Transitions between the terrestrial and epiphytic habit drove the evolution of seed-aerodynamic traits in orchids

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Running title: Evolution of seed-aerodynamic traits in orchids

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ABSTRACT

Orchids are globally distributed, a feature often attributed to their tiny dust-like seeds. They were ancestrally terrestrial, but in the Eocene expanded into tree canopies, with some lineages later returning to the ground, providing an evolutionarily replicated system. Because seeds are released closer to the ground in terrestrial species than in epiphytic ones, seed traits in terrestrials may have been under selective pressure to increase seed dispersal efficiency. In this study, we test the expectations that (i) seed air space –a trait known to increase seed floatation time in the air– is larger in terrestrial lineages and (ii) has increased following secondary returns to a terrestrial habit. We quantified and scored 20 seed traits in 121 species and carried out phylogenetically-informed analyses. Results strongly support both expectations, suggesting that aerodynamics traits even in dust seeds are under selection to increase dispersal ability, following shifts in average release heights correlated with changes in habit.

Key words: Dust seeds, seed air space, phylogenetic comparative methods, seed dispersal distance, wind dispersal.

Introduction

The fall rates of wind-dispersed plant diaspores, units that consist of one or more seeds and attached structures such as wings or plumes, can change with even minor morphological modifications (Greene and Johnson 1989, 1990; Cummins et al. 2018). This has been shown in experiments on a wide range of species (van der Pijl 1982; Nathan et al. 2002; Greene and Johnson 1989, 1990; Cummins et al. 2018). Especially important is the height at which a given diaspore is released into the air, but also external wind patterns and diaspore weight and aerodynamic features. Light wind-dispersed seeds, up to 45 mg, are typically carried by plumes and may float about at more than 100 m above the ground and be transported for hundreds of kilometers (reviewed in Renner 1992). A different type of light seeds are dust seeds, which are known from only twelve plant families including orchids, the largest clade with such seeds (Arditti and Ghani 2000; Eriksson and Kainulainen 2011). At the time of dispersal, an orchid's seed coat is just one cell layer thick and encloses an embryo in the shape of an ellipsoid cluster of cells, with a distinctive feature being the large internal air space between the embryo and the seed coat (Arditti et al. 1979, 1980; Arditti and Ghani 2000). Experiments in still air have shown that the time of orchid seed floatation increases with percent air space, and hence higher dispersal abilities (Arditti and Ghani 2000). This sets up the expectation that the contrasting atmospheric conditions experienced by terrestrial versus epiphytic species in terms of wind speeds and convectional uplift may have shaped their air space volumes over evolutionary time, with terrestrial species perhaps having larger air spaces than epiphytic species to compensate for lower release heights.

Today, orchids are globally distributed, a feature often attributed to excellent dispersal abilities conferred by their dust-like seeds (e.g., Givnish et al. 2015, 2016). Orchidaceae initially evolved as a terrestrial clade but in the Eocene expanded into tropical canopies as a new niche, with some lineages later returning to the ground (Benzing and Atwood 1984; Chomicki et al. 2015; Givnish et al. 2015, 2016). The family therefore includes independent epiphytic and terrestrial lineages that can be seen as evolutionary replicates, in principle permitting comparison of seed traits in terrestrial and epiphytic groups. Such a comparison in six species of *Liparis* showed that the two terrestrial species had larger air spaces and smaller embryos than the four epiphytic species (Tsutsumi et al. 2007), consistent with the expectation of enhanced uplift through larger air balloons in the terrestrial species. Floatation experiments in 12 other species (in 12 genera from throughout the Orchidaceae, but without the incorporation of phylogenetic information) further showed that for seeds of similar volume, it is probably seed air space that modulates floatation time (Arditti and Ghani 2000: Fig. 6b).

To address whether terrestrial and epiphytic orchids consistently differ in seed morphological traits, we measured 20 qualitative and quantitative seed traits in 121 species from 63 of the family’s 736 genera and analyzed the data in a comparative framework. Specifically, we wanted to address whether (i) evolutionary changes in seed traits parallel shifts between the terrestrial and epiphytic habit, and (ii) how seed traits correlate with one another. Our expectation was that terrestrial orchids should have relatively larger seed air spaces as their seed release height is much smaller than that of epiphytic orchids.

Materials and Methods

Study species and study site

Orchid species were identified using the Flora of China (http://www.efloras.org/florataxon.aspx?flora_id=2andtaxon_id=10638) and a published orchid species list from Xishuangbanna (Gao et al. 2014). Seeds were collected in the field from mature fruits (1-5 capsules) of orchids grown at the Xishuangbanna tropical research station in Yunnan, the tropical region of Southern China between Laos and Myanmar.

Seed trait assessment using photography and scanning electron microscopy

Seeds from collected fruits were dried for 4-6 days in a vacuum dryer filled with anhydrous calcium chloride. Seeds were kept in sealed tubes and preserved at -20°C before observations using Image-J (version 1.45). Because seed traits may vary with seed hydration, we measured size differences between dry and hydrated seeds in each of the 121 species. Dry seeds were directly gold-coated and submitted to scanning electron microscopy (SEM, EVO LS10, Germany) without any extra pretreatment. Detailed characteristics were scored from SEM photos (available as **Fig. S1**). Seed shape was categorized into five types including filiform

(Length/Wide ratio > 6.0), fusiform, spathulate, ovoid and circular (Arditti and Ghani 2000; Verma et al. 2014).

Because the water pore and testa cells are clear under SEM and the embryo is only visible under optical microscope (OM), we measured length and width of dry seeds, water pore width, and number, cell length and shape of epidermis cells on testa (seed coat at the longest axis) in five seeds per species in two replicates from SEM pictures, meaning ten measurements for each species.

To measure hydrated seeds, dry seeds were put in a water-saturated container for two days and then photographed under an optical microscope (Ste REO Discovery V20/ Axio Imager A2). Length and width of hydrated seeds, length and width of embryos were measured from 2 seeds in 2 replicates based on OM pictures (Arditti and Ghani 2000).

As embryos were generally elliptical in cross-section, their volume was calculated using the formula $4/3\times\pi\times (L/2) \times (W/2)^2$, where L is the embryo length and W the embryo width (Arditti and Ghani 2000). Seed volume was calculated based on seed shape. If it was elliptical, the same formula was used as for the embryo. If it was cylindrical, formula $2[(W/2)^2 \times (L/2) \times (\pi/3)]$ was applied, where W = seed width, L = seed length (Arditti et al. 1979). If seed shape was intermediate between those two shapes, formula $[4/3\times\pi\times (L/2) \times (W/2)^2]/2 + [(W/2)^2 \times (L/2) \times (\pi/3)]$ was used. The percentage of air space of hydrated seeds was calculated by subtracting the embryo volume from the seed volume of the same seed. Data were analyzed using SPSS 16.0 (SPSS Inc., USA) or R (R Team for statistical computing).

We measured 20 seed traits, namely (1) hydrated seed length, (2) hydrated seed width (3) hydrated seed length/width ratio, (4) hydrated seed volume, (5) hydrated embryo length, (6) hydrated embryo width, (7) hydrated embryo length/width ratio, (8) hydrated embryo volume, (9) dry seed length, (10) dry seed width, (11) dry seed length/width ratio, (12) dry seed volume, (13) cell number in longitudinal axis of seeds, (14) hydrated seed cell length, (15) dry seed cell length, (16) cell length ratio (hydrated/dry), (17) hydrated seed/embryo volume ratio, (18) hydrated seed air space (%), (19) seed water absorption ability estimated as $(Volume_{\text{hydrated seed}} - Volume_{\text{dry seed}})/Volume_{\text{dry seed}}$, and (20) water pore width. Trait 21 was growth habit. The final trait dataset generated for this study consists of 2640 data points (averages for quantitative traits; **Table S1**).

DNA isolation, sequencing, and phylogenetic analyses

About a quarter of the 121 species of which we studied the seeds under SEM had no sequences available in GenBank (NCBI https://www.ncbi.nlm.nih.gov/), and we therefore sequenced their nuclear Internal Transcribed Spacer (nrITS) region. DNA was isolated from silica-dried leaves of 32 species, using a modified CTAB protocol (Doyle 1991), and the entire ITS region (ITS 1 + 5.8S + ITS 2) was amplified using primers of Sun et al. (1994) designed for *Sorghum* (17SE and 26SE). The DNA was amplified using standard protocols and sequenced on an automated sequencer (Sangon Biotech Company, Shanghai, China). Each species is vouchered with a permanent herbarium specimen, and taxonomic authors, vouchers numbers, and species' geographic origin, as well as the GenBank accession numbers are shown in **Table S2**.

Our final DNA matrix included 111 of the 121 species whose seeds were studied, plus five outgroups from the families Alliaceae (*Allium*), Amaryllidaceae (*Crinum*), Iridaceae (*Sisyrinchium* and *Trimezia*) and Liliaceae (*Asparagus*). To improve topological resolution, we added sequences from the plastid genes *matK* and *rbcL*, and the *trnL-trnF* spacer region from GenBank for a total of 5816 aligned base pairs **(Table S2**). Sequences were aligned in MAFFT v7 (Katoh and Standley 2013) under standard settings, except for ITS which was aligned under the Q-IN-S, which takes secondary structure into consideration and is recommended for alignment of divergent nuclear RNAs. We performed maximum likelihood analyses using RAxML version 8 (Stamatakis 2014), under the GTR substitution model, with 25 gamma categories, and 100 bootstrap replicates. Tree support is shown in **Fig. S2**. Our dataset does not resolve several important nodes in the orchid backbone, which in the BEAST analyses (below) were therefore constrained to match the backbone topology retrieved in both the 9-gene dataset of Chomicki et al. (2015) and the plastid dataset of Givnish et al. (2015).

To generate an ultrametric tree, we used BEAST version 1.8.3 (Drummond and Rambaut 2007) and four fossil calibrations as in Chomicki et al. (2015). We used the same model of nucleotide substitution as before (GTR + G), a Yule tree prior, and an MCMC chain length of 40 million generations, sampling every 10,000 generations. Because our Xishuangbanna orchid sampling was comparatively small at the scale of orchids (covering only 63 of family's 736 genera), we used hard time constraints based on previous studies (Chomicki et al. 2015; Givnish et al. 2015). The oldest known fossil of the Asparagales (105 million years (myr); Walker and Walker 1984) was used as a maximal calibration point for the Orchidaceae and was given a large normal prior (offset = 105.3; SD = 8). A gamma distribution was used on each of the three ingroup fossil constraints (the offset value was set to the minimum age of each fossil and the standard deviation was set such that the maximum age was included in the 97.5% quantile). The fossil orchid *Meliochis caribea* (15–20 myr; Ramírez et al. 2007) was used as a minimal constraint for the monophyletic tribe Goodyerinae, under a normal prior (offset = 17.5; SD= 5), and two macrofossils (*Dendrobium winkaphyllum* and *Earina fouldenensis*; both 20–23 myr; Conran et al. 2009) were used as minimum constraints within Epidendroideae, with normal priors (offset = 20; SD= 4.5). The trees were summarized using TreeAnnotator version 1.8.0 (part of the BEAST package), with a 10% burn-in and a 0.98 posterior probability limit.

Ancestral state estimations

To map habitats and orchid seed traits, we used stochastic mapping, using the function ‘make.simmap’ in the phytools package (Revell 2012), which implements the stochastic character mapping approach developed by Bollback (2006). We estimated ancestral states under the ER model, and then simulated 1000 character-histories on the MCC tree. We summarized the 1,000 simulated histories using the function ‘describe.simmap’ and relied on the functions ‘fastAnc’ and ‘contMap’ in phytools. However, given the relatively small sample size, we consider these reconstructions more like mappings that visually show the patterns of seed trait evolution, rather than inferences of ancestral states.

Hierarchical Bayesian Modelling

To take into account phylogenetic distance in the analyses, we used a hierarchical Bayesian (HB) approach to test whether habit significantly influences seed air space (%) while simultaneously correcting for phylogenetic signal. Regression components of the model are the following:

$\mu_{Seed\ air\ space\ i} = \alpha 1 + \beta 1 \times S_{Terrestrial\ i}$

$\mu_{Seed\ air\ space\ i} = \alpha 2 + \beta 2 \times S_{Epiphyte\ i}$

where the term α refers to the intercept and β for the slope. We used mean seed air space as dependent variable. Phylogenetic information was integrated into the model through Bayesian phylogenetic regression by converting the ultrametric tree into a scaled (0-1) variance-covariance matrix, using the function ‘vcv.phylo’ of the ape package (Paradis et al. 2004). We adapted an R script using the JAGS package (Plummer 2003) and the R2JAGS package (Su and Yajima 2014) and ran three parallel MCMC chains for 20,000 iterations followed a 5000-iteration burn-in. Model convergence was evaluated with the Gelman and Rubin (1992) statistic using the ‘ggmcmc’ R package (Fernández-i-Marín 2013). Noninformative priors were specified for all parameter distributions, following Fridley and Craddock (2015).

Binary correlations between continuous seed traits

To test whether seed traits are correlated while accounting for phylogeny, we used the Bayesian version of the random walk (model A) implemented in BayesTraits V2 (Pagel and Meade 2013). For each of the possible correlations, we ran one correlated model (function 'CORREL') and another one where we set all correlations to zero using the function 'TESTCORREL'. To compare these non-nested models, we used Bayes Factors. The 15 continuous traits were seed length (dry), seed length (hydrated), seed width (dry), seed width (hydrated), final seed volume μm^3 (hydrated seeds), embryo length (hydrated), embryo width (hydrated), volume of hydrated embryo as elliptical (μm^3), final seed volume μm^3 (dry), cell number in longitudinal axis (dry), cell length in longitudinal axis um (hydrated), seed/embryo volume ratio (hydrated), hydrated seed air space (1 - embryo/final seed volume), seed water absorption ability, and water pore width (μm).

Determining the trait space of epiphytic vs. terrestrial orchids

To determine the trait space of epiphytic vs. terrestrial orchids, we performed a non-metric multidimensional scaling analysis (NMDS) in the R package vegan (Oksanen et al. 2013). We removed two highly correlated traits, namely seed length and width when dry and hydrated, and analyzed the remaining 13 continuous traits, using either the entire dataset of 121 species (**Tables S1, S2, Fig. S1**) or only the species included the concatenated DNA matrix. Results from the 121-species dataset were plotted using ggplot2 (Wickham 2009). For the reduced analysis, we extracted the NMDS1 and NMDS2 values for each species and used this as input data for a phylomorphospace graph (Revell 2012). This creates a projection of the phylogenetic tree into morphospace and allows to visualize how the tips in a phylogeny diverge and converge from ancestral nodes.

Results

Macroevolutionary evidence on the correlation of seed traits with the terrestrial or epiphytic habit

Visual inspection and quantitative and qualitative measurements of the 20 seed traits scored for the 121 species highlight striking differences among these dust seeds (**Table S1; Fig. S1** showing one seed per species under SEM). Ancestral state reconstructions revealed that our expectations that terrestrial orchids should have larger air space than epiphytic species and that evolutionary returns to a terrestrial habit (i.e., being rooted in soil) might favor returns to larger seed air space were met (**Fig. 1a, Fig. S3**). To test whether this association of seed air space with habit is significant, we used a Bayesian hierarchical model taking into account phylogenetic autocorrelation, which revealed a strong association of larger seed air space with the terrestrial habit (**Fig. 1b**).

Seed trait correlations in orchids

To describe the overall trait spaces of the epiphytic and terrestrial species, we first tested for evolutionary correlations among the continuous traits. This revealed that 70 of the 120 trait pairs are very highly correlated as supported by Bayes Factor scores (**Fig. 2, Table S3**). Air space is highly or very highly positively correlated with seed width, seed volume, embryo volume, seed length, embryo width, and cell number (and obviously seed/embryo volume ratio [**Fig. 2, Table S3**]). However, embryo length, cell length in longitudinal axis, water absorption ability and water pore width are barely correlated with seed air space (**Fig. 2, Table S3**). Notably, seed air space is not correlated with cell length (**Fig. 2, Table S3**), suggesting that shifts in cell division, rather than expansion mediate changes in seed air space.

The trait correlations seen on the phylogeny (**Fig. 1**) suggest that terrestrial species have distinct trait spaces, rather than merely differing by the size of their air space. To test this, we ran an NMDS analysis using the 13 continuous seed traits from our dataset. We indeed identified discrete trait spaces in epiphytic and terrestrial species, with their 95% confidence intervals covering non-overlapping trait space (**Fig. 3**).

Discussion

Larger seed air spaces in terrestrial than epiphytic species suggests dispersal limitations

Arditti and Ghani (2000: Fig. 6b) showed that seed air space enhances dispersal ability (by modulating floatation time) in orchids. Our comparative phylogenetic analyses now reveal that basal terrestrial orchids have larger seed air spaces compared to most epiphytic ones and that secondary returns to the terrestrial habit correlate with an increase in seed air space (**Fig. 1**). This suggests a seed dispersal limitation in terrestrial orchids, and the distinct trait spaces of epiphytic vs. terrestrial orchids (**Fig. 3**) are consistent with different selective regimes. Repeated evolutionary returns to terrestrial habitats have occurred in the orchid subfamily Epidendroideae (Chomicki et al. 2015; color-coded in **Fig. 1A**), and our results show that secondarily terrestrial Epidendroideae have large seed air spaces. This suggests that, initially, orchids' conquest of tree canopies in the Eocene (Chomicki et al. 2015) led to larger embryos and smaller seed air spaces (because of higher average seed release heights), and later returns to a terrestrial habit led to renewed selection for larger seed air space.

Local vs. Long-distance dispersal

The extremely large seed numbers and low recruitment rates in orchids have long puzzled researchers, perhaps starting with Darwin (1862). Because of orchids' endosperm-lacking seeds, germination is obligately dependent upon mycorrhizal fungi (Rasmussen 1995; Smith & Read 2008), and it was therefore long thought that presence of suitable fungi might limit orchid distribution (McCormick and Jacquemyn 2014). This view is being challenged by molecular data, showing that many terrestrial orchids can associate with many or widespread fungi (Swarts et al. 2010; Jacquemyn et al. 2011; Phillips et al. 2011). Germination experiments further show that proximity to the parent plant (and hence its fungus) may not be as important as thought

(McKendrick et al. 2000; Tesitelova et al. 2012; Phillips et al. 2011; De Hert et al. 2013; McKormick and Jacquemyn 2014). These results suggest that – at least in species with low specificity of fungal partners – distant seed dispersal may not be a problem for recruitment. However, data are biased towards Northern Hemisphere terrestrial species, and much more work is needed on germination in tropical epiphytic orchids.

The evolution of orchid dust seeds is among the most striking changes in seed weight in monocots (Moles et al. 2005), and orchids provide many examples of undoubted long-distance dispersal (Givnish et al. 2016; Pérez-Escobar et al. 2017). Nevertheless, they comprise <1% of the native vascular floras of 395 oceanic islands, while making up much larger percentages on the mainland, pointing to dispersal limitations, lacking fungal partners, or lacking pollinators preventing successful population maintenance (Taylor et al. 2019).

Limitation of this study and conclusions

A limitation of our study concerns the type of epiphyte and its micro-habitat. While our scoring of terrestrial species (i.e., rooted in soil or in the case of saprophytes connected to hosts) vs. epiphytic species (plants not rooted in soil) may seem like a clear distinction, it may not translate into two categories of average seed release heights. Ideally ,one would score seed traits for species occurring on trunks, lower canopy branches, the inner canopy, or the upper canopy, or better yet, treat epiphytism as a continuously varying trait (i.e., average height off the ground [which would require quantifying height in the natural habitat for every species sampled]). The extent to which seed air space impacts dispersal kernels under different wind conditions should also be studied experimentally.

Despite these limitations, our phylogenetic-comparative approach show that a key trait – seed air space – in secondarily terrestrial orchid clades is larger than in their immediate epiphytic ancestors, plausibly because of less uplift experienced by seeds released closer to the ground. Understanding the extent to which dispersal limitation might be important in terrestrial orchids, however, requires more work on how seed aerodynamics and travel distances influence recruitment success.

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Data Archiving

All DNA sequences have been submitted to GenBank (Table S2); all measurements are shown in Table S1.

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Figure Legends

Figure 1. The evolution of seed air space mirrors evolutionary shifts in growth habit in orchids. (**A**) Phylogeny for the 121 species used in this study (listed in Table S1), with habit and seed air space percentage. The color-coding of branches in the phylogeny refers to orchid subfamily, namely Apostasioideae (black), Orchidoideae (blue), and Epidendroideae (orange). (**B**) Estimated coefficient values from a Bayesian hierarchical model testing the effect of seed air space on habit, showing means and 95% confidence intervals (CI).

Figure 2. Correlations between the 120 pairs of continuous seed traits (15 traits) in a phylogenetic context. Colors refer to the strength of correlations as assessed by Bayes Factors.

Figure 3. The trait space of terrestrial and epiphytic orchids. Non-metric multidimensional scaling analysis of 13 continuous seed traits. The two ellipses show the 95% confidence internals for terrestrial and epiphytic orchids. The NMDS is plotted as a phylomorphospace graph depicting both phylogenetic relationships and divergence times.

Figure 1

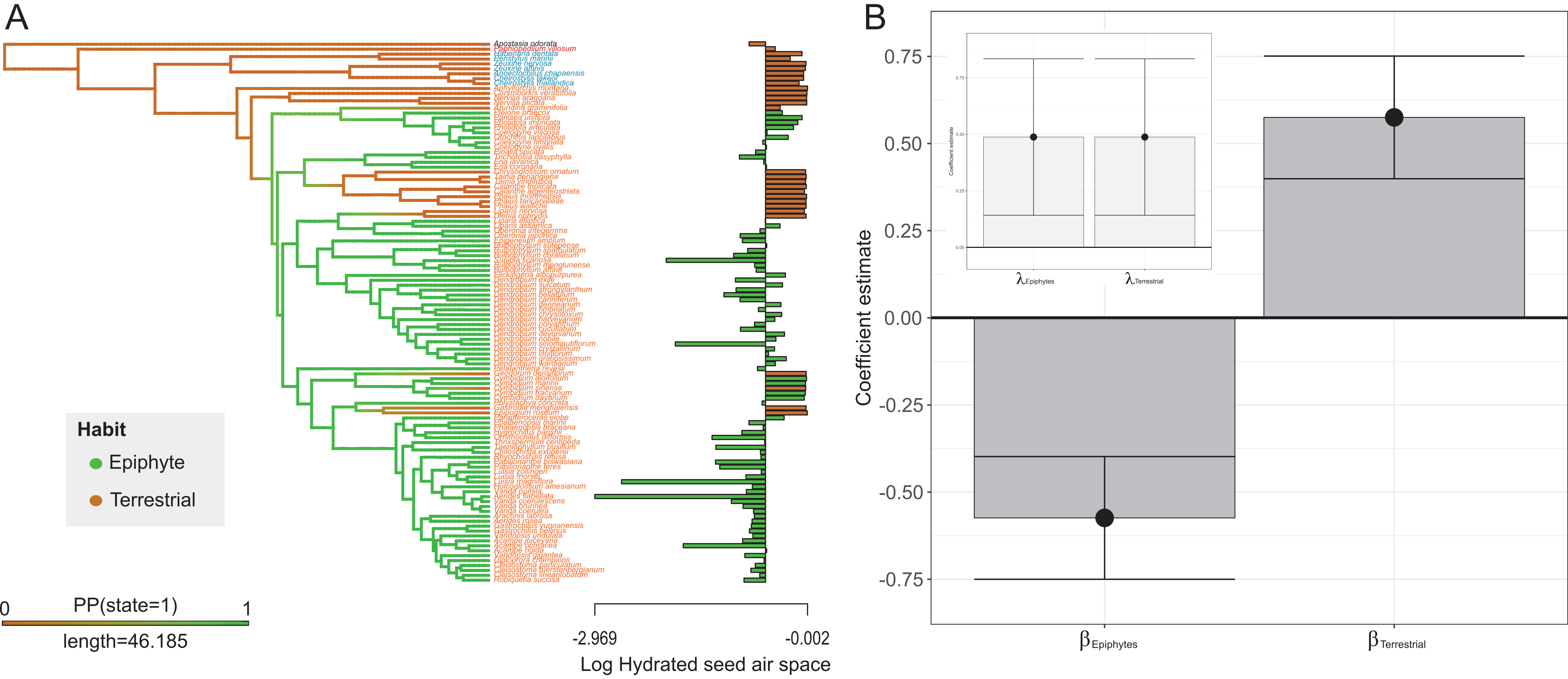

A
Apostasia odorata
Paphiopedilum villosum
Habenaria dentata
Peristylus mannii
Zeuxine nervosa
Zeuxine affinis
Anoectochilus chapaensis
Cheirostylis takeoi
Cheirostylis thailandica
Aphyllorchis montana
Corymborkis veratrifolia
Nervilia aragoana
Nervilia plicata
Arundina graminifolia
Pleione praecox
Panisea uniflora
Pholidota imbricata
Pholidota articulata
Coelogyne viscosa
Otochilus lancilabius
Coelogyne fimbriata
Coelogyne ovalis
Pinalia spicata
Trichotosia dasyphylla
Eria javanica
Eria coronaria
Chrysoglossum ornatum
Tainia penangiana
Tainia viridifusca
Calanthe triplicata
Calanthe argenteostriata
Phaius mishmensis
Phaius tancarvilleae
Phaius wallichii
Liparis nervosa
Dienia ophrydis
Liparis elliptica
Liparis assamica
Oberonia integerrima
Oberonia japonica
Epigeneium amplum
Bulbophyllum sutepense
Bulbophyllum spathulatum
Bulbophyllum corallinum
Sunipia scariosa
Bulbophyllum menglunense
Bulbophyllum affine
Flickingeria albopurpurea
Dendrobium exile
Dendrobium sulcatum
Dendrobium strongylanthum
Dendrobium bellatulum
Dendrobium cariniferum
Dendrobium denneanum
Dendrobium fimbriatum
Dendrobium chrysotoxum
Dendrobium harveyanum
Dendrobium polyanthum
Dendrobium cucullatum
Dendrobium devonianum
Dendrobium nobile
Dendrobium sinominutiflorum
Dendrobium crystallinum
Dendrobium lituiflorum
Dendrobium gratiosissimum
Dendrobium wardianum
Pelatantheria rivesii
Geodorum densiflorum
Cymbidium aloifolium
Cymbidium mannii
Cymbidium sinense
Cymbidium tracyanum
Cymbidium dayanum
Polystachya concreta
Gastrodia menghaiensis
Epipogium roseum
Parapteroceras elobe
Phalaenopsis mannii
Phalaenopsis braceana
Hygrochilus parishii
Ornithochilus difformis
Thrixspermum centipeda
Taeniophyllum pusillum
Chiloschista exuperei
Rhynchostylis retusa
Papilionanthe biswasiana
Papilionanthe teres
Luisia zollingeri
Luisia morsei
Luisia magniflora
Holcoglossum amesianum
Vanda pumila
Aerides flabellata
Vanda coerulescens
Vanda brunnea
Vanda coerulea
Arachnis labrosa
Aerides rosea
Gastrochilus yunnanensis
Gastrochilus bellinus
Vandopsis undulata
Acampe joiceyana
Acampe ochracea
Acampe rigida
Vandopsis gigantea
Diploprora championii
Cleisostoma paniculatum
Cleisostoma fuerstenbergianum
Cleisostoma linearilobatum
Robiquetia succisa
Habit
Epiphyte
Terrestrial
0
PP(state=1)
1
length=46.185
-2.969
-0.002
Log Hydrated seed air space
B
Coefficient estimate
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
$\beta_{\text{Epiphytes}}$
$\beta_{\text{Terrestrial}}$
Coefficient estimate
0.75
0.50
0.25
0.00
$\lambda_{\text{Epiphytes}}$
$\lambda_{\text{Terrestrial}}$

Figure 2

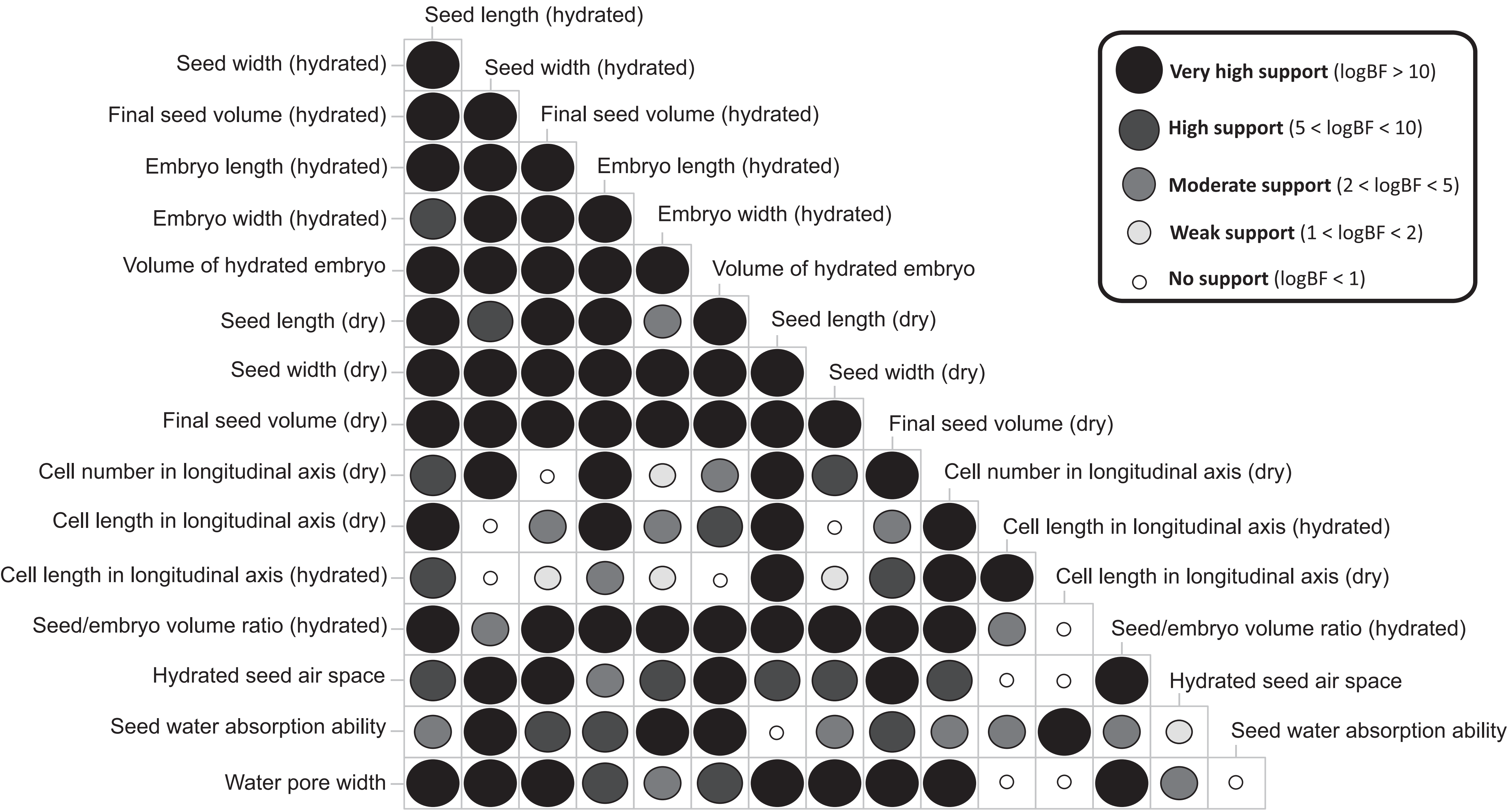

Seed length (hydrated)
Seed width (hydrated)
Final seed volume (hydrated)
Embryo length (hydrated)
Embryo width (hydrated)
Volume of hydrated embryo
Seed length (dry)
Seed width (dry)
Final seed volume (dry)
Cell number in longitudinal axis (dry)
Cell length in longitudinal axis (dry)
Cell length in longitudinal axis (hydrated)
Seed/embryo volume ratio (hydrated)
Hydrated seed air space
Seed water absorption ability
Water pore width
Very high support (logBF > 10)
High support (5 < logBF < 10)
Moderate support (2 < logBF < 5)
Weak support (1 < logBF < 2)
No support (logBF < 1)

Figure 2 (online-only)

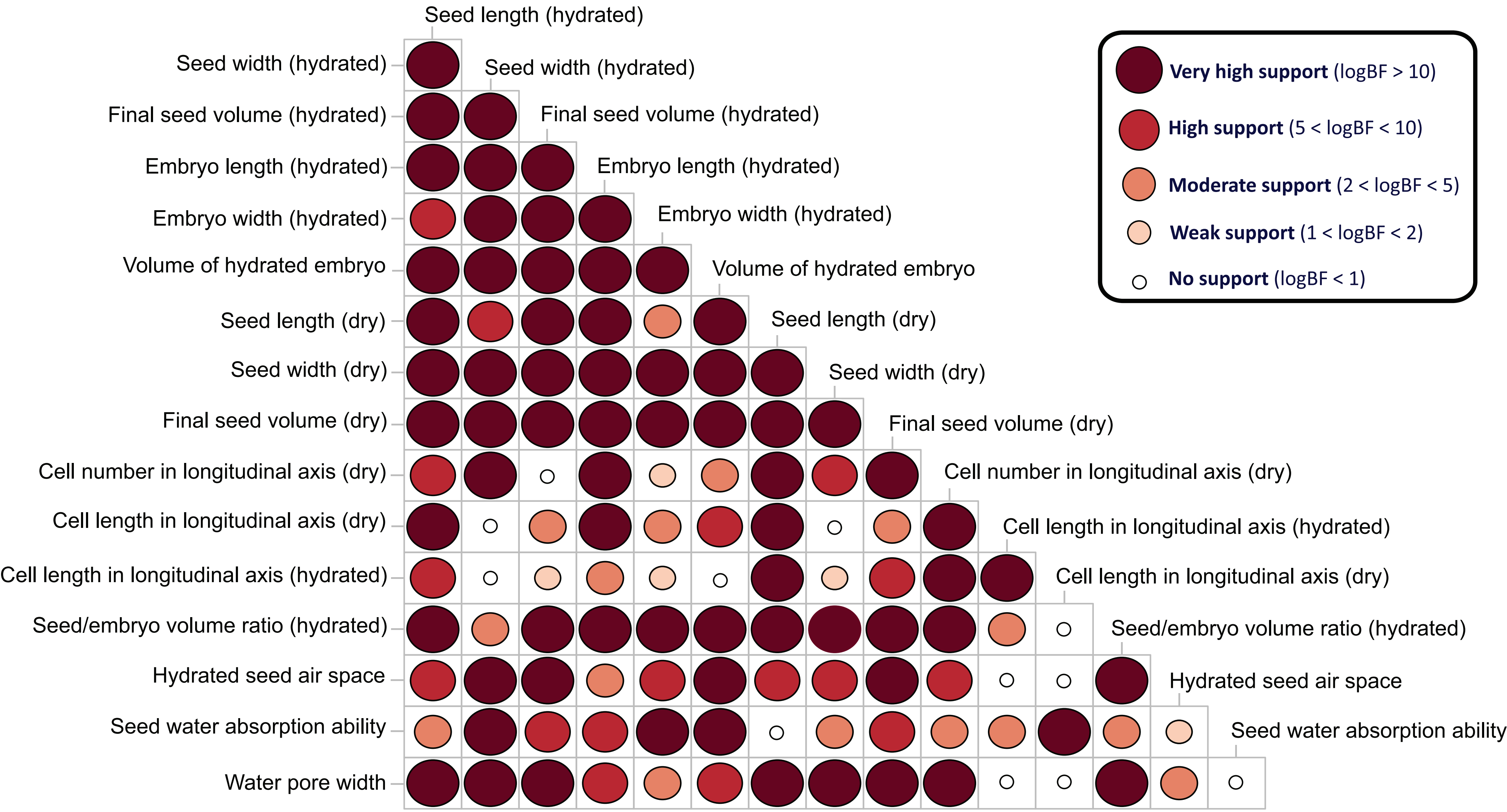
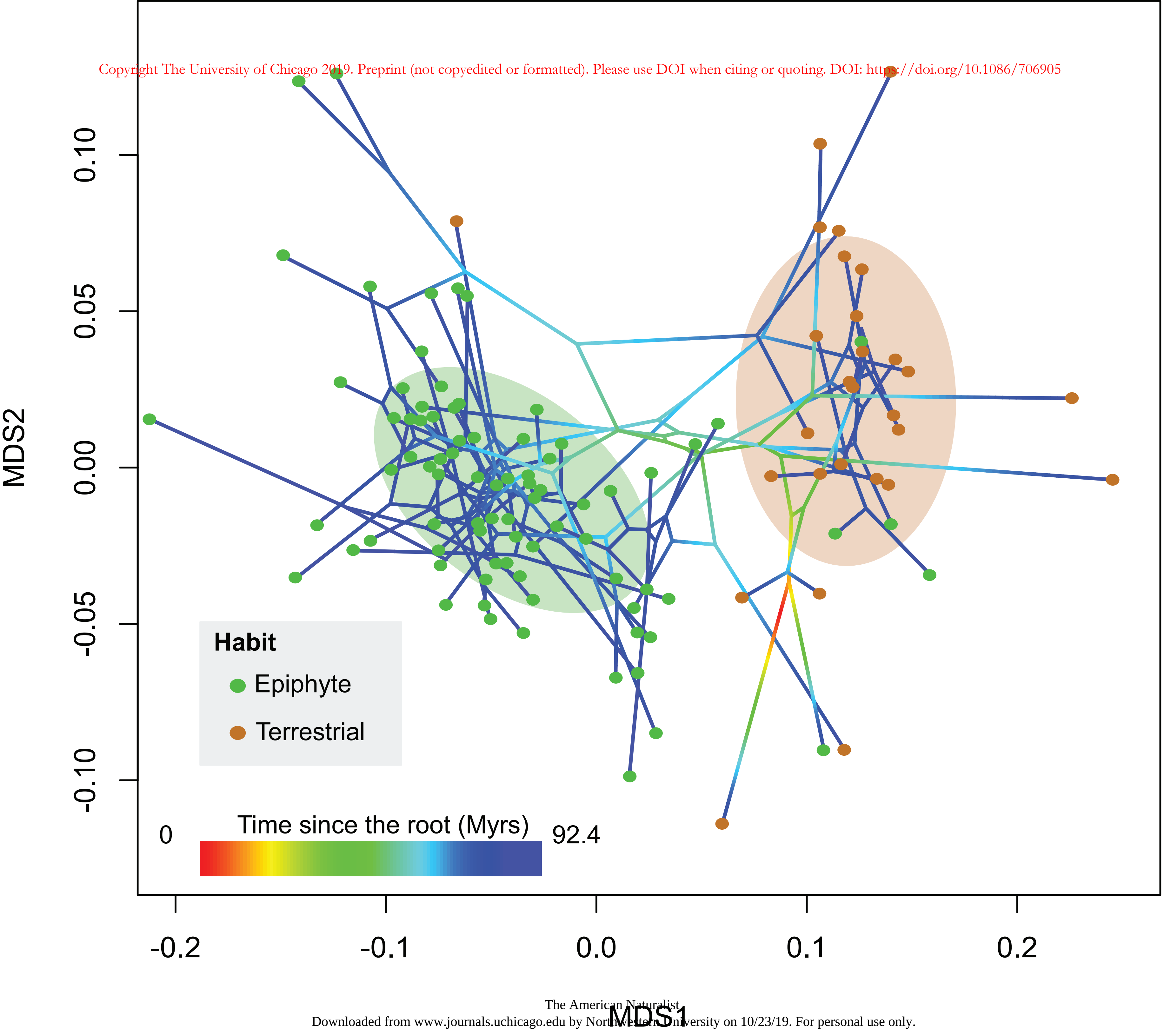


Figure 3


MDS2
0.10
0.05
0.00
-0.05
-0.10
MDS1
-0.2
-0.1
0.0
0.1
0.2
Habit
● Epiphyte
● Terrestrial
Time since the root (Myrs)
0
92.4