Moles et al. (2007) speculated that it might be due to latitudinal variation in plant size (with larger plants in the tropics supporting larger seeds). Large seed size may be an adaptation to low water availability (Leishman et al. 2000; Murray & Gill 2001) and/or low light availability (Leishman et al. 2000). These hypotheses predict that grass seed mass should (1) co-vary with plant size, (2) decrease with precipitation and/or (3) increase with shading. Among the grasses here, seed mass was indeed positively correlated with culm length at the species level, but only weakly at the county level and not at the plot

level. Thus, while culm length showed relatively strong relationships to temperature and precipitation, seed mass did not. Considering possibilities (2) and (3), the effects of precipitation and shading may be confounded for grasses because high precipitation is likely to lead to higher tree cover (e.g. Sankaran et al. 2005; Sandel & Svenning 2013) and shadier conditions for grass species. High water availability and low light should apply opposite selective pressures on seed mass, perhaps leading to a weak overall influence of precipitation on seed mass.

The decline in N_{area} with temperature, on the other hand, may reflect the fact that C_3 species have higher average N_{area} than C_4 species, while also being more common at cool temperatures. Indeed, there is almost no correlation between temperature and county mean N_{area} within C_3 species ($r = -0.062$) or within C_4 species ($r = -0.108$) alone, while the correlation with temperature across all grass species is strong ($r = -0.505$). This suggests that the temperature– N_{area} relationship arises because of geographic variation in the prevalence of C_4 photosynthesis, rather than a direct functional relationship between N_{area} and temperature. This highlights the difficulty of understanding geographic variation within traits in isolation, particularly when traits co-vary. The null model approach developed here to predict assemblage-level trait correlations from species-level correlations should be a generally useful tool to understand geographic patterns of trait composition in the context of species-level correlations.

Geographic patterns in trait means often depended strongly on whether plot-, county- or country-level assemblages were considered. For example, at the plot level, SLA and Seed both increased from the southeastern Southwest to the northwestern Southwest, which was hardly visible in the county-level assemblages. This is likely due primarily to the fact that plot-level calculations were weighted by abundance (and, across plots, were most heavily influenced by widespread species), which is likely to clarify the major patterns of community composition (e.g. Ackerly et al. 2002; but see Pakeman et al. 2009). On the other hand, models explaining the trait composition of plots generally had lower R^2 values than those for counties. This may reflect the fact that vegetation plot composition is subject to many constraints other than climate, for example local soil conditions, disturbance history and hydrology. This should add a great deal of variance to trait composition between nearby plots, which in this study is considered unexplained. In some cases, the shapes of relationships also changed markedly. For example, the proportion of C_4 species increased with precipitation among countries, but was U-shaped among plots (Appendix S7). In general, the distribution of C_4 species is primarily controlled by temperature (Ehleringer et al. 1997), so these idiosyncratic relationships with

precipitation may reflect different patterns of collinearity with temperature at different spatial extents.

Conclusion

In general, many of the major trait–trait correlations and trait–environment relationships that have been found for other plant groups were found for grasses. However, there were several notable exceptions, which involve the role of C_4 photosynthesis in the group, lineage-specific idiosyncrasies and the likely geographic variation in grass microhabitats. The simple approach for detecting unusual assemblage-level trait correlations from species-level correlations should be generally useful and contribute to improved understanding of trait–environment relationships and plant strategy evolution in general.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Skewness of the distributions of raw and log-transformed trait values.

Appendix S2. Proportional trait coverage at the species, country, county, county-from-plot and plot level.

Appendix S3. Trait-trait correlations (using Pearson’s correlation coefficient) and sample sizes.

Appendix S4. Maps of additional mean trait values at country (top row), county (middle row) and plot (bottom row) grass assemblages.

Appendix S5. PCA results using all 14 traits, with isoclines of mean annual precipitation shown in red.

Appendix S6. As Figure 4, but for countries rather than counties.

Appendix S7. Pairwise relationships between climate and additional trait means at the country level (green), county level (blue) or county-from-plot level (red).

Appendix S8–S10. Pairwise relationships among six traits used in the main PCA (Figure 3) at Plot, County and Country levels.

Appendix S11. Trait references.