

# Phylogeny more than plant height and leaf area explains variance in seed mass

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## Abstract

Although the leaf-height-seed (LHS) scheme states that plant height and leaf area are closely correlated with seed mass; phylogeny, genome size, growth form, and leaf N may also explain variations in seed mass. Till now, there has been little information on the relative contributions of these factors. We compiled data consisting of 1071 plant species from the literature to quantify the relationships between seed mass, explanatory variables and phylogeny. Strong phylogenetic signals of these explanatory variables reflected inherited ancestral traits of the plant species. Without controlling phylogeny, growth form and leaf N are associated with seed mass. However, this association disappeared when accounting for phylogeny. Plant height, leaf area, and genome size showed consistent positive relationship with seed mass irrespective of phylogeny. Using partial R<sup>2</sup>s, phylogeny explained 50.89% of the variance in seed mass, much more than plant height, leaf area, genome size, leaf N, and growth form explaining only 7.39%, 0.58%, 1.85%, 0.06% and 0.09%, respectively. Our study is the first to disentangle the contributions of phylogeny and plant attributes to the variance in seed mass, providing a novel avenue for better understanding variation in traits across plant species.

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**Authorship statement**

XY conceived and designed the study. FY, YW and YN-W compiled the dataset. FY, and YW analyzed the data. XY, HZ and FY wrote the manuscript. All authors reviewed the final manuscript.

## Data accessibility

Compiled datasets in Appendix S1 in the Supplementary Material are archived in Figshare and can be accessed freely at [10.6084/m9.figshare.21270249](https://figshare.com/10.6084/m9.figshare.21270249).

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## Conflict of interests

The authors declare no competing interests.

## Abstract

Although the leaf-height-seed (LHS) scheme states that plant height and leaf area are closely correlated with seed mass; phylogeny, genome size, growth form, and leaf N may also explain variations in seed mass. Till now, there has been little information on the relative contributions of these factors. We compiled data consisting of 1071 plant species from the literature to quantify the relationships between seed mass, explanatory variables and phylogeny. Strong phylogenetic signals of these explanatory variables reflected inherited ancestral traits of the plant species. Without controlling phylogeny, growth form and leaf N are associated with seed mass. However, this association disappeared when accounting for phylogeny. Plant height, leaf area, and genome size showed consistent positive relationship with seed mass irrespective of phylogeny. Using partial  $R^2$ s, phylogeny explained 50.89% of the variance in seed mass, much more than plant height, leaf area, genome size, leaf N, and growth form explaining only 7.39%, 0.58%, 1.85%, 0.06% and 0.09%, respectively. Our study is the first to disentangle the contributions of phylogeny and plant attributes to the variance in seed mass, providing a novel avenue for better understanding variation in traits across plant species.

**Keywords:** seed mass, plant height, leaf area, genome size, leaf N, growth form, phylogeny

## Introduction

Seed mass, a key ecological trait that affects many aspects of plant ecology (Moles et al., 2005a, b; Mason et al., 2008), has great influences on the regeneration strategies of plants, including seed output for a given amount of energy, seed dispersal and seedling survival (Leishman et al., 2000). Variation in seed mass reflects the fundamental trade-off between seed number and seed mass (Henery & Westoby, 2001) and between seed mass and persistence in the seed bank (Thompson et al., 1993). An increasing body of evidence has shown that large-seeded species produce less seeds than those bearing small seeds (Henery & Westoby, 2001; Moles et al., 2004). Compared to small-seeded species, large-seeded species are more likely to produce large seedlings that are supposed to survive better than small seedlings under a variety of hazardous environments (Armstrong & Westoby, 1993; Leishman & Westoby, 1994a, b; Burke & Grime 1996; Westoby et al., 1996, 2002; Harms & Dalling, 1997; Leishman et al., 2000; Dalling & Hubbell, 2002; Moles & Westoby, 2004; Dainese & Sitzia, 2013). Despite the advantages associated with large seeds, seed masses of present-day species have been observed to range over 11.5 orders of magnitude, from the 0.0001-mg dust-like seeds of orchids to the 20-kg seeds of the double coconut (Michelle et al., 1995). Therefore, to reveal the internal mechanism and influencing factors of the changes in seed mass will help us to better understand the ecological history of plants.

As proposed by the leaf-height-seed (LHS) scheme of plant ecology strategy (Westoby, 1998), plant height and leaf area are closely correlated with seed mass. As a crucial component of a plant species' ecological

strategy, plant height not only determines a plant's ability to compete for light but also a species' carbon gain strategy, which is supposed to play an important role in another life-history trait, seed mass (Moles & Leishman, 2008). A pioneering study by Levin (1974) found that the mean seed mass of 832 plant species increase along the growth form: herbs, shrubs, vines, shrubby trees, and trees. Leishman et al. (1995) showed that seed masses are consistently correlated with plant height across 1659 species, representing a worldwide flora. Carly et al. (2009) found positive linear correlations between plant height and seed mass of 15 species at the community level in the northeast Galilee region of Israel. Moles et al. (2004) analyzed the trait data of 2026 species across 150 families and revealed a positive correlation between seed mass and plant height, representing large-scale evidence for the relationship between seed mass and plant height. However, Grime et al. (1997) found no significant correlation between plant height and seed mass across 43 common British species. Thompson & Rabinowitz (1989) analyzed 816 plant species around Sheffield and found significant relationships between seed mass and plant height within some families (Poaceae, Caryophyllaceae, Asteraceae and Fabaceae), but not in other taxa like Scrophulariaceae, Apiaceae, Lamiaceae, *Calophyllum*, *Pinus*, and *Quercus*. In a southeastern Sweden flora, seed mass was only marginally correlated with plant height of 126 species (Bolmgren & Cowan, 2007). Rees (1996) analyzed 382 species of Sheffield flora and found that the relationship between seed mass and plant height is inconsistent and dependent on dispersal modes. Therefore, much uncertainty still remains to be tackled possibly due to the limitation of plant species sampled in previous studies, although plant height has been considered one of the strongest correlates of seed mass (Leishman et al., 1995; Moles et al., 2004).

As the main organ of plants that contributes to photosynthesis (Bazzaz et al., 2000), leaves act as a key determinant of the amount of energy available for reproduction (Wright et al., 2004). Although leaves may vary in their traits (e.g., area, morphology, anatomy, physiology and N nutrition) in response to growing conditions (Givnish, 1987; Witkowski & Lamont, 1991; Ackerly & Reich, 1999; Cornelissen et al., 2003; McDonald et al., 2003; Xu et al., 2009; Milla & Reich, 2011), a strong connection between total leaf mass and net annual reproductive biomass has been observed (Niklas & Enquist, 2002, 2003). Therefore, the ecological significance of leaf traits may relate to resource capture in productive organs, implying that leaf area and seed mass should be positively correlated (Westoby & Wright, 2003). Midgley & Bond (1989) found that leaf area was positively correlated to cone size in 18 species from the *Leucadendron* genus in South Africa. Hodgson et al. (2017) also found positive linear relationships between leaf area and seed mass of 2400+ species from England and Spain. Although it was not specifically stated in the studies by Laughlin et al. (2010), seed mass appears to be positively correlated with leaf area of 133 plant species in northern Arizona, USA. Rather than a linear relationship, Cornelissen (1999) showed a triangular relationship between leaf area and seed mass of 58 woody species from Europe. Recently, Santini et al. (2017) showed that the triangular relationship also holds for 401 annual plants belonging to 37 families from the United Kingdom. However, Westoby & Wright (2003) failed to find the triangular relationship between leaf area and seed mass as reported by Cornelissen (1999), indicating that the pattern seems not universal between seed mass and leaf area.

In addition, seed mass is not independent of growth form, which is often a predictor of other plant traits (Moles et al., 2005a, b). Plant growth form, like seed mass, may also be phylogenetically controlled (Li et al., 2017). Evidence has shown that woody plants are more likely to have larger seeds, while non-woody species are more likely to produce small seeds (Jurado et al., 1991). Therefore, the phylogenetic conservatism of plant growth form might have an indirect impact on the variations in seed mass. Furthermore, genome size appears to be one of the most studied factors that are related to variations in seed mass. Although there is no significant linear regression relationship between genome size and seed mass across 1222 species from 139 families and 48 orders of seed plants, Beaulieu et al. (2007) found that species with very large genome sizes never had small seeds. Therefore, apart from the influence of plant height and leaf area, phylogeny, growth form and genome size may also contribute to seed mass variations.

Phylogenetic conservatism in plant traits has been well studied (Wiens et al., 2010; Baskin & Baskin, 2014; Cornwell et al., 2014; Tozer et al., 2015) and such studies are helping to illuminate the role of the evolutionary past in determining the characteristics of species. Seed mass has been accepted as an ecologically important

trait phylogenetically constrained within local floras. This may also be true for plant height and leaf area. Therefore, it should be obligatory to extract variations in plant traits associated with phylogeny, before analyzing relationships between seed mass and other plant ecological attributes, e.g., growth form, plant height, and leaf area. However, the potential influence of phylogeny on the leaf-height-seed (LHS) plant ecology strategy scheme has not previously been well evaluated (Cornelissen, 1999; Laughlin et al., 2010; Hodgson et al., 2017).

Despite previous data on the relationship between plant traits across the world, published literature failed to incorporate phylogeny and plant traits into the analysis of the variations in seed mass (Chase & Pippen, 1990; Mustart & Cowling, 1992; Lord et al., 1995; Kang & Primack, 1999; Zhang et al., 2004; Vandelook et al., 2018). The rapid accumulation of databases on plant traits provides us an ideal opportunity to illustrate a general pattern of the relationship between plant traits, which helps us to have a better understanding of the leaf-height-seed (LHS) plant ecology strategy scheme. In the present study, we first used phylogenetic partial  $R^2$ s (Ives, 2019) to tease apart the effects of multiple plant traits (plant height, leaf area, genome size, growth form and leaf N) and phylogeny, to quantify extent to which they contribute to variations in seed mass of plant species when each predictor variable and the phylogeny is removed one-by-one.

## Materials and Methods

### Data collection

Plant traits were derived from the large currently available databases (Kattge et al., 2020; Royal Botanic Gardens Kew, 2022) and the published literature (Westoby & Wright, 2003; Diaz et al., 2016; Santini et al., 2017). We took advantage of big data and compiled a global dataset containing 1071 species, 553 genera, 136 families. Plant traits included: 1) seed mass ( $\text{mg seed}^{-1}$ ), plant height (m), genome size (1C, pg), leaf area ( $\text{mm}^2$ ), leaf N ( $\text{mg/g}$ ), and growth form. The growth form was split into two functional groups: “woody” and “non-woody”. We obtained 404 woody and 667 non-woody species with known trait values. Following Westoby (1998), all variables were log10-transformed prior to analysis to correct for skewness in trait distributions because trait values can vary by several orders of magnitude, and are often lognormally distributed between species. A full list of species, data and data sources was provided in Appendix S1 in the Supplementary Material.

### Phylogenetical signal

Phylogenetic signal in seed mass, plant height, leaf area, growth form and leaf N was constructed from a mega-tree (GBOTB.extended.tre) containing 10587 genera and 74533 vascular plant species. This mega-tree is the largest phylogeny for vascular plants so far (Zanne et al., 2014; Smith & Brown, 2018). The R package ‘V. PhyloMaker’ was used because it can generate very large phylogenies for vascular plants at a relatively fast speed (Jin & Qian, 2019). Species names in this study were standardized to The Plant List v.1.1 (<http://www.theplantlist.org/>).

Pagel’s lambda ( $\lambda$ ) estimates the strength of phylogenetic signal in a continuous trait, therefore, we calculated Pagel’s  $\lambda$  to quantitatively estimate if the similarity of seed mass, plant height, genome size, leaf area, and leaf N among species is correlated with the phylogenetic similarity of plant species. We utilized a randomization test by running the package ‘phytools’ (Revell, 2012) in R to test for the significance of  $\lambda$ . In our study, Pagel’s  $\lambda$  can range from 0 to 1, with a  $\lambda$  of 0 indicating no phylogenetic signal and whereas a  $\lambda$  of 1 indicating the strongest phylogenetic signal (Pagel, 1999).

We tested the strength of the phylogenetic signal in growth form using the D statistic that is for binary traits (Fritz & Purvis, 2010), using the package ‘caper’ in R (Orme et al., 2013). Growth form of the 1071 species is supposed to come from the time of their independent evolution if the D is not significantly different from 0 ( $P_{\text{Brownian}} > 0.05$ ). Whereas, if D value is equal to or not significantly different from 1 ( $P_{\text{random}} > 0.05$ ), which indicates that the interspecific differences in growth form are distributed randomly across a phylogenetic tree.

### Statistical analysis

All analyses were conducted in R (R Development Core Team, 2021). As plant traits vary with growth form, we analyzed for differences in plant traits between woody and non-woody species after accounting for growth form. We employed the general linear model to detect the differences in seed mass, plant height, genome size, leaf area, leaf N between plant species with different growth forms (woody vs non-woody). We also constructed generalized linear model (GLM) to see the association between seed mass, plant height, growth form, genome size, leaf area and leaf N across plant species and groups, with the seed mass as dependent variable and other plant traits as independent variables. To investigate which plant traits were more important to variations in seed mass across plant species, we applied a multi-variable phylogenetic generalized linear mixed model (PGLMM) to incorporate phylogenetic information and then correct for phylogenetic effects among species, as closely related organisms are more likely to share similar biological traits. We used a Gaussian distribution with phylogenetic trees, implemented in the R packages ‘phyr’ and ‘ape’ (Paradis & Schliep, 2019; Li et al., 2020). We considered plant height, leaf area, genome size, growth form and leaf N as predictor variables, seed mass as the response variable and phylogeny as a random intercept.

To tease apart the relative contributions of plant traits and phylogeny to the variation in seed mass of the plant species, we used partial  $R^2$ s for the logistic regression model (Ives, 2019) implemented by the R package ‘rr2’ (Ives & Li, 2018). The partial  $R^2_{\text{lik}}$  for each factor was calculated by comparing the full model with reduced models in which a given factor was removed, and measuring the consequent reduction in the likelihood (Wang et al., 2022).

## Results

By analyzing worldwide variation in several plant traits, we found strong and statistically significant phylogenetic signal of seed mass, plant height, genome size, leaf area, leaf N and growth form across the plant species ( $\lambda = 0.976$ ,  $P < 0.001$ ;  $\lambda = 0.964$ ,  $P < 0.001$ ;  $\lambda = 0.956$ ,  $P < 0.001$ ;  $\lambda = 0.883$ ,  $P < 0.001$ ;  $\lambda = 0.771$ ,  $P < 0.001$ ;  $D = -0.190$ ,  $P_{\text{random}} = 0$ ,  $P_{\text{Brownian}} = 0.982$ ; Fig. 1 and 2), showing that plant traits covary in direct proportion to their shared evolutionary history.

General linear model showed that seed mass and plant height were higher in the woody plants than in the non-woody species ( $t = -6.676$ ,  $P < 0.001$ ;  $t = -38.42$ ,  $P < 0.001$ ; Fig. 3a, b). Although there was a trend for woody plants to have larger genome size and leaf area than non-woody species, this was not significant ( $t = 0.735$ ,  $P = 0.462$ ;  $t = 0.595$ ,  $P = 0.552$ ; Fig. 3c, d). However, leaf N was lower in the woody plants than in the non-woody species ( $t = 8.782$ ,  $P < 0.001$ ; Fig. 3e).

Without controlling phylogeny, we identified statistically significant relationships between seed mass and plant height across 1071 species based on multi-variable generalized linear model ( $t = 3.299$ ,  $P = 0.001$ ; Table 1). Although seed mass and leaf area were positively correlated ( $t = 6.961$ ,  $P < 0.001$ ; Table 1), we detected significant interactive effect of plant height and leaf area on variations in seed mass ( $t = 2.204$ ,  $P = 0.028$ ; Table 1). Significant relationship was found between seed mass and genome size ( $t = 5.034$ ,  $P < 0.001$ ; Table 1) but not between seed mass and leaf N in the absence of phylogeny ( $t = 1.646$ ,  $P = 0.099$ ; Table 1). Growth form, however, well predicted variations in seed mass across the plant species ( $t = 5.784$ ,  $P < 0.001$ ; Table 1).

In analysis that controlled for the phylogeny, plant height, leaf area, and genome size alone appeared to be a reliable predictor of variations in seed mass ( $z = 4.268$ ,  $P < 0.001$ ;  $z = 2.549$ ,  $P = 0.011$ ;  $z = 4.514$ ,  $P < 0.001$ ; Table 1). After correcting for phylogenetic effects, growth form and leaf N failed to predict variations in seed mass ( $z = 0.838$ ,  $P = 0.402$ ;  $z = 0.850$ ,  $P = 0.395$ ; Table 1). There was no significant interactive effect of plant height and leaf area on seed mass in the presence of phylogenetic considerations ( $z = 0.437$ ,  $P = 0.662$ ; Table 1).

Phylogeny explained the vast majority of seed mass variation across the plant species (partial  $R^2_{\text{lik}} = 50.89\%$ ,  $\Delta\log\text{Lik} = 380.8$ ,  $P < 0.001$ ), while plant height, leaf area, genome size explained a minority of variation ( $R^2_{\text{lik}} = 7.39\%$ ,  $\Delta\log\text{Lik} = 41.1$ ,  $P < 0.001$ ;  $R^2_{\text{lik}} = 0.58\%$ ,  $\Delta\log\text{Lik} = 3.1$ ,  $P = 0.01$ ;  $R^2_{\text{lik}} = 1.85\%$ ,  $\Delta\log\text{Lik} = 10.0$ ,  $P < 0.001$ ; Fig. 4). Leaf N and growth form failed to explain the variance in seed mass ( $R^2_{\text{lik}} =$

0.06%,  $\Delta\log\text{Lik} = 0.3$ ,  $P = 0.41$ ;  $R^2_{\text{lik}} = 0.09\%$ ,  $\Delta\log\text{Lik} = 0.5$ ,  $P = 0.33$ ; Fig. 4).

## Discussion

By conducting a meta-analysis of studies of 1071 plant species, our results suggest phylogenetic conservatism for the majority of plant traits tested in this study, i.e., seed mass, plant height, leaf area, genome size, and leaf N, as observed in previous studies (Moles et al., 2005; Swenson & Enquist, 2009; Davies et al., 2013; Wang et al., 2022). This is most likely due to the similar traits of phylogenetically closely related species rather than the similarity of traits at higher taxonomic levels. Apart from phylogenetic signal of these traits, we showed that growth form of the 1071 species was not randomly distributed but followed a Brownian model of trait evolution, indicating that the closely related species are more likely to have similar growth form than might be expected by chance (Kerckhoff et al., 2006). The phylogenetic signal carried by plant growth form may potentially explain the differences in seed mass, plant height, and leaf N between the woody and non-woody plant species.

Previous studies have looked at the patterns of associations of seed mass with other plant traits (Westoby, 1998; Guo et al., 2010; Santini et al., 2017), however, few studies have incorporated phylogenetic affiliations in gauging the correlations between seed mass and several attributes. By controlling phylogeny, plant height appears to be a reliable predictor of seed mass across species based on the results of PGLMM. Although dispersal mode and growth form may modify the pattern of association of plant height with seed mass (Thompson & Rabinowitz, 1989; Leishman & Westoby, 1994c; Leishman et al., 1995), we found consistent positive correlation between seed mass and plant height. The positive relationship between seed mass and plant height may facilitate long-distance seed dispersal because seed dispersal distance is more strongly correlated with plant height than with seed mass (Thomson et al., 2011).

Plant height is also closely related to leaf area (Falster & Westoby, 2003), therefore positive relationships between leaf area and plant height are likely to lead to a positive correlation between seed mass and leaf area. In our study, there were also consistent and positive correlations between seed mass and leaf area, suggesting that the correlations between leaf area and seed mass are conserved across life-forms. These patterns accord well with independently gathered data on the relationship between seed mass and leaf area both in the woody and annual species (Senn et al., 1992; Niinemets & Kull, 1994; Cornelissen, 1999; Santini et al., 2017). The positive relationship between seed mass and leaf area may reflect the great contribution of photosynthetic capacity and nitrogen content of leaves.

The role of the relationship between genome size and seed mass has gained much less attention over the two decades (Moles et al., 2005a, b; Beaulieu et al., 2007). Despite several studies that found a quadratic relationship between genome size and seed mass (Beaulieu et al., 2007; Knight & Beaulieu, 2008; Krahulcová et al. 2017), our GLM and PGLMM models showed positive association between genome size and seed mass across 1017 species. This discrepancy is largely due to the fact that previous studies failed to incorporate phylogeny into this consideration. To understand the forces shaping the evolution of seed mass, we will also need to consider other plant traits, such as leaf N and growth form. Without controlling phylogeny, seed size was associated with growth form and woody plants tended to have larger seeds than smaller herbaceous plants, possibly due to the larger height of woody plants than of herbaceous species (Jurado et al., 1991). However, incorporating phylogenetic affiliations into the model failed to detect the clear association between seed mass and growth form across the plant species, indicating that phylogeny conceals the effect of growth form on the variation in seed mass. This finding may not be in agreement with the observation that variations in seed mass are consistently associated with those in growth form (Mole et al., 2005).

Despite the strong phylogenetic signal in several plant traits, our meta-analysis successfully teased apart the relative contributions of phylogeny, plant height, leaf area, genome size, leaf N and growth form on explaining variations in seed mass across the plant species. We first showed that phylogeny had much more power to explain variations in seed mass than did other plant traits, whereas plant height, leaf area and genome size only explained the minority of these variations although the leaf-height-seed (LHS) scheme states that plant height and leaf area are closely correlated with seed mass (Westoby, 1998). Growth form

and leaf N explained little variation in seed mass, reflecting the main effect of phylogeny on affecting seed mass variation. Therefore, our study suggests that divergences in seed mass have been more closely correlated with phylogeny than with divergences in other plant traits. If this pattern holds equally for plants of different taxa, investigation on the correlations between plant traits should not ignore the contribution of phylogeny.

Together, our results indicate that although there is a significant phylogenetic signal in plant traits (seed mass, plant height, leaf area, genome size, leaf N and growth form), phylogeny appears to explain variations in seed mass better than these explanatory variables. This implies that phylogeny has acted as one of the most important factors that govern the variations in seed mass across plant species. Our work is expected to open the door to further investigate the contributions of phylogeny and explanatory attributes to the variation in given plant traits.

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**Table 1.** Multivariate models (PLGMM and GLM) constructed with seed mass of the 1071 species as response variable.

Model	AIC	Predictor variable	Estimate (SE)	Z	P
PGLMM	1976.6	Intercept	0.614 (0.893)	0.688	0.492
		Plant height	0.409 (0.096)	4.268	<0.001
		Leaf area	0.071 (0.028)	2.549	0.011
		Genome size	0.304 (0.067)	4.514	<0.001
		Leaf N	0.103 (0.121)	0.850	0.395
		Growth form	0.075 (0.089)	0.838	0.402
		Plant height*Leaf area	0.015 (0.035)	0.437	0.662
Model	AIC	Predictor variable	Estimate (SE)	t	P
GLM	2731.5	Intercept	-0.822 (0.233)	-3.522	<0.001
		Plant height	0.330 (0.100)	3.299	0.001
		Leaf area	0.231 (0.033)	6.961	<0.001
		Genome size	0.281 (0.056)	5.034	<0.001
		Leaf N	0.271 (0.165)	1.646	0.099
		Growth form	0.527 (0.091)	5.784	<0.001
		Plant height*Leaf area	0.081 (0.037)	2.204	0.028

### Figure legends

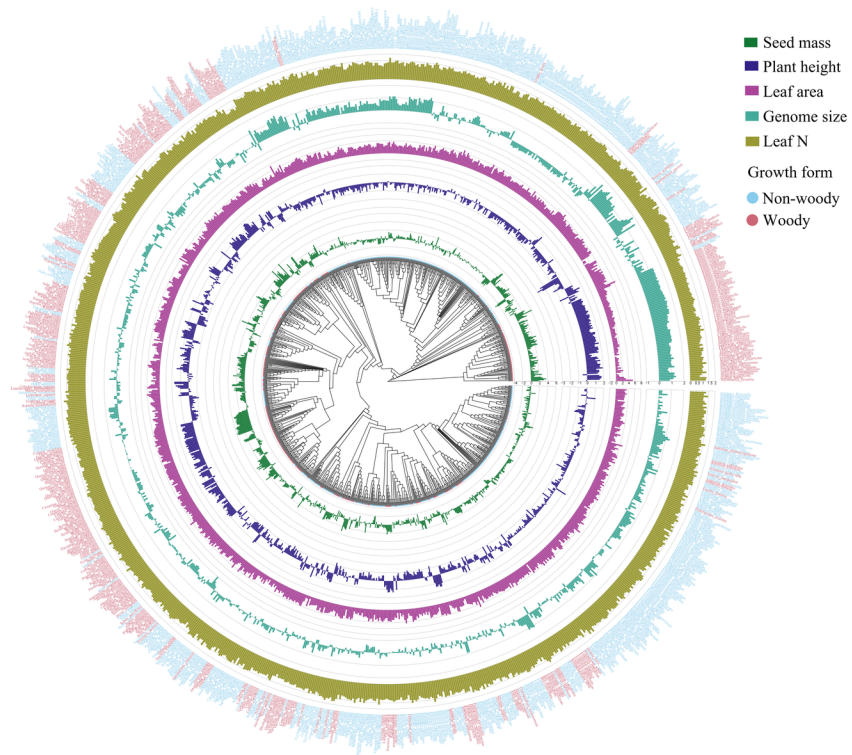
**Fig. 1.** Plant traits (seed mass, plant height, leaf area, genome size, leaf N, and growth form) mapped onto a plant phylogeny. Note that data were log 10-transformed prior to mapping.

**Fig. 2.** Tests of phylogenetic signal in plant traits. A statistically significant phylogenetic signal was detected in seed mass (a,  $\lambda = 0.976$ ,  $P < 0.001$ ), plant height (b,  $\lambda = 0.964$ ,  $P < 0.001$ ), genome size (d,  $\lambda = 0.956$ ,  $P < 0.001$ ), leaf area (c,  $\lambda = 0.883$ ,  $P < 0.001$ ), leaf N (e,  $\lambda = 0.771$ ,  $P < 0.001$ ), and growth form (f,  $D = -0.148$ ,  $P_{\text{random}} = 0$ ,  $P_{\text{Brownian}} = 0.982$ ) of 1071 plant species.

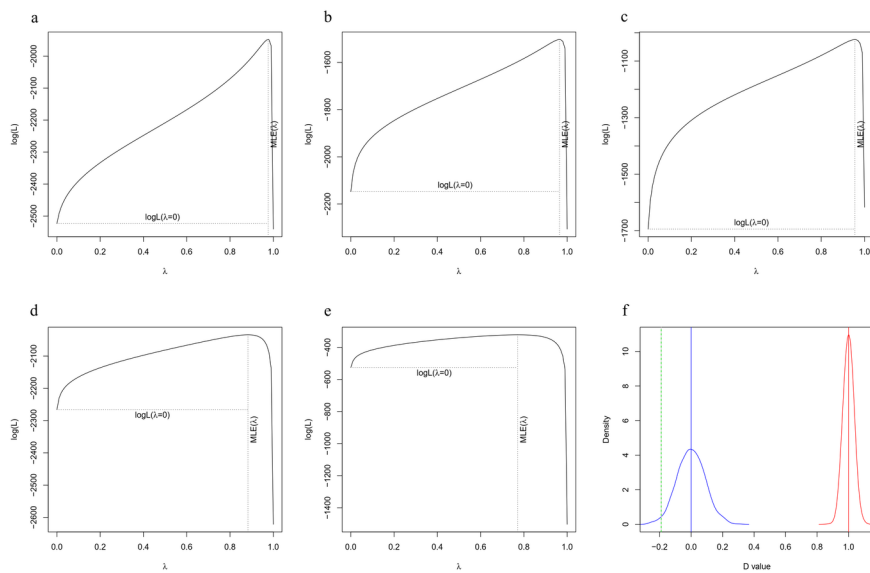
**Fig. 3.** Comparison of seed mass, plant height, leaf area, genome size and leaf N between plant species with different growth forms (woody vs non-woody) derived from general linear model (GLM).

**Fig. 4.** The relative contribution of different factors to the variation in seed mass using partial  $R^2$ s for the logistic regression model.

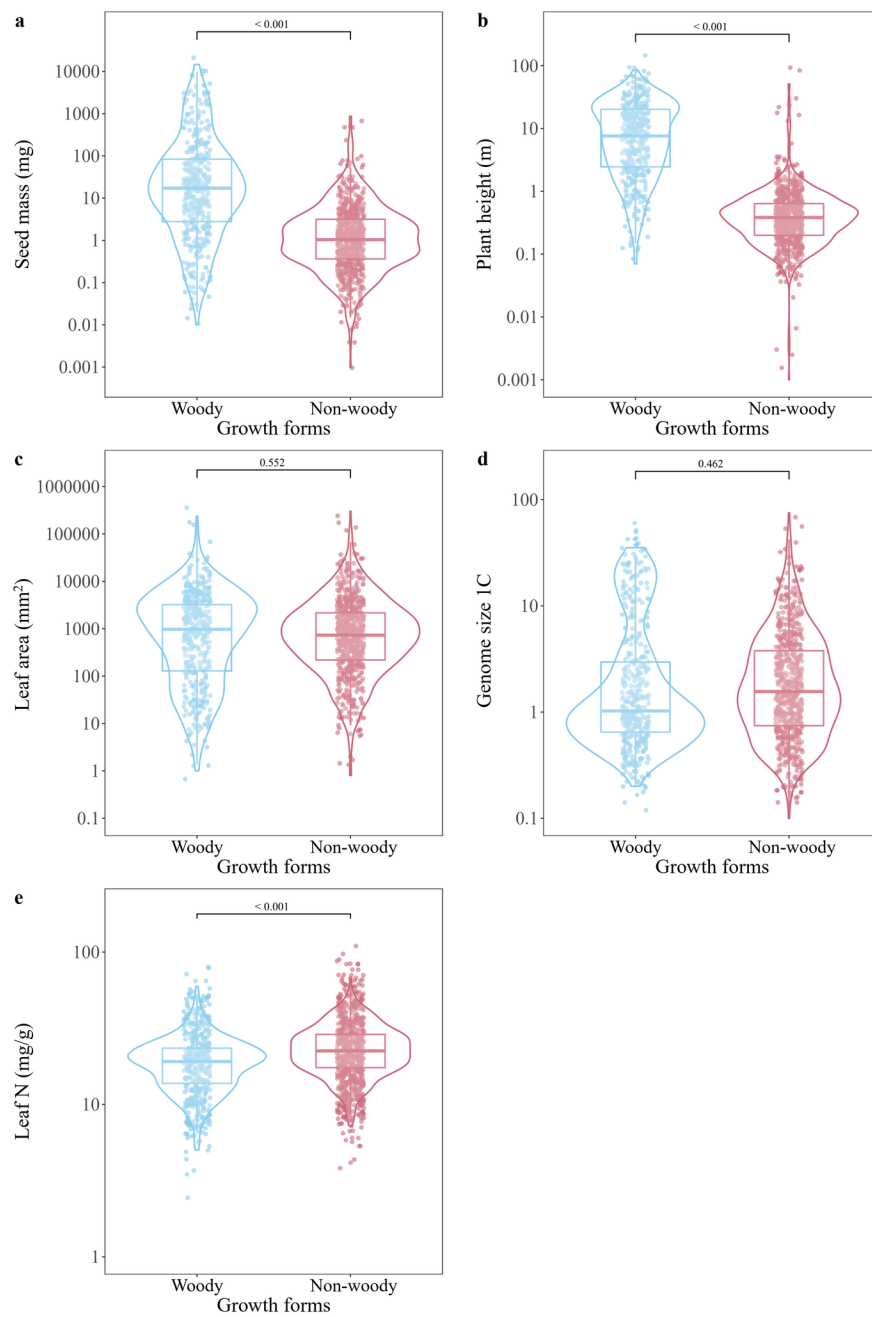
**Fig. 1.**



**Fig. 2.**



**Fig. 3.**



**Fig. 4.**

