

Clade-specific differences in leaf-height-seed strategy scheme

Fei Yu¹, Shijia Fu¹, Yang Wang¹, and Xianfeng Yi²

¹Henan Normal University

²Qufu Normal University

December 6, 2022

Abstract

The leaf-height-seed (LHS) plant ecology strategy scheme posits that functional traits such as leaf size, stem height and seed mass play a key role in life history of plants. Although many studies have explored the LHS scheme across plant species, to our knowledge, no study has so far linked functional trait patterns across different plant clades. Here, we first explored the LHS scheme of several plant clades, i.e., palms, other monocots, dicots and gymnosperms, to understand how potential forces drive variation of plant functional traits. We showed that phylogeny constrains plant functional traits and appears to be the most decisive factor that controls variation in seed mass irrespective of plant clades. Apart from phylogeny, a majority of variation in seed mass was explained by leaf size in palms clade, whereas by plant height in other monocots and dicots. Neither leaf size nor plant height well explained variation in seed mass of gymnosperms clade. Our study strongly suggests that different plant clades exhibit distinct LHS schemes, paving a new avenue for better understanding evolution and correlation between functional traits across sets of plant species.

Title page

Clade-specific differences in leaf-height-seed strategy scheme

Abstract

The leaf-height-seed (LHS) plant ecology strategy scheme posits that functional traits such as leaf size, stem height and seed mass play a key role in life history of plants. Although many studies have explored the LHS scheme across plant species, to our knowledge, no study has so far linked functional trait patterns across different plant clades. Here, we first explored the LHS scheme of several plant clades, i.e., palms, other monocots, dicots and gymnosperms, to understand how potential forces drive variation of plant functional traits. We showed that phylogeny constrains plant functional traits and appears to be the most decisive factor that controls variation in seed mass irrespective of plant clades. Apart from phylogeny, a majority of variation in seed mass was explained by leaf size in palms clade, whereas by plant height in other monocots and dicots. Neither leaf size nor plant height well explained variation in seed mass of gymnosperms clade. Our study strongly suggests that different plant clades exhibit distinct LHS schemes, paving a new avenue for better understanding evolution and correlation between functional traits across sets of plant species.

KEYWORDS

LHS scheme, palms, other monocots, dicots, gymnosperms, phylogeny

INTRODUCTION

Plant functional traits (i.e., plant height, leaf area and seed size) have been considered as potentially powerful indicators of the ecological processes of species, which can also be used as indicators or reference for the maximum information of plant growth and resource utilization strategies (Adler et al., 2013; Kooyima et al., 2010; Navarro et al., 2010; Wilson et al., 1999). Plant traits have become a core attribute to determine plant

strategies and then to understand and predict the evolution, distribution as well as ecological strategies of plant species at the scale of population, community and ecosystem (Chapin et al., 2000; Gaudet & Keddy, 1988; Kunstler et al., 2015), because they directly affect the basic behavior and function of plants, and reflect the survival strategies formed by plants adapting to environmental changes (Ackerly & Cornwell, 2007). Plant strategies can be quantified by measuring various functional characteristics that affect plant fitness and ecological processes (Lavorel & Garnier, 2002). Westoby chose the plant ecological strategy scheme (LHS), i.e., the use of three functional traits (Westoby, 1998), specific leaf area (SLA), plant canopy height and seed mass as representing three fundamental and relatively independent axes of a plant's ecological strategy to classify plants according to meaningful axes of plant specialization (Díaz et al., 2015; Laughlin et al., 2010; Vendramini et al., 2002). Later on, ecologists have carried out a number of studies on the relationship between plant height, leaf area and seed mass (Lavergne et al., 2003; Wang et al., 2014; Wolf et al., 2022), and found consistent relationship between plant traits, which further improves our understanding of plant adaptation strategies (Koch et al., 2004).

Plant traits represent an outcome of evolutionary processes, therefore its distribution reliably reflects their evolutionary history and phylogenetic constrains (Larson et al., 2020; Reinhart et al., 2012; Wang et al., 2008). Phylogenetically related species share a common evolutionary history and may therefore have similar traits (Ibanez et al., 2016; Losos, 2008). Although the whole point of the scheme is that the LHS variables are not necessarily correlated with each other, much of the literature has provided evidence that the correlated evolutionary divergence of traits has led to trait correlations across plant species (Gingerich, 1974; Revell et al., 2008; Xia et al., 2022), such as correlation between leaf area and seed mass (Laughlin et al., 2010)¹². McCarthy et al. (2007) and Reich et al. (2014) have shown that woody gymnosperms invest relatively more in leaves than woody angiosperms. Poorter et al. (2012) provided further evidence that herbaceous monocots have lower leaf mass fractions than herbaceous eudicots because dicots invest relatively more than monocots in leaves. Moreover, Damour et al. (2016) showed that dicots had higher seed mass than monocots. Differing from the other monocots (Raven, 1988; Tomlinson, 2006), palms build their tall primary stature and exhibit unique features such as leaf development and anatomical characteristics, and possibly the correlation of seed mass with leaf area and plant height (Cámara-Leret et al., 2017; Moore, 2003; Sampaio & Scariot, 2008). Therefore, it remains debatable if plant species from different clades will follow a specific LHS scheme at a higher classification level (e.g., genus), though variety of ecological strategy schemes have been proposed across plant species.

An important goal of plant ecology is to separate the key dimensions of ecological variations across species and then to understand how and why they function and vary between species. For example, the widely used LHS scheme of Westoby propose that each dimension of LHS vary widely between species at any given level of the other two, but it is not sufficient to describe the main axes of trait variation of temperate woody species (Westoby, 1998). Therefore, investigating the correlation of trait characters in different plant clades will provide a sound basis further our understanding of the evolution of functional characters among plants (Pierce et al., 2014; Reich et al., 1999; Tjoelker et al., 2005). However, to our knowledge, no study has so far investigated plant trait variation across different clades, especially using large datasets in the context of LHS scheme and phylogeny.

Consequently, it is still highly uncertain whether traits of different plant clades will fit a specific LHS scheme. Or, do all plant species within a specific clade support a plant ecological strategy scheme (LHS)? Although several authors have investigated LHS scheme within each clade such as palms, angiosperms, gymnosperms, annuals, perennials, herbaceous or woody plants (Cámara-Leret et al., 2017; Falster & Westoby, 2005; Kawai & Okada, 2020; Laughlin et al., 2010), but to our knowledge no study has so far used large datasets to investigate correlations of plant traits across different plant clades (i.e., palms, other monocots, dicots, and gymnosperms). We addressed these questions by conducting a meta-analysis of functional traits (plant height, leaf size, and seed mass) from four plant clades, i.e., palms, other monocots, dicots and gymnosperms with contrasting growth forms. The primary aim of the current study was to understand if and how the different plant clades are coordinated along the plant ecological strategy scheme. Specifically, we first used phylogenetic generalized linear mixed models (PGLMM) and partial R²lik logistic regression model, to explore how

potential forces drive variation in plant traits between different clades, so as to better understand evolution and correlation between functional traits among sets of plant species (Zheng et al., 2009). We expected that each clade of plant species will share the same plant ecological strategy scheme, while LSH scheme would differ across different plant clades.

MATERIALS AND METHODS

Data collection

Using Westoby’s leaf-height-seed (LHS) model of plant functional types (Westoby, 1998), we clustered the plant species studied into four clades: palms, other monocots, dicots, and gymnosperms. We extracted trait data of 2558 palm species 160 genera from a species-level functional trait database of palms, Palm Traits 1.0 (Kissling et al., 2019), complemented with data from published literature (Gödel et al., 2015). Here, we focused on leaf size (maximum blade length in mm), stem height (maximum height in m), and fruit size (maximum fruit width in mm) to represent these major trait axes for palms. We used blade length as a proxy of leaf size of palms because it is commonly used in analyses of leaf traits (Gödel et al., 2015). Fruit size was used as a proxy for seed size because 1) little information of seed size is available for palms, 2) many palm genera are mainly 1-seeded, 3) fruit and seed size are often positively correlated (Fig. S1). Therefore, palms traits we collected are in line with the traits of the LHS plant ecology strategy scheme.

For all species of other monocots, dicots, and gymnosperms, we derived data of leaf size (in mm²), maximum plant height (in m) and seed mass (in mg) from TRY plant trait database (Kattge et al., 2020) and BEIN dataset (Fraser, 2020), complemented it with data from recent publication, representing the leaf–height–seed plant strategy scheme of Westoby (1998). In total, 836 species 279 genera of other monocots, 4290 species 1602 genera of dicots, and 112 species 40 genera of gymnosperms were collected. All data of plant species were averaged at genus level before analysis, which will reduce the effect of environmental scales on plant functional traits.

Statistical analysis

Pagel’s lambda (λ) is a robust estimate of the strength of phylogenetic signal in a continuous trait (Münkemüller et al., 2012; Pagel, 1999; Molina-Venegas & Rodríguez, 2017). In our study, Pagel’s λ can range from 0 to 1, a λ of 0 indicates that there is no phylogenetic signal in the focal traits, whereas a λ of 1 indicates high phylogenetic signal in which the focal trait evolved according to Brownian motion. We calculated Pagel’s to quantify the strength of the phylogenetic signal in plant traits (plant height, leaf size, seed mass, fruit width, blade length and stem height) of palms, other monocots, dicots and gymnosperms (Cadotte et al., 2013). We evaluated the importance of through randomized tests implemented in the function `phylosig` of the R package ‘phytools’ (Revell, 2011).

We used a Gaussian distribution with phylogenetic trees, implemented in the R packages ‘phyr’ and ‘ape’. The multivariate phylogenetic generalized linear mixed models (PGLMM) were used to test the effects of leaf size and plant height on seed mass while controlling for phylogeny.

The location of palms, other monocots, dicots, and gymnosperms in a multivariate trait space illustrated by the first two axes of the PCA based on traits of seed mass (fruit width), leaf size (blade length), and plant height (stem height) (Duras, 2020).

The partial R² for the logistic regression model (Ives & Helmus, 2011) implemented by the R package “rr2” was used to tease apart the relative contributions of leaf size, plant height and phylogeny to the variation in seed mass of palms, other monocots, dicots, and gymnosperms. The partial R²lik 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.

RESULTS

The phylogenetic signals in seed mass and leaf size were moderate and statistically significant across palms, other monocots, dicots, and gymnosperms (Table 1; Fig 2), indicating that seed mass and leaf size have a

common evolutionary history with species. We detected a strong phylogenetic signal in plant height of other monocots, dicots and gymnosperms but not palms (Table 1; Fig 2).

When controlling for phylogeny, seed mass showed significantly positive correlation with leaf size across plant species (Table 2; Fig 3). However, plant height was positively correlated with seed mass in other monocots and dicots rather than palms and gymnosperms (Table 2, Fig 3).

The first two axes of the Principal Component Analysis (PCA) together accounted for 87.3% of variability in the functional traits of plant species ($P < 0.001$, $R^2 = 0.154$, permutations = 999). The principal axis (PC1) was determined positively by seed mass and plant height. The second axis was significantly and positively correlated with leaf area (Fig 4). Thus, dicots were ordinated in a triangle of multivariate space, while palms, gymnosperms and other monocots were ordinated in three separated spaces, with large-seeded palms at the positive extreme of PC1 and small-leaved gymnosperms at the negative extreme of PC2 (Fig 4).

The partial R^2 for the logistic regression model showed that leaf size and phylogeny explained the vast majority of variation in seed mass across palm species (partial $R^2_{\text{lik}} = 15.79\%$, $\Delta\log\text{Lik} = 13.7$, $P < 0.001$; $R^2_{\text{lik}} = 16.92\%$, $\Delta\log\text{Lik} = 14.8$, $P < 0.001$; Fig 5), while phylogeny and plant height explained variation in seed mass of species of other monocots and dicots ($R^2_{\text{lik}} = 42.91\%$, $\Delta\log\text{Lik} = 78.2$, $P < 0.001$; $R^2_{\text{lik}} = 6.36\%$, $\Delta\log\text{Lik} = 9.2$, $P < 0.001$; $R^2_{\text{lik}} = 33.81\%$, $\Delta\log\text{Lik} = 330.5$, $P < 0.001$; $R^2_{\text{lik}} = 7.32\%$, $\Delta\log\text{Lik} = 60.9$, $P < 0.001$; Fig 5). Phylogeny rather than leaf size explained a majority of variation in seed mass in gymnosperms ($R^2_{\text{lik}} = 16.35\%$, $\Delta\log\text{Lik} = 3.6$, $P = 0.008$; $R^2_{\text{lik}} = 8.51\%$, $\Delta\log\text{Lik} = 1.8$, $P = 0.059$; Fig 5).

DISCUSSION

In this study we presented the first systematic quantification of major plant functional traits for palms, other monocots, dicots and gymnosperms and analyzed their relationships to leaf size, plant height and seed mass. Phylogenetic signal in functional traits of all plant clades distributed unimodally, except for stem height in the palm clade (Herben et al., 2008). Weak phylogenetic signal of stem height of palms indicates that phylogeny fails to constrain plant height across palm species, reflecting the uniqueness of functional traits of palms across the world (Barrett et al., 2019; Ma et al, 2015; Sylvester & Avalos, 2013). There has been growing consensus that strong phylogenetic signal across species is due to the similar traits of phylogenetically closely related species (Aizen et al., 2015; Fuzessy et al., 2021). The strong phylogenetic signal observed in plant height, leaf size and seed mass essentially reflects the four dominant phylogenetic groups that differ in major functional traits (Collyer et al., 2021; Zheng et al., 2017).

Much progress has been made in recent years outlining the LHS strategy scheme at species level (Klimešová et al., 2015; Westoby & Wright, 2006), but relatively little attention has been given to functional trait patterns across plant clades, especially at genus level. Although trait relationships will become weak when species groupings are merged (Falster & Westoby, 2005), our results provide evidence that seed mass, even at genus level, is positively and closely correlated to plant height and leaf area across plant species within the clade of dicots and other monocots, suggesting the covariations between functional traits among plant species (Falster et al., 2018; Moles et al., 2005). The close correlations between functional traits in these two plant clades support the notion that LHS scheme is unable to describe the major variation of plant traits of dicots and other monocots. Although broad leaves have evolved in gymnosperms, we failed to detect any correlation between seed mass, leaf area and plant height among the clade gymnosperms, implying that the LHS scheme appears to hold for understanding the trait spectra of gymnosperms (Cornelissen, 1999). However, palms appear to be unique phylogenetic group because leaf size rather than plant height is consistently and positively correlated with seed mass (Gödel et al., 2015), suggesting that leaf size is a key driver of variation of seed mass in the palm clade (Wright et al., 2004). Our partial R^2 for the logistic regression model provided further evidence that leaf size (i.e., blade length) rather than stem height explained a majority of variation in seed mass across palm species, while plant height contributed more to variation in seed mass than leaf size across species within dicots and other monocots. Moreover, the PCA ordinated

identified palms, other monocots, dicots, and gymnosperms in the respective location in a multivariate trait space. Trait correlations within each clade are considered to be caused by divergent patterns of correlated evolution of traits that inherited by its descendant lineages (Messier et al., 2010; Westoby et al., 2002). Therefore, the findings of the current study show that plant species exhibit unique strategy scheme within each clade but variety of ecological strategy schemes across the different plant clades, i.e., palms, other monocots, dicots and gymnosperms.

Seed mass is an important ecological character affecting many aspects of plant ecology (Moles et al., 2005), because its variation can span 10 orders of magnitude across plant species (Rees & Venable, 2007). It is generally believed that seed mass has been the representative of dispersal ability, competitiveness and survival (Zhang et al., 2020), imposing great impacts on plant regeneration strategies and diversity of community. We showed that plant height scales positively with seed mass both in the clades of dicots and other monocots, which is consistent with previous meta-analyses of functional traits showing that plant size and seed mass pattern positively (Díaz et al., 2015; Moles et al., 2005; Pierce et al. 2014). However, a positive relationship between leaf size and seed mass observed in dicots and other monocots is contrary to previous studies demonstrating that seed size does not scale consistently with leaf size (Cornelissen, 1999; Wright et al., 2007). Quantifying plant traits at genus level among different clades or large dataset of species involved in our study may partially explain this discrepancy. By comparing palms with other monocots, however we found that leaf size rather than plant height appears to be a consistent function of variation in seed mass (Santini et al., 2017; Winkel et al., 2001). As the main organ of photosynthesis in plants (Price et al., 2014), the limited numbers of large leaves of palms contribute a lot to seed development (Givnish, 1987; Onstein et al., 2017). The correlation of leaf size with seed mass may reflect strong natural selection for shade tolerance in understory palms (Gödel et al., 2015; Ma et al., 2015). In our study, there is a lack of close correlation of seed mass with plant height and leaf size in the extant gymnosperms, implying that variation in seed size of gymnosperms is mainly structured by dispersal syndrome and cone morphology (Leslie et al., 2017). Another possible explanation can be that extant gymnosperms exhibit a narrow range of seed sizes and lack very small seeds (Moles et al., 2005).

In conclusion, our meta-analysis provides strong support to our prediction that the LHS strategy scheme does not consistently identify plant functional trait patterns across plant clades. However, LHS scheme captures a substantial part of the same spectra of strategy variation within each plant clade. The findings of our study provide important insights into better understanding seed mass correlations with plant height and leaf size across plant clades. These findings also add to our knowledge on the evolution and variation of plant functional traits, which are important in shaping plant life history strategies.

References

- Aizen, M.A., Gleiser, G., Sabatino, M., Gilarranz, L.J., Bascompte, J. & Verdu, M. (2015) The phylogenetic structure of plant-pollinator networks increases with habitat size and isolation. *Ecology Letters* , 19, 29–36.
- Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013) Trait-based tests of coexistence mechanisms. *Ecology Letters* , 16, 1294–1306.
- Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* , 10, 135–145.
- Barrett, C.F., McKain, M.R., Sinn, B.T., Ge, X.J., Zhang, Y.Q. & Antonelli, A. et al. (2019) Ancient polyploidy and genome evolution in palms. *Genome Biology and Evolution* , 11, 1501–1511.
- Collyer, M.L., Baken, E.K. & Adams, D.C. (2021) A standardized effect size for evaluating and comparing the strength of phylogenetic signal. *Methods in Ecology and Evolution* , 13, 367–382.
- Cámara-Leret, R. Faurby, S., Macía, M.J., Balslev, H., Gödel, B. & Svenning, J.C. et al. (2017) Fundamental species traits explain provisioning services of tropical American palms. *Nature Plants* , 3, 16220.
- Cadotte, M., Albert, C.H. & Walker, S.C. (2013) The ecology of differences: assessing community assembly

with trait and evolutionary distances. *Ecology Letters* , 16, 1234–1244.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M. & Reynolds, H.L. et al. (2000) Consequences of changing biodiversity. *Nature* , 405, 234–242.

Cornelissen, J.H.C. (1999) A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* , 18, 248–255.

Duras, T. (2020) The fixed effects PCA model in a common principal component environment. *Communications in Statistics Theory and Methods* , 1, 1–21.

Damour, G., Guerin, C. & Dorel, (2016) M. Leaf area development strategies of cover plants used in banana plantations identified from a set of plant traits. *European Journal of Agronomy* , 74, 103–111.

Díaz, S. Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S. & Dray, S. et al. (2015) The global spectrum of plant form and function. *Nature* , 529, 167–171.

Fuzessy, L., Silveira, F.A.O., Culot, L., Jordano, P. & Verdu, M. (2021) Phylogenetic congruence between Neotropical primates and plants is driven by frugivory. *Ecology Letters* , 25, 320–325.

Fraser, L.H. (2020) TRY— A plant trait database of databases. *Global Chang Biology* , 26, 189–190.

Falster, D.S., Duursma, R.A. & FitzJohn, R.G. (2018) How functional traits influence plant growth and shade tolerance across the life cycle. *Proceedings of the National Academy of Sciences of the United States of America* , 115, 6789–6798.

Falster, D.S. & Westoby, M. (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* , 93, 521–535.

Gödel, B., Kissling, W.D. & Svenning, J.C. (2015) Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World. *Botanical Journal of the Linnean Society* , 179, 602–617.

Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* , 334, 242–243.

Givnish, T.J. (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* , 106, 131–160.

Gingerich, P. (1974) Stratigraphic record of Early Eocene *Hyopsodus* and the geometry of mammalian phylogeny. *Nature* , 248, 107–109.

Herben, T., Klimesova, J. & Chytrý, M. (2018) Effects of disturbance frequency and severity on plant traits: An assessment across a temperate flora. *Functional Ecology* , 32, 799–808.

Ibanez, S., Arène, F. & Lavergne, S. (2016) How phylogeny shapes the taxonomic and functional structure of plant–insect networks. *Oecologia* , 180, 989–1000.

Ives, A.R. & Helmus, M.R. (2011) Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs* , 81, 511–525.

Kawai, K. & Okada, N. (2020) Leaf vascular architecture in temperate dicotyledons: correlations and link to functional traits. *Planta* , 251, 1–12.

Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C. & Leadley, P. et al. (2020) TRY plant trait database-enhanced coverage and open access. *Global Chang Biology* , 26, 119–188.

Kissling, W.D., Balslev, H., Baker, W.J., Dransfield, J., Gödel, B. & Lim, J.Y. et al. (2019) Palm Traits 1.0, a species-level functional trait database of Arecaceae plants worldwide. *Scientific Data* , 6, 178.

- Klimešová, J., Tackenberg, O. & Herben, T. (2015) Herbs are different: clonal and bud bank traits can matter more than leaf-height-seed traits. *New Phytologist* , 210, 13–17.
- Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R. & Laughlin, D.C. et al. (2015) Plant functional traits have globally consistent effects on competition. *Nature* , 529, 204–207.
- Kooyman, R., Cornwell, W. & Westoby, M. (2010) Plant functional traits in Australian subtropical rain forest: partitioning within-community from cross-landscape variation. *Journal of Ecology* , 98, 517–525.
- Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. *Nature* , 428, 851–854.
- Leslie, A.B., Beaulieu, J.M. & Mathews, S. (2017) Variation in seed size is structured by dispersal syndrome and cone morphology in conifers and other nonflowering seed plants. *New Phytologist* , 216, 429–437.
- Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* , 24, 493–501.
- Lavergne, S., Garnier, E. & Debussche, M. (2003) Do rock endemic and widespread plant species differ under the Leaf–Height–Seed plant ecology strategy scheme? *Ecology Letters* , 6, 398–404.
- Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* , 16, 545–556.
- Molina-Venegas, R. & Rodriguez, M.A. (2017) Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? *BMC Evolutionary Biology* , 17, 1–10.
- Ma, R.Y., Zhang, J.L., Cavaleri, M.A., Sterck, F., Strijk, J.S. & Cao, K.F. (2015) Convergent evolution towards high net carbon gain efficiency contributes to the shade tolerance of palms (Arecaceae). *PloS ONE* , 10, e0140384.
- Munkemuller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T. & Schiffers, K. et al. (2012) How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* , 3, 743–756.
- Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* , 13, 838–848.
- McCarthy, M.C., Enquist, B.J. & Kerkhoff, A.J. (2007) Organ partitioning and distribution across the seed plants: assessing the relative importance of phylogeny and function. *International Journal of Plant Sciences* , 168, 751–761.
- Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Pitman, A.J. et al. (2005) Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences of the United States of America* , 102, 10540–10544.
- Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Westoby, M. (2005) A brief history of seed size. *Science* , 307, 576–580.
- Moore, P. (2003) Palms in motion. *Nature* , 426, 26–27.
- Navarro, T., El Oualidi, J., Taleb, M.S., Pascual, V., Cabezudo, B. & Milla, R. (2010) Leaf patterns, leaf size and ecologically related traits in high Mediterranean mountain on the Moroccan High Atlas. *Plant Ecology* , 210, 275–290.
- Onstein, R.E., Baker, W.J., Couvreur, T.L.P., Faurby, S., Svenning, J.C. & Kissling, W.D. (2017) Frugivory-related traits promote speciation of tropical palms. *Nature Ecology and Evolution* , 1, 1903–1911.
- Price, C.A., Wright, I.J., Ackerly, D.D., Niinemets, U., Reich, P.B. & Veneklaas, E.J. (2014) Are leaf functional traits “invariant” with plant size and what is “invariance” anyway? *Functional Ecology* , 28, 1330–1343.

- Pierce, S., Bottinelli, A., Bassani, I., Ceriani, R.M. & Cerabolini, B.E.L. (2014) How well do seed production traits correlate with leaf traits, whole-plant traits and plant ecological strategies? *Plant Ecology* , 215, 1351–1359.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P. & Mommer, L. (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* , 193, 30–50.
- Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature* , 401, 877–884.
- Reich, P.B., Luo, Y.J., Bradford, J.B., Poorter, H., Perry, C.H. & Oleksyn, J. (2014) Temperature drives global patterns in forest biomass allocation in leaves, stems and roots. *Proceedings of the National Academy of Sciences of the United States of America* , 111, 13721–13726.
- Reinhart, K.O., Wilson, G.W.T. & Rinella, M.J. (2012) Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits. *Ecology Letters* , 15, 689–695.
- Revell, L.J. (2011) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* , 3, 217–223.
- Revell, L.J., Harmon, L.J. & Collar, D.C. (2008) Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* , 57, 591–601.
- Rees, M. & Venable, D.L. (2007) Why do big plants make big seeds? *Journal of Ecology* , 95, 926–936.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C. & Volin, J.C. et al. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* , 80, 1955–1969.
- Raven, P. (1988) Reading palms. *Nature* , 334, 482.
- Santini, B.A., Hodgson, J.G., Thompson, K., Wilson, P.J., Band, S.R. & Jones, G. et al. (2017) The triangular seed mass-leaf area relationship holds for annual plants and is determined by habitat productivity. *Functional Ecology* , 31, 1770–1779.
- Sylvester, O. & Avalos, G. (2013) Influence of light conditions on the allometry and growth of the understory palm *Geonoma undata* subsp. *edulis* (Arecaceae) of neotropical cloud forests. *American Journal of Botany* , 100, 2357–2363.
- Sampaio, M.B. & Scariot, A. (2008) Growth and reproduction of the understory palm *Geonoma schottiana* Mart. in the gallery forest in Central Brazil. *Revista Brasileira de Botanica* , 31, 433–442.
- Tomlinson, P.B. (2006) The uniqueness of palms. *Botanical Journal of the Linnean Society* , 151, 5–14.
- Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B. & Tilman, D. (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* , 167, 493–508.
- Vendramini, F., Diaz, S., Gurvich, D.E., Wilson, P.J., Thompson, K. & Hodgson, J.G. (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* , 154, 147–157.
- Wolf, S. Mahecha, M.D., Sabatini, F.M., Wirth, H., Bruelheide, H. & Kattge, J. et al. (2022) Citizen science plant observations encode global trait patterns. *Nature Ecology and Evolution* , 1–10.
- Wang, Y.J., Wang, J.J., Lai, L.M., Jiang, L.H., Zhuang, P. & Zhang, L.H. et al. (2014) Geographic variation in seed traits within and among forty-two species of *Rhododendron* (Ericaceae) on the Tibetan plateau: relationships with altitude, habitat, plant height, and phylogeny. *Ecology and Evolution* , 4, 1913–1923.
- Wang, J.H., Baskin, C.C., Cui, X.L. & Du, G.Z. (2008) Effect of phylogeny, life history and habitat correlates on seed germination of 69 arid and semi-arid zone species from northwest China. *Evolutionary Ecology* , 23, 827–846.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G. & Martinez-Ramos, M. et al. (2007) Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* , 99, 1003–1015.

Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* , 21, 261–268.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z. & Bongers, F. et al. (2004) The worldwide leaf economics spectrum. *Nature* , 428, 821–827.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* , 33, 125–159.

Winkel, T., Payne, W. & Renno, J.F. (2001) Ontogeny modifies the effects of water stress on stomatal control, leaf area duration and biomass partitioning of *Pennisetum glaucum* . *New Phytologist* , 149, 71–82.

Wilson, P.J., Thompson, K. & Hodgson, J.G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* , 143, 155–162.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* , 199, 213–227.

Xia, L.M. Miao, Y.Z., Cao, A., Liu, Y., Liu, Z.H. & Sun, X.L. et al. (2022) Biosynthetic gene cluster profiling predicts the positive association between antagonism and phylogeny in *Bacillus* . *Nature Communications* , 13, 1023.

Zhang, C.H., Li, J.Y., Willis, C.G. & Ma, Z. (2020) Among-population variation in seed mass for 190 Tibetan plant species: Phylogenetic pattern and ecological correlates. *Global Ecology and Conservation* , 23, e01163.

Zheng, J.M., Guo, Z.W. & Wang, X.P. (2017) Seed mass of angiosperm woody plants better explained by life history traits than climate across China. *Scientific Reports* , 7, 2741.

Zheng, L., Ives, A.R., Garland, T., Larget, B.R., Yu, Y. & Cao, K.F. (2009) New multivariate tests for phylogenetic signal and trait correlations applied to ecophysiological phenotypes of nine *Manglietia* species. *Functional Ecology* , 23, 1059–1069.

TABLE 1 Phylogenetic signal of functional traits of palms, other monocots, eudicots, and gymnosperms as measured by Pagel’s λ (1999).

Taxon	Lambda value (P)	Lambda value (P)	Lambda value (P)
	Seed mass (fruit width)	Leaf size (blade length)	Plant (stem) height
Palms	0.711 (< 0.001)	0.582 (< 0.001)	0.000 (1.000)
Other monocots	0.915 (< 0.001)	0.718 (< 0.001)	0.928 (< 0.001)
Dicots	0.944 (< 0.001)	0.757 (< 0.001)	0.960 (< 0.001)
Gymnosperms	0.793 (< 0.001)	0.840 (< 0.001)	0.938 (< 0.001)

TABLE 2 Multivariate models (PGLMM) constructed with seed mass (fruit width) as response variable.

Taxon	AIC	Predictor variable	Estimate (SE)	Z	P
Palms	19.4	Blade length	0.127 (0.023)	5.539	< 0.001
		Stem height	0.023 (0.021)	1.102	0.271
Other monocots	574.9	Leaf size	0.140 (0.050)	2.831	0.005
		Plant height	0.242 (0.054)	4.487	< 0.001
Dicots	3743.0	Leaf size	0.162 (0.026)	6.283	< 0.001
		Plant height	0.390 (0.033)	11.935	< 0.001
Gymnosperms	105.8	Leaf size	0.345 (0.172)	1.998	0.046

Taxon	AIC	Predictor variable	Estimate (SE)	Z	P
		Plant height	0.056 (0.150)	0.371	0.711

Figure legends

FIGURE 1 Plant key traits (plant height, leaf size, seed mass, fruit width, blade length and stem height) of (a) palms, (b) other monocots, (c) dicots, and (d) gymnosperms mapped onto a plant phylogeny. Bars at the phylogenetic tree indicate seed mass or fruit width (olive), leaf size or maximum blade length (green) and maximum plant or stem height (dark brown).

FIGURE 2 Phylogenetic signal test of key traits of palms (a: fruit width; b: blade length; c: stem height), other monocots (d: seed mass; e: leaf size; f: plant height), dicots (g: seed mass; h: leaf area; i: plant height), and gymnosperms (j: seed mass; k: leaf area; l: plant height).

FIGURE 3 Significant correlation of seed mass (or fruit width) with leaf size (or blade length) and plant height (or stem height) across palms (a and b), other monocots (c and d), dicots (e and f), and gymnosperms (g and h). Significant effect was detected based on phylogenetic generalized linear mixed models (PGLMM, see Table 2).

FIGURE 4 The location of palms, other monocots, dicots, and gymnosperms in a multivariate trait space illustrated by the first two axes of a principal component analysis (PCA) based on trait information on seed mass (fruit width), leaf size (blade length), and plant height (stem height). All data were log-transformed. Nonparametric multivariate analysis of variance (per-MANOVA) shows significant overall shifts in community structure ($P < 0.001$, $R^2 = 0.154$, permutations = 999). PC1 and PC2 together account for 87.3% of the variability in the data.

FIGURE 5 The relative contribution of different factors to the variation in seed mass (fruit width) of (a) palms, (b) other monocots, (c) dicots, and (d) gymnosperms using partial R^2 for the logistic regression model.

FIGURE S1 Correlation of fruit width with seed width (a) and fruit volume (b) of palms. Log transformation was performed on the data.

FIGURE 1

Hosted file

image1.emf available at <https://authorea.com/users/512479/articles/610368-clade-specific-differences-in-leaf-height-seed-strategy-scheme>

Hosted file

image2.emf available at <https://authorea.com/users/512479/articles/610368-clade-specific-differences-in-leaf-height-seed-strategy-scheme>

FIGURE 2

FIGURE 3

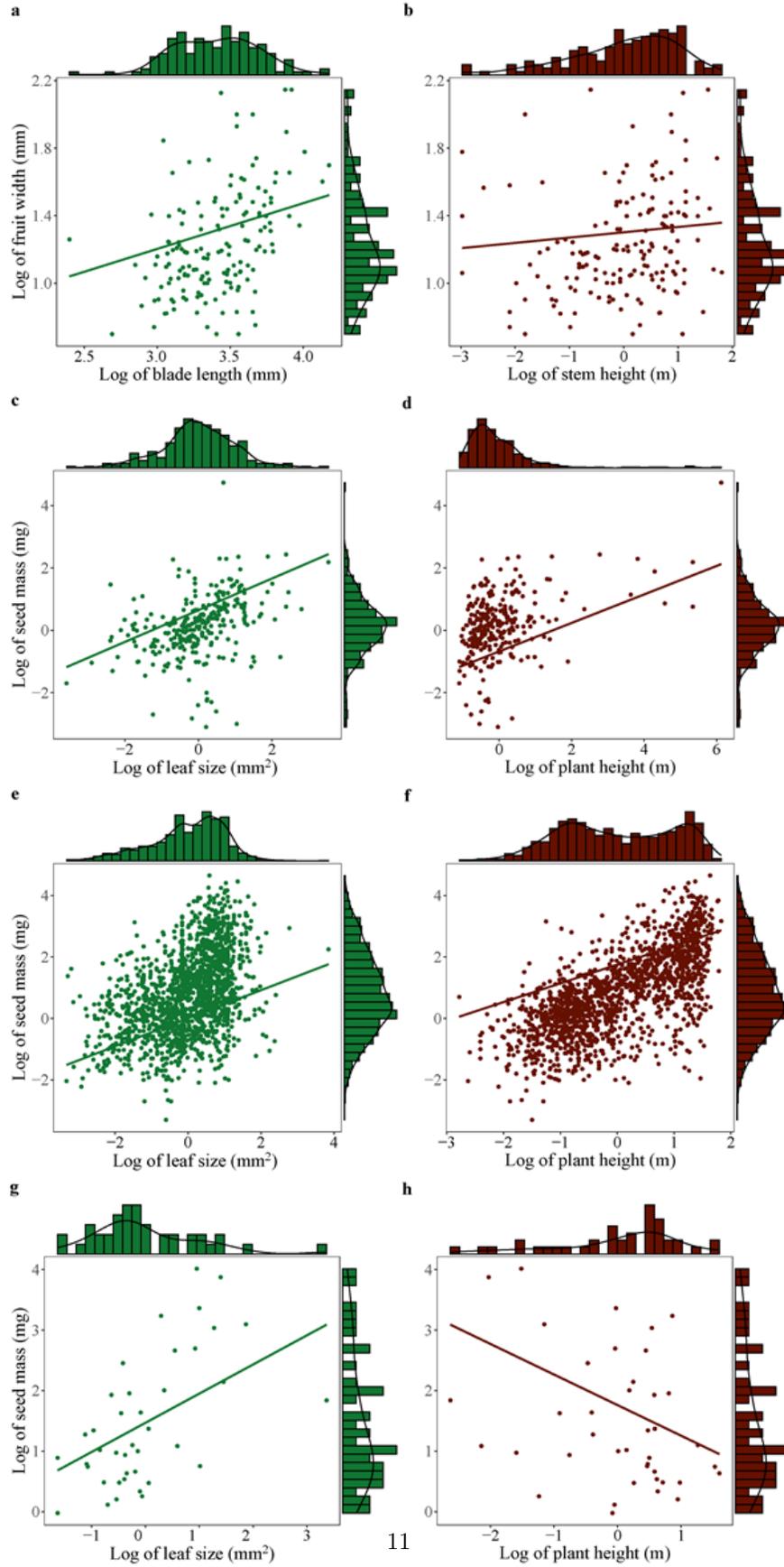


FIGURE 4

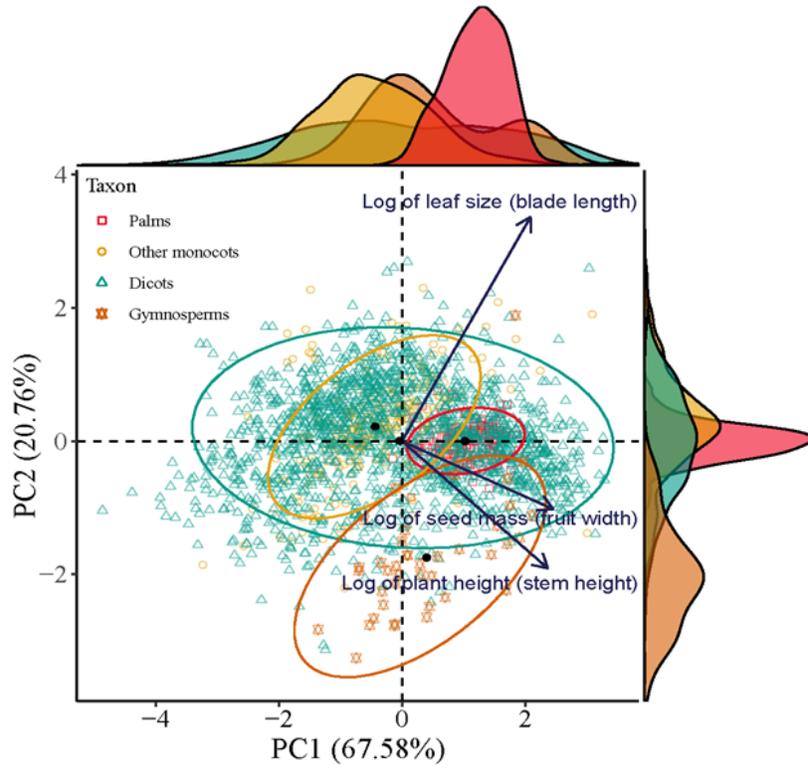


FIGURE 5

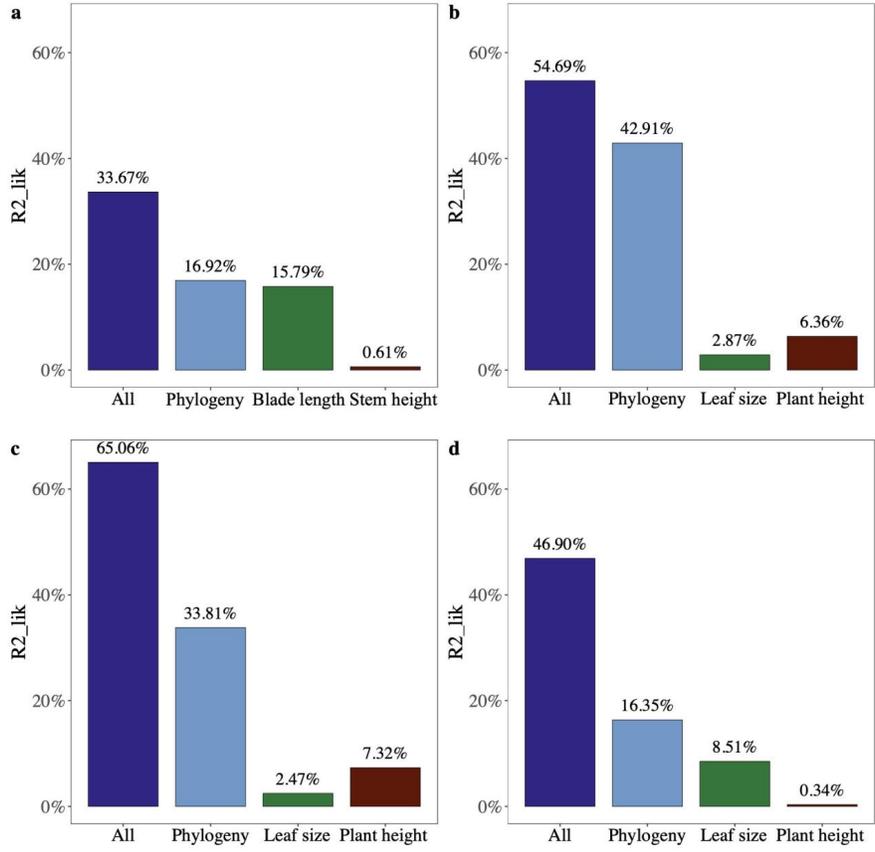


FIGURE S1

