



# A targeted phylogenetic approach helps explain New World functional diversity patterns of two eudicot lineages

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## Abstract

**Aim:** Large-scale functional diversity studies typically examine isolated traits, often without phylogenetic context. Here, we integrate data from five life-history traits with phylogeny and occurrence records to assess: (a) correlated latitudinal gradients of trait combinations; (b) which traits show phylogenetic conservatism and (c) quantitative, clade-specific differences in trait syndromes, illustrating the phylogenetic scale of observable variation in ecological strategies.

**Location:** The Americas.

**Taxon:** Ericales (Asterids) and Fabales (Rosids).

**Methods:** We used publicly available trait data sets on height, seed mass, wood density, leaf mass per area (LMA) and growth form, an open-source phylogeny, and georeferenced occurrence records to investigate functional diversity patterns. We employed phylogenetic generalized least squares and phylogenetic principal components analyses (pPCA) to assess correlated trait evolution and quantify the trait syndrome, respectively. We employed the InfoMap Ecoregions web app to cluster species by bioregions. We used standard statistical tests and randomization simulations to assess statistical significance of results.

**Results:** Ericales and Fabales exhibited a biogeographically consistent, phylogenetically conserved trait syndrome. Moving poleward, species exhibited progressively smaller trait values and more herbaceous and shrubby growth forms (except for LMA, which showed no consistent pattern). We quantified latitudinal variation in this trait syndrome using pPCA, and provide evidence for correlated trait evolution.

**Main conclusions:** We demonstrate a functional trait syndrome involving height, seed mass, wood density and growth form, but not LMA. Functional trait values showed consistent latitudinal patterns and evidence of correlated evolution, suggesting an underlying ecological strategy. Furthermore, the two clades showed quantitative differences in the manifestation of this trait syndrome. Variation in the syndrome was best observed among species from con-ordinal families. We interpret this trait syndrome as a strategy of resource acquisition in which habitats with relatively greater soil nutrient content and a shorter growing season favour shorter stature, lower seed mass and wood density, and shrubby or herbaceous growth form.



## KEY WORDS

angiosperms, cold tolerance, Ericales, Fabales, functional diversity, latitudinal gradient, life-history traits

## 1 | INTRODUCTION

Functional traits mediate numerous aspects of plant ecology (Grime, 2006), and there has been extensive interest in categorizing the distributional patterns of functional trait values. Such patterns represent the confluence of differing ecological strategies and interactions, selection pressures, physiological constraints, abiotic filtering and historical contingency (Reich et al., 2003). Nevertheless, understanding the underlying biological reasons for the observed patterns remains elusive. Strong latitudinal gradients in many life-history traits, sometimes assessed across all angiosperms or seed plants, have given researchers a first glimpse into continental-scale patterns of functional diversity (Moles et al., 2005, 2007, 2009; Swenson et al., 2012), which might provide crucial insight into the integrated ecological strategies employed by particular taxa (Grime, 2006).

Despite these advances, important gaps in our syntheses of these trait patterns remain (Moles, 2018). Large-scale analyses of functional diversity often look at only a single trait (Moles et al., 2005, 2007, 2009), or include phylogeny in only a limited context (Swenson et al., 2012; Swenson & Weiser, 2010). However, ecological strategies might manifest in the combination of traits a plant exhibits (Grime, 2006; Pierce et al., 2017), and functional trait values will vary among different clades, and can be influenced by evolutionary history (e.g. phylogenetic constraint). For example, although trees may be taller on average in the tropics, what constitutes tall may vary among different lineages. Thus, one important and outstanding question is the extent to which traditional functional traits show evidence of phylogenetic signal/conservatism (Blomberg et al., 2003; Wiens et al., 2010). Indeed, phylogenetic niche conservatism, in general, has been upheld as the primary driver of present-day distributional patterns among New World trees (Segovia et al., 2020). Understanding the extent to which the functional trait values which contribute to a plant's niche are conserved, therefore, has significant implications for understanding modern biodiversity.

Another important consideration is the extent to which certain functional traits correlate, or group together, potentially indicating an integrated strategy. In part, this is a practical concern, since if two traits are tightly correlated, but only one of the pair is easily measured, then it may suffice to measure only that trait for which data acquisition is simpler. However, biologically, it might also be the case that a plant's ecological strategy is better understood in the context of multiple traits and that phylogenetic niche conservatism might manifest as coordinated evolution among multiple characters. Underpinning both the question of phylogenetic signal and coordinated evolution of traits is the question of appropriate evolutionary scale: at what phylogenetic scale is variation in ecological strategies observed?

To begin addressing these questions, we examined five life-history traits that relate to ecological strategies and are linked to plant and ecosystem function: height, seed mass, wood density, leaf mass per area (LMA) and growth form. Plant height is important for its relationship to carbon sequestration (Conti & Díaz, 2013; Moles et al., 2009) and competition for light (Moles & Leishman, 2008), as well as influencing habitat type available for animal species (e.g. closed canopy forest versus open woodland). Seed mass is one determinant of dispersal syndrome (Muller-Landau et al., 2008; Westoby et al., 2002) and contributes to fecundity-survival (Muller-Landau, 2010) and shade tolerance trade-offs (Wright et al., 2010). Wood density provides mechanical support and forms a 'wood economics spectrum' (Chave et al., 2009). Leaf traits relate directly to photosynthetic strategy and the leaf economics spectrum (Wright et al., 2004, 2010). Leaf mass per area (LMA) represents a fundamental part of a plant's carbon-investment strategy and has been correlated with leaf life span in woody plants.

While previous work on continental-scale diversity patterns (Moles et al., 2007, 2009; Swenson et al., 2012; Swenson & Weiser, 2010) has found a signal for latitudinal gradients for several traits, the inclusion of phylogeny has been limited. On the other hand, studies that have related functional trait patterns to phylogeny (Moles et al., 2005; Zanne et al., 2014) have utilized very broad phylogenetic scales (the entire seed plant or angiosperm phylogeny; but see Hawkins et al., 2014). These extremely broad studies may obscure the underlying biological explanations for observed patterns. Here, we adopt a targeted approach that allows us to account for individual histories of particular lineages and provides a clearer understanding of empirical patterns.

We examine the geographic distribution of this suite of life-history traits across the Americas within two angiosperm clades: Ericales (Asterids) and Fabales (Rosids). Ericales is a large clade within the Asterids, containing 22 taxonomic families and comprised of ~12,000 known species (The Angiosperm Phylogeny Group, 2016; Stevens, 2001). Although resolution of deep divergences remains contentious, the clade likely began diversifying between 100 and 125 million years ago (MYA; cf. Magallón et al., 2019; Rose et al., 2018; Stevens, 2001), providing not only ample opportunity for phenotypic diversification but also for species to be exposed to several changes in habitat types and climate regimes. Similarly, Fabales represents a ~80–100 MYA clade (Li et al., 2015; Stevens, 2001; Wikström et al., 2001) that has diversified into numerous ecosystems across the globe. Additionally, Fabales are of particular note for their involvement with nitrogen-fixing bacteria (Sprenst, 2009), of which the Fabaceae contributes greatly to the global nitrogen cycle.

Both Ericales and Fabales are present throughout the Americas and contribute to the structure and diversity of a wide range of ecosystems, including tropical rainforests, forest understories,

open habitats and polar environments (Hedwall et al., 2013; Moquet et al., 2017; ter Steege et al., 2006; Stevens, 2001). Therefore, we expected that each of these two clades would show sufficient variation in functional trait values to address the question of which traits show phylogenetic conservatism and evidence of correlated evolution. Nevertheless, because these clades are relatively distantly related (separated by over 100 MY), we expected clade-specific quantitative differences in the trait values characterizing each clade, even if overall qualitative phenotypic patterns were similar.

## 2 | MATERIALS AND METHODS

### 2.1 | Phylogenies & species lists

We obtained species-level Ericales and Fabales phylogenies from the Smith and Brown (2018) seed plant phylogeny, and left polytomies unresolved. Species lists from this phylogeny were used to query trait and geographic occurrence record databases (see below). To investigate the interaction between traits and biogeographic distribution, we pruned each larger phylogeny (Ericales or Fabales) based on trait data availability to create subtrees for each trait, yielding the following species-by-trait coverage after data cleaning and processing (per cent indicates fraction of species for which trait data were available). Growth form: 2,362 (Ericales, 14.9%) and 4,052 (Fabales, 16.5%). Plant height: 558 (Ericales, 3.5%) and 593 (Fabales, 2.4%). Seed mass: 412 (Ericales, 2.6%) and 1,014 (Fabales, 4.1%). Wood density: 314 (Ericales, 1.9%) and 367 (Fabales, 2.4%). LMA: 451 (Ericales, 2.8%) and 625 (Fabales, 2.6%).

We illustrated the correspondence between species' trait values and their farthest latitudinal extent from the equator (see Section 2.2 below) with phylogenetic heatmaps for which we painted ancestral state reconstructions on branches and latitudinal categories surrounding each phylogeny. Phylogenies were visualized using the R statistical computing environment (R Development Core Team., 2011) with 'GGTREE' (Yu et al., 2017) and 'TREEIO' (Wang et al., 2020) packages; reconstructions were calculated with 'PHYTOOLS' (Revell, 2012).

To determine phylogenetic clustering (niche conservatism) of species within latitudinal categories, we calculated the average phylogenetic distance among species found in each category. To assess whether these average distances were more extreme than expected by chance, we performed 1,000 random draws of  $n$  taxa from the phylogeny and calculated the average distance among them for each draw (where  $n$  equals the number of species in a category). Observed phylogenetic distances were deemed significant if they were more extreme than 95% of distances obtained from these simulations.

We used phylogenetic principal component analyses (pPCA) to quantify our trait syndrome, calculated with 'PHYTOOLS' and visualized with 'PCA3D' (Weiner, 2015). pPCA accounts for the covariance structure of the phylogeny during ordination (Polly et al., 2013),

allowing one to measure the degree of correlation among variables beyond what is expected from Brownian motion. We performed pPCA on the subsets of taxa for which complete trait data were available (86 Ericales, 220 Fabales species), although we did not include growth form (categorical trait) in the ordination. For these subsets, correlated evolution among traits was assessed by phylogenetic generalized least squares (PGLS), using the variance-covariance matrix of the subtree as the expected correlation structure, in order to quantify the degree of correlation between traits beyond what would be expected solely from a Brownian motion model of trait evolution.

### 2.2 | Occurrence records

Ericales and Fabales georeferenced occurrence records across all American countries were obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and processed using the 'COORDINATECLEANER' package (Zizka et al., 2019) in R to remove suspect coordinates, fossil records and match taxa to country. Records were further processed by removing those with fewer than two decimal precision (~1.1 km) and matching all names to those from the Smith and Brown (2018) phylogeny. From these records, each species was assigned a unique latitudinal category based on the farthest *absolute* distance it was found from the equator. We required at least three records within a category in order to assign a species to it. Categories were as follows: beyond 60° (polar); between 60° and 50° (hemi-boreal); between 50° and 40° (temperate); between 40° and 20° (subtropical) and between 20° and 0° (tropical). Results were robust to changes in the boundaries of these latitudinal categories (data not shown).

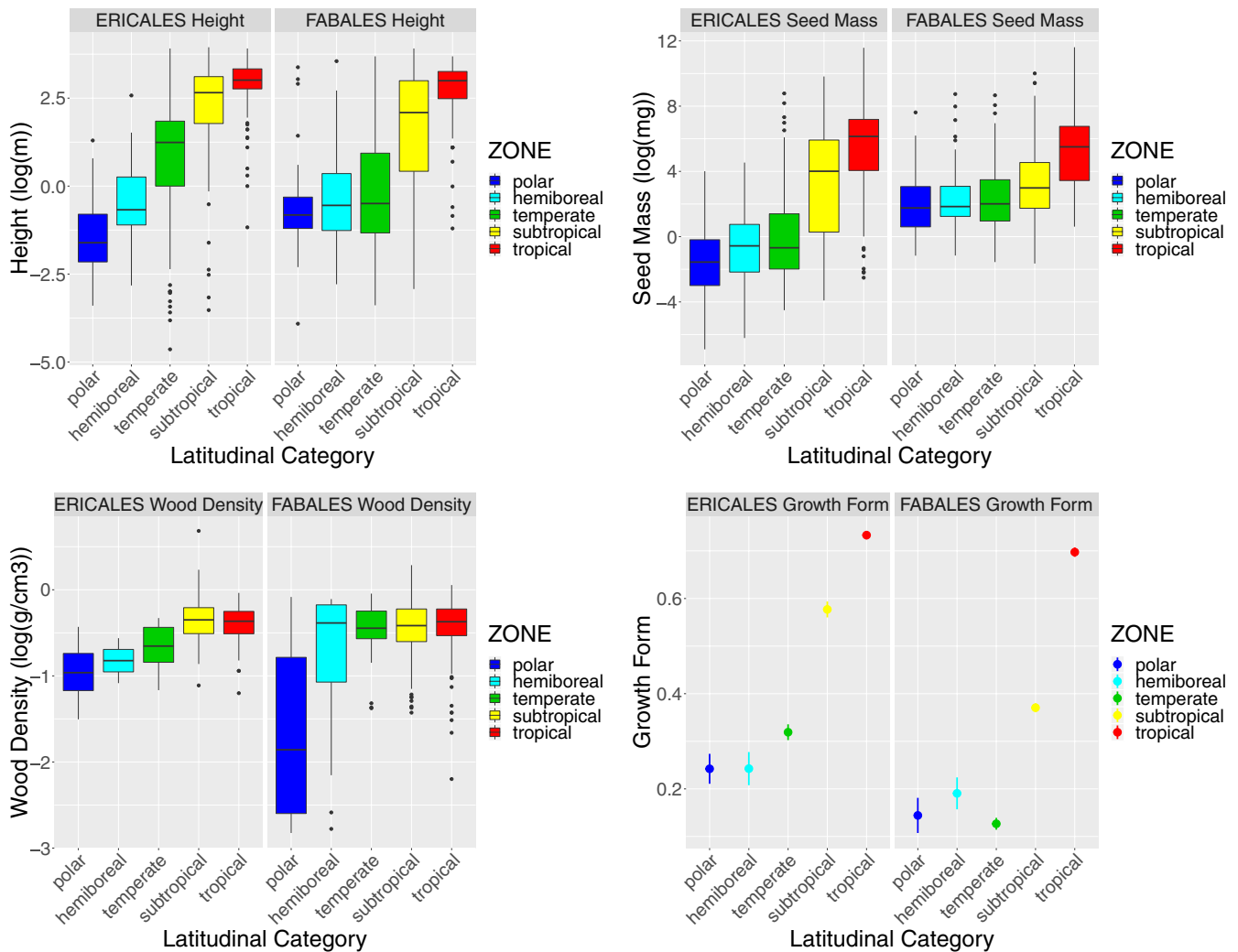
Latitudinal gradients were visualized with 'GGPLOT2' (Wickham, 2016) in R. Trait disparity maps were constructed as follows. For each clade and trait, we calculated standardized effect size

as  $SES = (X - \bar{X}) / \sigma_x$ , where  $X$  denotes species' trait value,  $\bar{X}$  the mean

clade-wide trait value (Figure S1) and  $\sigma_x$  is the standard deviation of the trait distribution. We calculated the average SES found within a 0.5 degree grid cell in order to visualize 'hot spots' where trait values differ significantly from the overall clade average. Positive (negative) values indicate grid cells with average trait values much larger (smaller) than the clade-wide average. Scores are in units of standard deviations and can be interpreted as a Z-score. American terrain maps were obtained from stamen maps (Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under CC BY SA) via the 'GGMAP' API (Kahle & Wickham, 2013).

### 2.3 | Trait and climate data

Trait data were obtained from the TRY Plant Trait Database (Kattge et al., 2020), by querying all traits related to plant height, seed mass,



**FIGURE 1** Latitudinal gradients for each clade (Ericales, left panels; Fabales, right panels) and functional trait (height, seed mass, wood density, growth form). For both clades, taxa confined to tropical latitudes show significantly higher trait values than those which reach polar latitudes ( $p < 0.05$  in all cases), and there is a tendency for a graded increase in trait values with decreasing distance from the equator. This trend is interpreted as a trait syndrome since it manifests across multiple traits. We omit LMA here because it did not show a strong latitudinal gradient (see Figure S2 for LMA results), although tropical taxa still possess higher median LMA values than polar ones. Differences between Fabales and Ericales are discernible, indicating quantitative differences in the manifestation of this trait syndrome (see Section 4). (Boxplots indicate median values. Growth form is plotted using average values (points) and standard deviations (lines) because this trait was treated differently than others in the analyses (see Section 2).) [Colour figure can be viewed at wileyonlinelibrary.com]

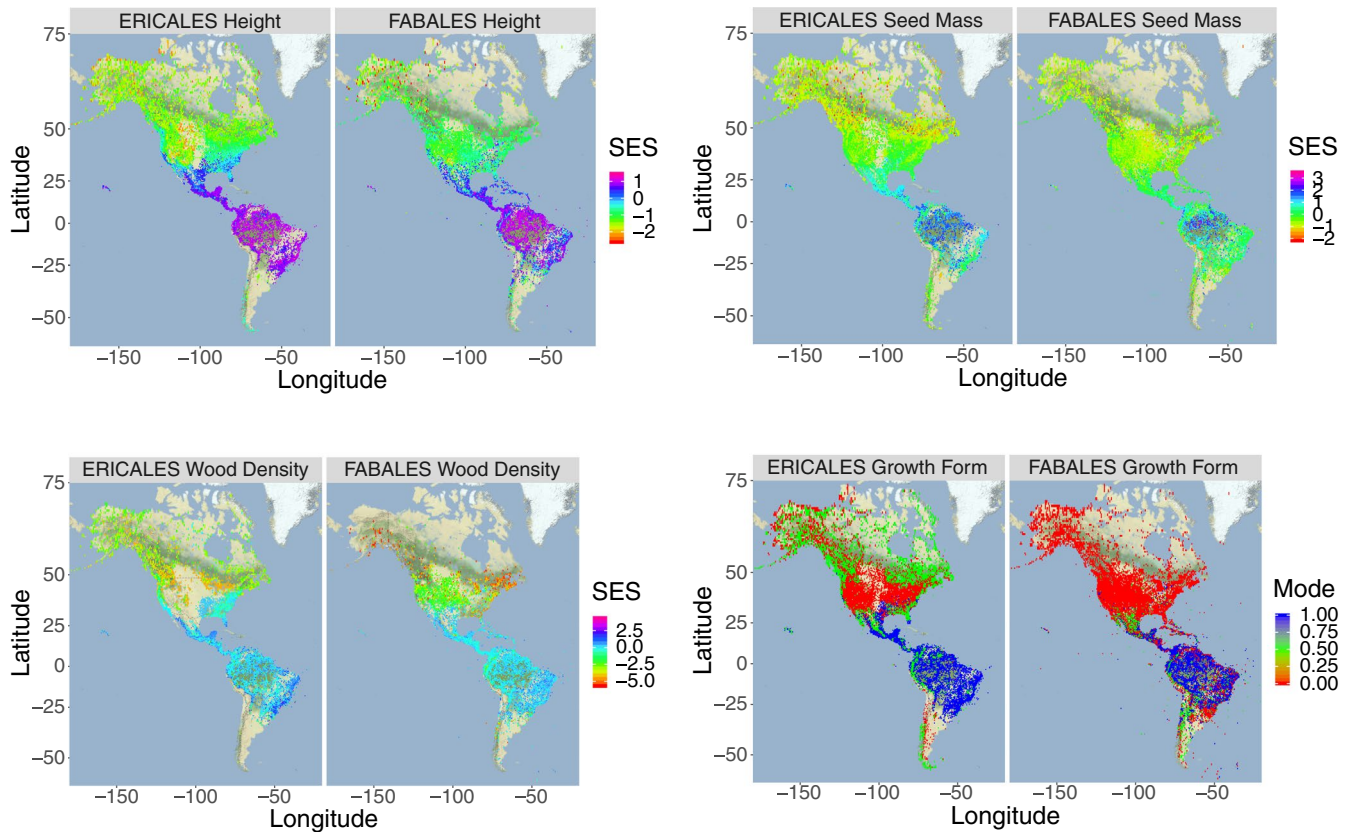
wood density, LMA and growth form for our Ericales and Fabales species lists. Trait data were converted into standard units (seed mass – mg; height – m; wood density –  $g/cm^3$ ; LMA –  $mg/mm^2$ ; growth form – unitless, see below), entries flagged with risk factor  $>4$  by TRY removed and remaining trait values averaged for each species. We log-transformed all traits, except growth form, prior to analyses. Growth form, instead, was coded numerically as: 0 – herbaceous, 0.5 – shrub/climber; 1 – tree; NA – other; however, we did not use such values as ordinated points.

We downloaded 30-s climate data from worldclim.org (Fick & Hijmans, 2017) describing mean annual temperature (MAT), precipitation (MAP) and elevation (ELV) of the Americas. We then extracted MAT, MAP and ELV values for each species' location using the 'RASTER' package in R, and calculated the minimum

MAT, MAP and maximum ELV for each species across all of its sites.

## 2.4 | Bioregion mapping and trait distributions

For those species with complete functional trait information, we used their georeferenced occurrence records to cluster species by biogeographical regions (bioregions), using the Infomap Bioregions web application (<https://bioregions.mapequation.org>). Briefly, this algorithm takes species' point occurrences as input and uses an information-theoretic clustering algorithm, Infomap (Edler et al., 2016; Rosvall & Bergstrom, 2008), to form a bipartite network mapping species to different bioregions. Rather than binning species by latitudinal extrema,



**FIGURE 2** Geographic heatmaps (Mercator projection) showing the extent of trait disparity for each clade (Ericales, *left panels*; Fabales, *right panels*) and functional trait (height, seed mass, wood density, growth form). LMA is omitted because it did not show a strong latitudinal gradient (see Figure S2). Except for growth form, grid cell colors indicate the extent to which the average trait value in that grid cell differs from the overall average across the entire clade (standard deviation units, e.g. z-score; see Methods), with red (purple) grid cells indicating values much lower (higher) than the average. For growth form, grid cells are colored by the most common (modal) growth habit in that cell (blue: tree; green: shrub; red: herbaceous). In general, South American tropics have trait values higher than the average and are dominated by trees (though many more Fabales are herbs here), while polar latitudes have trait values lower than the average and a greater proportion of herbs (though many more Ericales are shrubs here). Maps for the same trait share a common legend, however, maps of different traits do not and so colors are not directly comparable between different traits. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

this approach allowed the entirety of species' ranges to define potentially biologically relevant geographical boundaries that might separate groups of species using different ecological strategies. Parameters used for clustering each clade by bioregion are given in Table S1. To examine the relationship between functional traits and the bioregions identified by the Infomap algorithm, we calculated mean and standard error of functional trait values for all species assigned to each bioregion.

### 3 | RESULTS

#### 3.1 | Correspondence between geography and traits

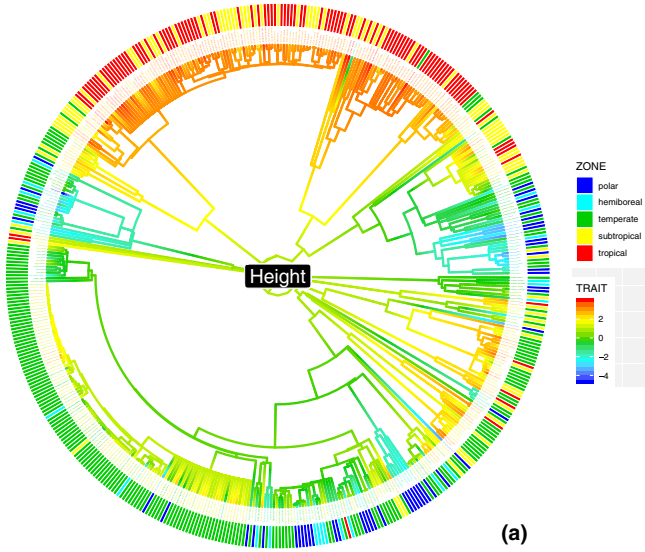
From an initial set of 1,854,067 GBIF records, data cleaning methods yielded a final set of 1,170,770 records (~63% retained). Among these, we observed a strong relationship between species'

**FIGURE 3** Phylogenetic conservatism of functional trait values and latitudinal extrema for Ericales (*left column*) and Fabales (*right column*). Species names are coloured according to observed trait values. Colors along phylogenetic branches depict the ancestral state reconstruction for each functional trait, with warmer (cooler) colors indicating larger (smaller) trait values. Coloured bars surrounding each phylogeny illustrate the assigned latitudinal category. Bar colors are as in Figure 1: polar (blue), hemiboreal (cyan), temperate (green), subtropical (yellow) and tropical (red). In order to maintain readability, for traits with data available for more than 500 species, only a random sample of 500 tips is included in this figure (see Figure S4 for phylogenies without any tips excluded). However, for all analyses, we included all species. For traits other than LMA, trait values are conserved, with closely related species having similar trait values. Species also tend to show conservation of latitudinal category, meaning that similarly coloured bars around each phylogeny tend to be grouped together. Furthermore, clades within each lineage tend to show conserved suites of traits when one looks across multiple traits within each column. The distribution of both functional trait values and of latitudinal category differs noticeably between Ericales and Fabales. Although similar fractions of each clade are represented in each latitudinal category (Figure S5), extra-tropical Fabales taxa cluster together in one portion of the phylogeny, whereas they are distributed throughout the Ericales phylogeny [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

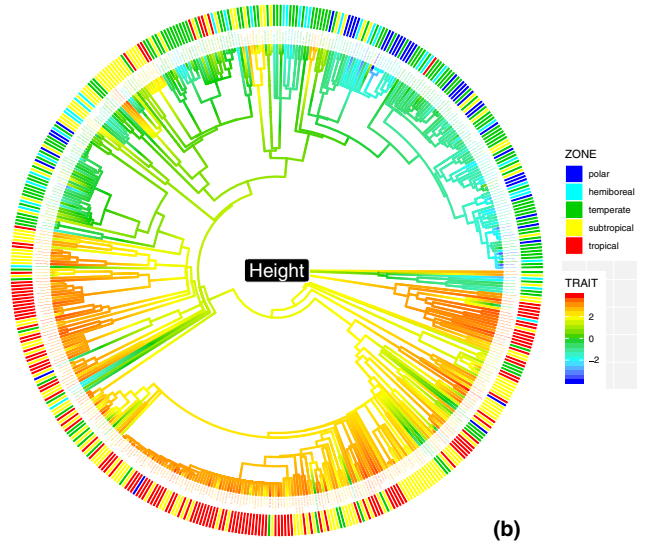


ERICALES

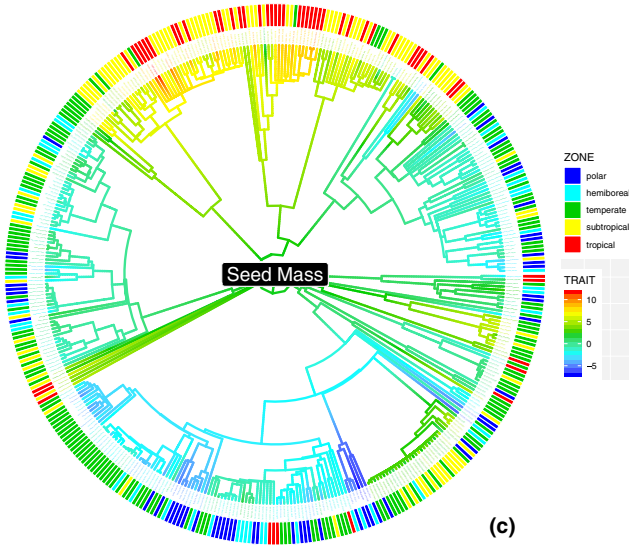
FABALES



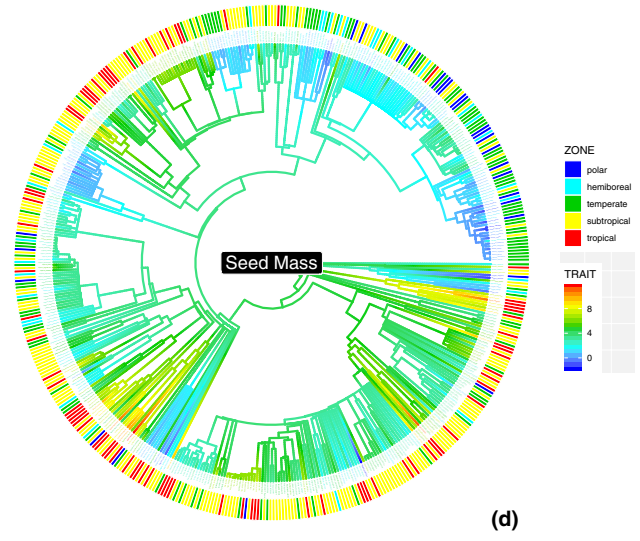
(a)



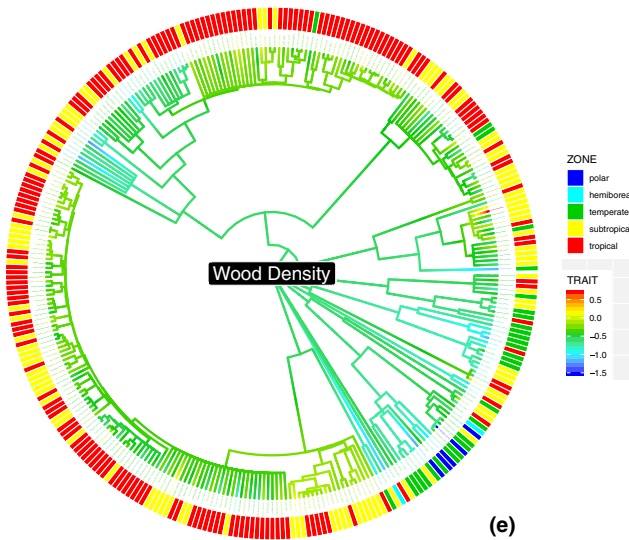
(b)



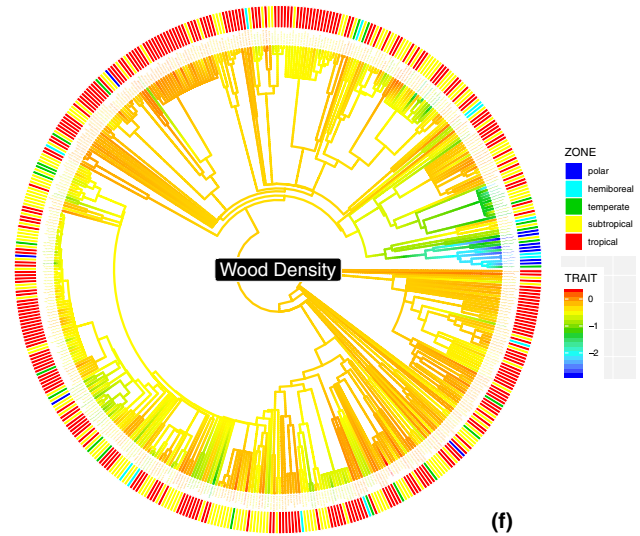
(c)



(d)



(e)



(f)

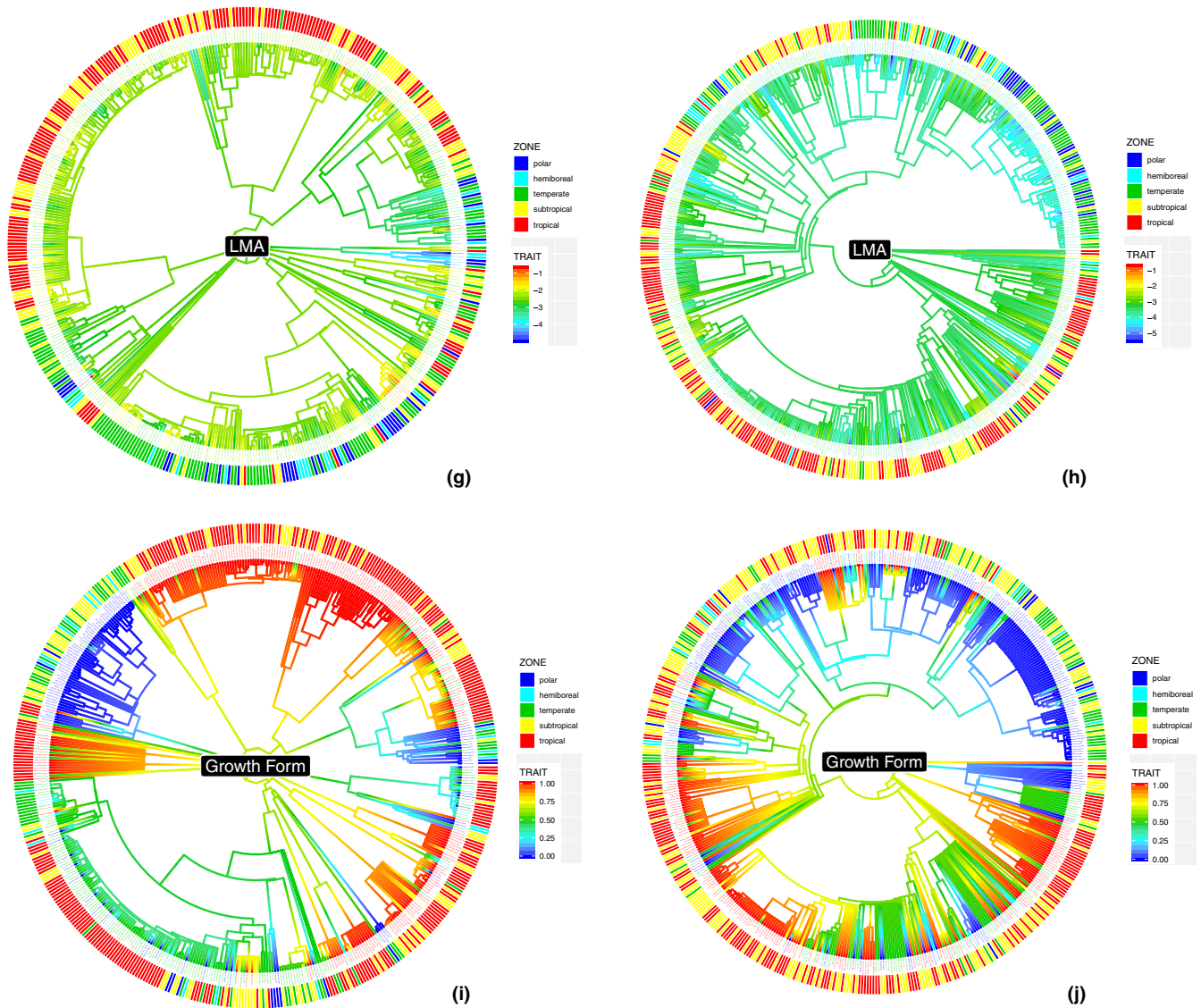


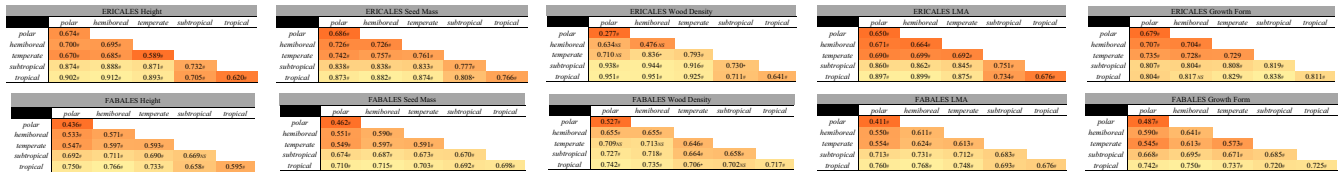
Figure 3 (Continued)

latitudinal category and most life-history trait values (Figure 1), LMA being an exception (Figure S2). Both Ericales and Fabales occurring at more extreme latitudes (particularly beyond 50° from the equator) exhibited a high-latitude trait syndrome characterized by the production of smaller seeds, shorter stature, lower wood density, being herbaceous or shrubby and lower LMA. The converse was generally true for taxa confined to within 20° of the equator. Production of larger seeds, higher wood density and stature, and tree growth form typified the lower-latitude manifestation of this trait syndrome.

Quantitatively, we found a latitudinal gradient in trait values for each trait and clade (Figure 1), with the exception of LMA (Figure S2), which showed a comparatively modest trend. Although both clades showed a graded tendency towards lower trait values at progressively higher latitudes, the quantitative trait values within each latitudinal category differed between Fabales and Ericales. For example, for both groups, species at polar latitudes were significantly shorter than those at tropical latitudes ( $p < 0.05$ ); however,

at polar latitudes Fabales species were significantly taller than Ericales species ( $p < 0.05$ ; see Section 4). We also note that Fabales tended to produce larger seeds, on average, than Ericales (Figure S1). Furthermore, there was a strong drop in median Fabales wood density at polar latitudes, which was not present for Ericales. To some extent, these clade-specific differences might be attributable to differences in how Fabales and Ericales are distributed with regards to temperature, precipitation and elevation (Figure S3).

We found variation in the intensity of trait disparity for each clade and trait, using a standardized effect size metric (see Section 2; Figure 2). In general, for both clades, grid cells at higher (lower) latitudes show average trait values that were significantly lower (higher) than the within-clade average. Clade-specific differences in the extent of relative trait disparity were also apparent. For example, while both groups had lower average wood density at polar latitudes, Fabales species at polar latitudes showed significantly lower wood density compared to Ericales taxa ( $p < 0.05$ ), and Ericales taxa had a higher proportion of shrub taxa in polar regions than Fabales.



**FIGURE 4** Mean pairwise phylogenetic distances (MPD) among taxa within each latitudinal category, for Ericales (*top row*) and Fabales (*bottom row*). Matrices are symmetrical, and we show only the lower triangle of each. Darker (lighter) colour indicates smaller (larger) phylogenetic distances, indicating species are more (less) closely related on average. In general, species in the same latitudinal category tend to be more closely related (i.e. the diagonal elements are usually darker colour than other elements in the same row/column), and polar species tend to be more closely related to each other than any other combination (i.e. the polar-polar element is usually one of the smallest values in the table). More generally, species outside of the tropics tend to be more closely related to each other than to tropical or subtropical species (the converse is also true). Most values were statistically significant (see Section 2). (<sup>#</sup>*p* < 0.001; \**p* < 0.05; NS: not significant) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3.2 | Correspondence among traits, phylogeny and geography

Species demonstrated phylogenetically conserved life-history trait values (Figure 3). In addition to showing conserved *individual* trait values, clades within each lineage also showed conserved *suites* of trait values. For example, Sapotaceae (Ericales) tended to be tall trees with large seeds and higher wood density, while *Trifolium* (Fabales) tended to be shorter statured, herbaceous or with lower wood density, and produce smaller seeds. Overall, congeneric species were similar in their functional trait values, indicating that within-genus comparisons would generally not provide observable variation in the functional traits we examined here. However, comparisons of con-ordinal species from differing families (e.g. comparing Sapotaceae, Ericaceae and Primulaceae) permitted observable variation in functional trait values, indicating that this phylogenetic scale is better suited for this trait syndrome. Comparisons made by grouping Ericales and Fabales together, however, could obscure the ability to see variation in this syndrome (see Section 4).

In general, there was also phylogenetic conservatism of latitudinal categories (coloured bars surrounding phylogenies in Figure 3; Figure 4). Species tended to be significantly more closely related to species in the same latitudinal category (i.e. diagonal elements in Figure 4 tend to have lower values than other elements in the same row or column). Additionally, species inhabiting polar latitudes tended to be more closely related to each other than to species in other categories (i.e. the average polar-polar phylogenetic distance is usually among the smallest values in each table). Overall, therefore, taxa showed phylogenetically conserved life-history trait syndromes, which corresponded to the latitudinal extrema at which the species are found. LMA was an exception to this trend, however; this trait showed little connection to phylogeny or latitudinal extrema.

Although data from both Ericales and Fabales were consistent with these trends, there were notable differences between the two clades in terms of how trait values and latitudinal extrema were distributed along their respective phylogenies. For example, although both clades had similar fractions of tropical species sampled for plant height (Figure S5 for proportion of species in each

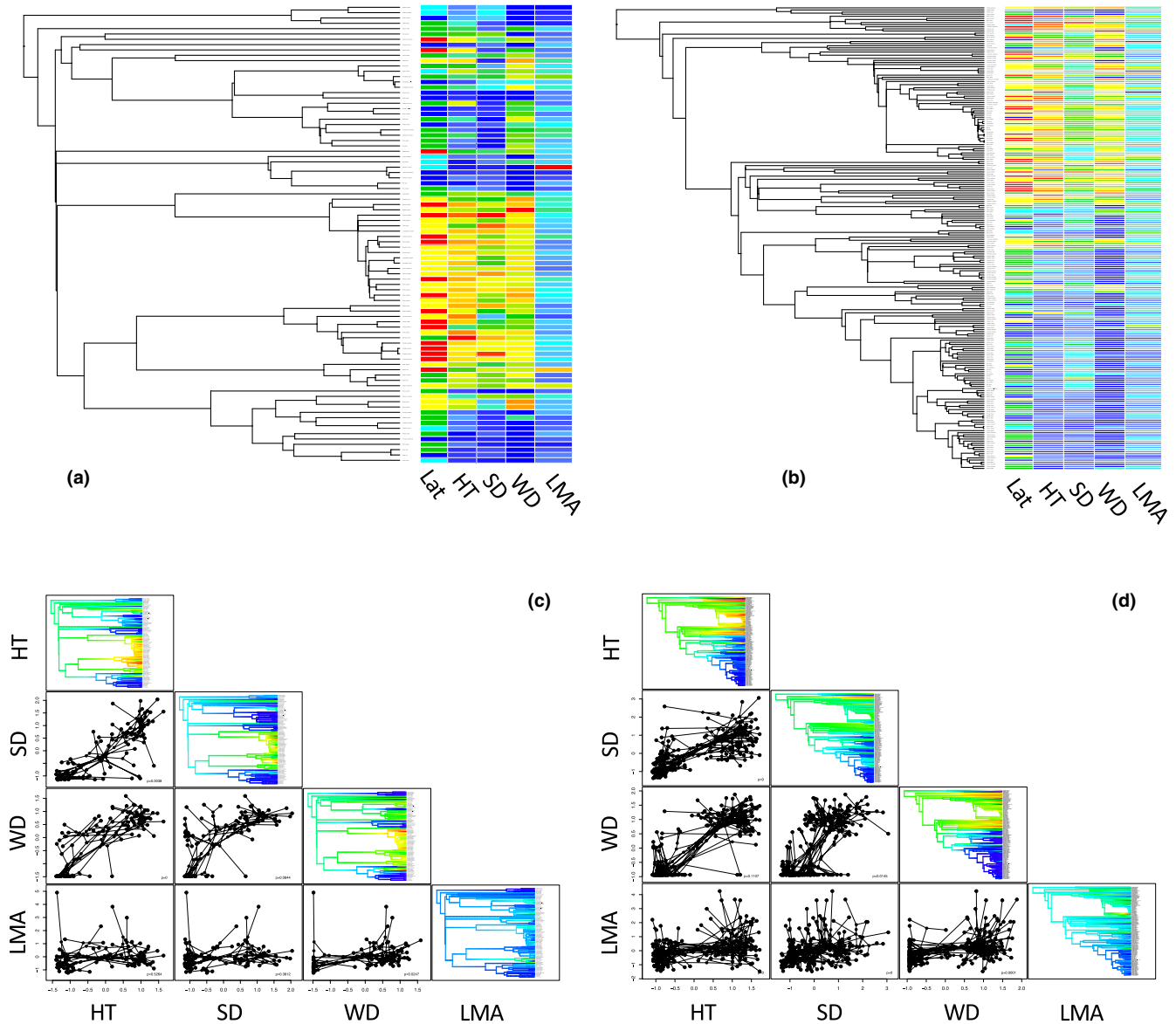
latitudinal category), tropical Fabales typically were clustered in the phylogeny, whereas tropical Ericales were distributed throughout multiple clades. The overall effect was that Ericales trait syndromes generally corresponded to Linnaean families, whereas the Fabales did not fall as easily into typical family or tribe categories (see Section 4).

### 3.3 | Categorizing trait syndromes

Although not every species was represented for every trait (see Section 2), by examining multiple traits across each plant clade, the correspondence between phylogeny and functional trait values suggested clades could be categorized by trait syndromes (Figure 5a,b). In general, the phylogenies showed that clusters of species exhibited shared suite of traits, indicating phylogenetic conservatism of this functional trait syndrome. LMA is an exception to this pattern, appearing instead as a 'barcode' pattern with very little relationship to phylogeny (Figure 5a,b). This trait syndrome was quantified using phylogenetic principal components analysis (pPCA; Figure 6). For both clades, the first two principal components (PCs) accounted for over 88% of the total variance, although we include the first three here (>95% variance explained; Figure 6). For Fabales, tropical and subtropical species clustered separately from temperate and boreal species, and this separation is visible in all three PCs, suggesting two broad trait patterns at the transition from tropical to temperate latitudes. For Ericales, there was greater separation between temperate taxa and those found in boreal latitudes (3 groups). Thus, the manifestation of the trait syndrome differs between these two clades (see Section 4).

We also examined the evidence for correlated evolution of functional trait values. We illustrated this graphically in Figure 5c,d, where phylogenies are mapped onto the trait space of each pairwise trait combination. For many trait combinations, there was a visually apparent correlation between the traits examined. Furthermore, we utilized PGLS to ask whether or not these correlations were significant *beyond* what we would expect under a Brownian motion model of trait evolution (*p*-values in lower right corner of each plot). Most, but not all, PGLS correlations were found to be significant. LMA, in particular, did not show evidence of correlated evolution.



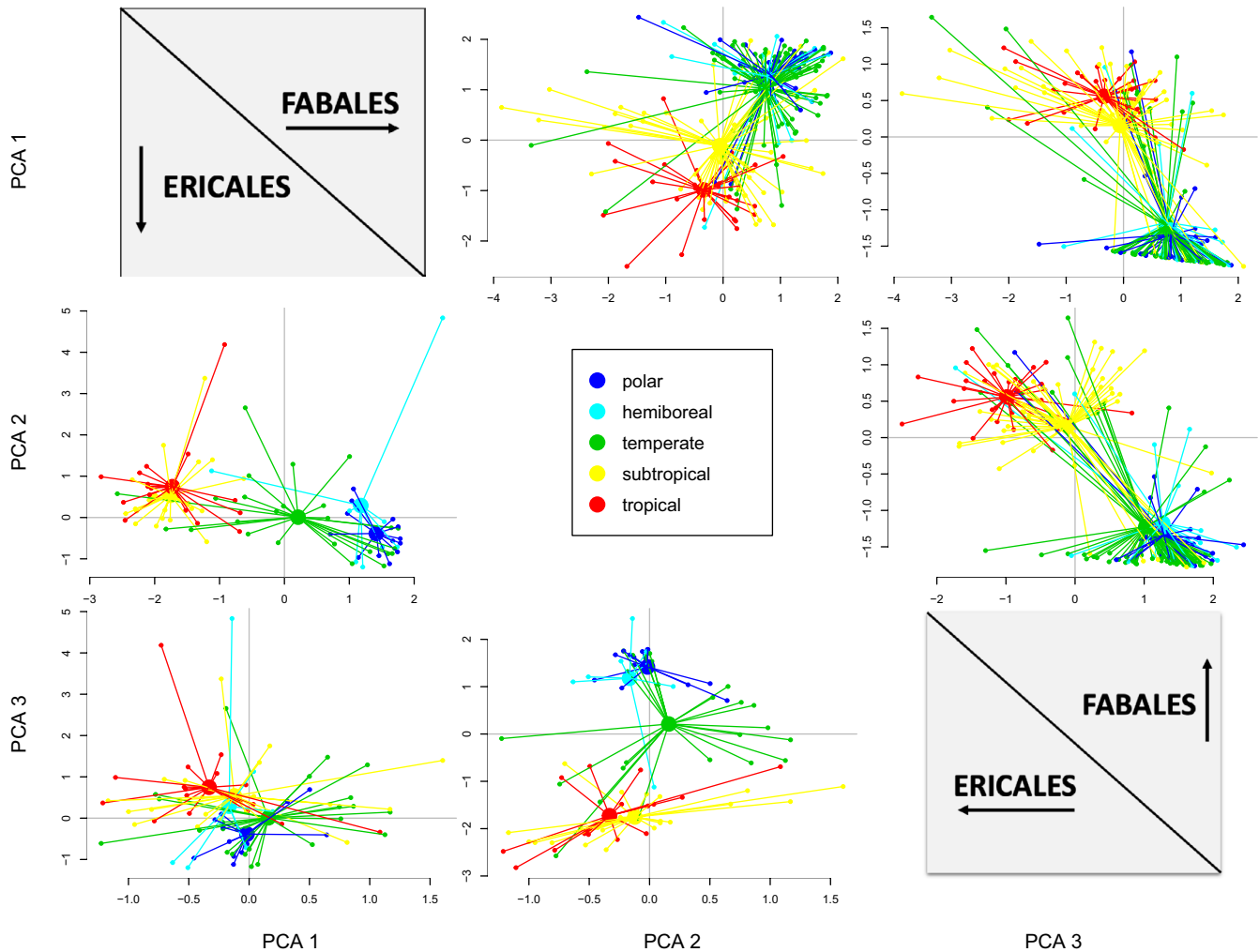


**FIGURE 5** Top panels: Phylogenetic heatmaps for (a) Ericales and (b) Fabales taxa for which complete trait information is available, indicating a conserved trait syndrome. The first column of trait values (*Lat.*) corresponds to the latitudinal extrema (colours are as in Figures 1 and 3). For functional traits, we include height (*HT*), seed mass (*SD*), wood density (*WD*) and *LMA* here because these traits were used in tests of correlated evolution (bottom panels) and phylogenetic principal components analysis (pPCA, Figure 6). Growth form was excluded in those analyses because it is not an ordinated trait. Colors for each trait are as in the ancestral state reconstructions of Figure 3, and bottom panels of this same figure. In general, but with the exception of *LMA*, species tend to show blocks of trait values consistent with a trait syndrome. This trait syndrome corresponds well to species' assigned latitudinal category. Bottom panels: Tests for correlated evolution among those functional traits depicted in top panels for Ericales (c) and Fabales (d) taxa. The grids show correlations of each pairwise trait combination, with the phylogeny mapped onto the two-dimensional trait space. Along the diagonal of the grid, we plot ancestral state reconstructions for each trait on the phylogenies shown in (a) and (b) above. With the exception of *LMA*, correlations between traits are discernible. We utilized phylogenetic generalized least squares (PGLS) to determine if correlations were significant beyond what would be expected under a Brownian motion model of trait evolution (*p*-values indicated in lower right corners of each plot). Correlations with *LMA* were generally not significant, whereas other correlations were. Although relatively few species have sufficient trait data to allow for these comparative methods, this is consistent with correlated evolution of these traits – thus, indicating that the relative trait values defining the syndrome we describe here might have evolved in concert [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Our results suggest that clades possess a shared suite of functional trait values that may have evolved in a correlated manner, although greater coverage of these functional traits would help strengthen this claim.

### 3.4 | Bioregion mapping and trait distributions

In addition to latitudinal categories, for those species with complete functional trait information, we also allowed species' ranges



**FIGURE 6** Phylogenetic principal components analysis (pPCA) among height, seed mass, wood density and LMA, for Ericales and Fabales taxa (as indicated by arrows in the plot). Growth form was excluded in the ordination because it is not an ordinated trait. For both clades, the first two principal components capture > 88% of the total variance, but we include the first three components here (>92% total variance). Small points indicate individual species, while larger circles indicate centroids of each group. The groups are coloured based on latitudinal category (colors are as in Figure 1). For both Ericales and Fabales, species within different latitudinal categories cluster separately in the composite trait space. This is consistent with the latitudinally graded multi-trait syndrome we describe here. However, there are differences between the two clades. Fabales shows two main clusters, with tropical and subtropical species clustering separately from temperate, hemiboreal and polar ones. Ericales, however, shows greater separation between temperate and hemiboreal/polar taxa (three clusters). Thus, the manifestation of the trait syndrome differs between these two groups [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

to define biogeographical clusters (see Section 2), which in turn might be expected to use different functional-trait strategies. For both clades, we obtained a similar number of clusters (Ericales: 11; Fabales: 10), and clusters converged on similar geographic regions (Figure S6). When measuring average trait values among all species assigned to each cluster, we found that clusters tended to exhibit consistent trait patterns (e.g. all low or all high trait values, excepting LMA, as in above analyses; insets of Figure S6). Additionally, geographically adjacent regions tended to exhibit similar trait values. Seed mass, however, showed an abrupt transition dividing tropical clusters (large average seed mass) from extra-tropical (low average seed mass) ones. Both trait data limitations and sparse sampling from certain regions (e.g. southern South America) influenced the

biogeographical clusters obtainable in this analysis and enhanced data collection should continuously update and refine the clusters, thus, identified.

#### 4 | DISCUSSION

Our results provide evidence among New World Ericales and Fabales of a latitudinally graded (Figures 1 and 2) and phylogenetically conserved (Figures 3–5) functional-trait syndrome involving height, seed mass, wood density and growth form, but not LMA. Moving poleward, species tend to exhibit progressively shorter stature, smaller seeds, lower wood density and become predominantly

herbaceous or shrubby. pPCA for those taxa with complete trait data suggest that this trait syndrome can be classified based on the clustering of species into separate groups in trait-space (Figure 6). Additionally, the comparative analyses provide evidence that the life-history traits involved in this syndrome may have evolved in a correlated manner (Figure 5c,d).

Our results also highlight quantitative, clade-specific, differences in the manifestation of this syndrome, illustrating the need for targeted phylogenetic approaches and examining potential patterns at different phylogenetic scales. While previous studies have made strides in examining broad intersections of ecological function and plant traits, they have typically incorporated phylogeny in a limited sense (e.g. Swenson et al., 2012), or used an extremely broad phylogenetic scale (e.g. Zanne et al., 2014). However, just as ecological studies have gained appreciation for the appropriate choice of spatial scale in study design, choice of phylogenetic scale can also be an important decision. To observe variation in the trait syndrome we describe here required looking beyond the level of congeners, which, for those traits we examined, tended to have very similar trait values, and our results suggest that comparisons of species sampled from con-ordinal families provided the best scale at which this trait syndrome could be quantified.

The importance of scale can be illustrated by examining seed mass measurements. If Fabales and Ericales seed mass measurements are lumped together, latitudinal differences among species whose ranges extend to temperate, boreal and polar areas are largely obscured due to the statistically significant differences in average seed mass between the two groups (Figure S1). There are also clade-specific differences in plant height among taxa within the same latitudinal category. For example, among polar-latitude species, Fabales are significantly taller than Ericales ( $p < 0.05$ , Figure 1, compare blue boxes), but at temperate latitudes, the situation is reversed and Ericales are taller ( $p < 0.05$ , Figure 1, compare green boxes). In Figure S3, we show that, at polar latitudes Ericales occur at sites with lower average temperature and higher average elevation than Fabales. In contrast, in temperate regions, Ericales tend to occur at sites with lower average elevation and higher average precipitation. These differences in how taxa are distributed according to smaller-scale climatic factors that might help explain some of the clade-specific differences in the manifestation of the trait syndrome described here, particularly height and seed mass. We also note that other trait syndromes might be best observed at quite different phylogenetic scales. For instance, the disparity in traits relating to chemical defence against herbivory among co-occurring congeneric species of *Inga* is known to be quite high (Sedio et al., 2018). Thus, careful and study-specific choice of phylogenetic scale can be important in teasing out processes of interest.

Unlike Ericales (Asterids), Fabales (Rosids) are part of the nitrogen-fixing clade (Friis et al., 2011), and form root nodules in association with Rhizobia bacteria to fix atmospheric nitrogen. Furthermore, in higher-latitude environments, Fabales tend to preferentially produce indeterminate nodules, whereas determinate nodules are

utilized more in tropical forests (Sprent, 2009). Thus, Fabales taxa show a distinct high-latitude nitrogen-fixing phenotype. It is possible that such differences in the nitrogen-fixation mode also contribute to differences in how these two clades manifest this trait syndrome and how they are arrayed along elevational and precipitation gradients, particularly at higher latitudes, where nitrogen may be more limiting (Reich & Oleksyn, 2004).

Although we focused on latitudinal categories for species, we also clustered species into bioregions using the InfoMap algorithm (see Section 2; Figure S6; Edler et al., 2016). That both Ericales and Fabales species clustered into a similar number of roughly geographically convergent bioregions could suggest these regions represent areas with distinct ecological strategies. Indeed, the functional trait values for height, seed mass and wood density within each bioregion tended to coincide with the presence of the functional trait syndrome we describe here, and LMA showed little relationship with any of the bioregions. Geographically proximate bioregions tended to have similar trait values, suggesting that clustering species by bioregions supplemented rather than supplanted the latitudinally based analyses, and that both methods of organizing species illustrate the occurrence of a similar trait syndrome. Clade-specific differences were also apparent in the bioregions analysis. Most notably, tropical Ericales were divided into two bioregions, whereas tropical Fabales formed a single, large cluster.

The manifestation of this trait syndrome, occurring under a variety of geographically based delimiting methods, could have originated under a variety of scenarios. For instance, this trait syndrome may represent a resource acquisition strategy whose manifestation is primarily influenced by soil nutrient availability and growing season length (i.e. the time in which available nutrients can be utilized). In particular, we note that, at higher latitudes, the manifestation of this trait syndrome is qualitatively similar to the suite of traits associated with 'pioneer', or early successional-stage, tropical species (e.g. smaller stature, lower seed mass, LMA and wood density; Wright et al., 2010). 'Pioneer', here, refers to those plants that colonize disturbed patches or gaps first and display enhanced growth rates under favourable conditions. In tropical soils, nutrient availability is generally lower than at higher absolute latitudes (Reich & Oleksyn, 2004). Treefall gaps can help to unlock some of these nutrients and make them available for early colonizers employing a resource-acquisitive strategy. As succession proceeds, plant growth within the gap again sequesters those nutrients and the manifestation of the resource-acquisition strategy changes, typically characterized by taller stature trees with larger seeds and higher wood density.

At higher latitudes, soil nutrients are relatively more abundant than in tropical soils (Reich & Oleksyn, 2004), and recent glaciation cycles have further helped to enhance deposition of these nutrients (Chadwick et al., 1999; Van Andel, 1994). However, also at progressively higher latitudes, the incident angle of light changes, resulting in a shorter effective growing season for plants. This, in turn, limits the time over which plants can utilize these available



nutrients, and might favour a more resource-acquisitive strategy in these areas as well. The effects of light seasonality are latitudinally graded and would pre-date the onset of global cooling in the Eocene (Graham, 2011). Additionally, temperature seasonality imposes limits on growing-season length at higher latitudes, favouring a more resource-acquisitive strategy as well.

The manifestation of the trait syndrome we describe, and its similarity to a tropical pioneer species strategy, might, therefore, be explained as a strategy to deal with both light and temperature seasonality in a relatively nutrient-rich environment with a short growing season. This trait syndrome could have arisen in several different ways. For example, it may have originated through the dispersal of tropical pioneer lineages pre-adapted to have a more resource-acquisitive strategy. Or it might have arisen independently at higher latitudes in response to light seasonality prior to the onset of global cooling, when the flora at such latitudes consisted of both boreal and tropical elements (e.g. boreotropical forests; Dick & Pennington, 2019; Graham, 2011). Under this hypothesis, lineages found in colder environments might represent longer-lasting endemics of past, non-analogous biomes, whose ecological strategies for addressing light seasonality became advantageous for temperature seasonality as well. Since light seasonality pre-dates global cooling, and a similar trait syndrome occurs among tropical pioneers, where cold tolerance is not a factor, it may be that the higher-latitude trait syndrome we observe is not a direct cold adaptation per se. Further work investigating timing of shifts in trait values with the biogeographic history of lineages undergoing those shifts would be invaluable to tease apart these scenarios or discover alternative explanations.

Our ability to describe the correlated evolution among this collection of (rather than individual) traits was limited significantly by data availability. In particular, wood density measurements were primarily for tropical tree species, and the extreme southern latitudes of South America and regions of the Amazon basin suffered from relatively poor species sampling. Given the destructive and labour-intensive methodology required for obtaining wood density, it is perhaps unsurprising that this trait would be limiting. However, greater sampling of temperate and boreal wood densities for angiosperm species would have greatly enhanced our dataset. We suggest that as an avenue for further data collection, along with greater species sampling at extreme southern latitudes for Ericales and Fabales.

## 5 | CONCLUSION

We suggest the tendency for a biogeographically consistent and phylogenetically conserved functional trait syndrome involving height, seed mass, wood density and growth form (and excluding LMA) among Ericales (Asterids) and Fabales (Rosids) New World taxa. By focusing on specific lineages, we are able to illustrate that variation in this trait syndrome is best observed by sampling species from con-ordinal families. Quantitative differences in the

manifestation of this trait syndrome among Ericales and Fabales taxa occurring in similar regions highlight the importance of matching phylogenetic scale with the research question(s) and pose potential new research avenues. We interpret the manifestation of this trait syndrome at higher latitudes as a resource-acquisitive strategy adapted to relatively high soil nutrient content coupled with a short growing season, a situation somewhat analogous to that faced by gap specialists in tropical forest communities which exhibit a similar suite of traits.

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## DATA AVAILABILITY STATEMENT

Species lists, subtrees and trait tables are available for download from Dryad Digital Repository: <https://doi.org/10.5061/dryad.wdbrv15mg>.

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## BIOSKETCH

**Hector Figueroa** endeavours to understand how historical contingency and physiological constraint drive current patterns of phenotypic distribution. Leveraging a background in biochemistry and physiology, he asks community assembly questions bridging ecology and evolutionary biology. By incorporating phylogeny and natural history into ecological hypotheses, questions of coexistence and biodiversity can be framed in biologically meaningful ways. His current research focuses on the distribution of angiosperm life-history traits across the Americas in relation to survival in extreme environments, such as polar climates, alpine summits, and arid deserts.

**Stephen A. Smith** aims to better understand the evolution of innovation and complexity in plants and how those changes intersect with molecular evolution. This often requires working with new data types as well as the development of new approaches and techniques. Currently, his research focuses on the evolution of several large eudicot lineages and how movements into new environments correspond to morphological and genomic changes.

Author contributions: H.F. conceived of the study and analysed the data. H.F. and S.A.S. collected some of the data. H.F. wrote the first draft of the manuscript. H.F. and S.A.S. contributed to editing and revising the final version of the manuscript.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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