

Retracing the contours of the early angiosperm environmental niche

Robin Pouteau^{1,2,*}, Santiago Trueba^{2,3} and Sandrine Isnard²

¹Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China,

²UMR AMAP, IRD, CIRAD, CNRS, INRA, Montpellier University, Noumea, New Caledonia and ³School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

*For correspondence. E-mail robin.pouteau@uni-konstanz.de

Received: 9 April 2019 Returned for revision: 31 May 2019 Editorial decision: 19 July 2019 Accepted: 25 July 2019

Published electronically 12 August 2019

- **Background and Aims** Our aim was to understand the environmental conditions of the emergence and radiation of early angiosperms. Such a question has long remained controversial because various approaches applied in the past have drawn conflicting images of early angiosperm ecology.
- **Methods** We provided a new perspective on the question by using support vector machines to model the environmental niche of 51 species belonging to ten genera of extant lineages that diverged early during angiosperm evolution (basal angiosperms). Then, we analysed the resulting pattern of niche overlap and determined whether this pattern deviates from what would be expected on the basis of a null model or whether it might mirror a legacy of a common primitive niche based on a phylogenetic reconstruction.
- **Key Results** The niche of three-quarters of the species and all genera converged towards tropical montane cloud forests (TMCFs). The latitudinal pattern of basal angiosperm richness indeed culminated in the tropics, and the elevational pattern revealed a humpback curve peaking between 2000 m and 3500 m when accounting for the effect of area. At first glance, this diversity pattern does not significantly differ from null predictions. However, we revealed a tendency for the basal-most taxa to occur in TMCFs so that phylogenetic reconstructions indicated that the niche of the common ancestor of the sampled basal angiosperms had a probability of 0.85–0.93 to overlap with TMCFs.
- **Conclusions** Our new approach indicates that the environmental convergence of extant basal angiosperms towards TMCFs would reflect a legacy of an ancestral niche from which the least basal taxa would have diverged following a random pattern under geometric constraints.

Key words: Angiosperm evolution, biogeography, biome, life-history traits, maximum likelihood phylogenetic reconstruction, macro-ecology, mid-domain effect, niche modelling, relict angiosperms, species distribution models.

INTRODUCTION

Flowering plants (angiosperms) are undoubtedly the most species-rich and ecologically dominant clade of plants that has ever occurred. Their diversity and abundance in most ecosystems worldwide mirror their evolutionary success. The rapid diversification of angiosperms during the Cretaceous has fascinated generations of botanists since the time of Charles Darwin who referred to them as an ‘abominable mystery’ (Darwin and Seward, 1903; Friedman, 2009). Despite many attempts to depict the conditions in which angiosperms emerged within ecosystems formerly dominated by gymnosperms and ferns, the nature of the environment in which this radiation has begun remains enigmatic.

The long-held approaches based on fossil plant records have generated a variety of hypotheses about the habitat from which early angiosperms have radiated, sometimes thought to be semixerophytic shrublands (Stebbins, 1974), stream-channel margins at the early successional stage in arid regions (Doyle and Hickey, 1976; Hickey and Doyle, 1977), coastal deltas, lagoons and tidal flats (Retallack and Dilcher, 1986) or swampy woodlands (Coiffard *et al.*, 2007). It is perhaps not surprising that no emerging consensus has been delivered regarding the

challenging task of reliably reconstituting paleoenvironments from fossils of extinct plants and their life-history traits.

Another historical image of the early angiosperm ecology has been inferred from current distributional patterns of modern representatives of angiosperm groups thought to be ‘primitive’ (Takhtajan, 1969; Thorne, 1976). This approach led to the view that the ancestral habitat of flowering plants would have borne a resemblance to extant tropical rain forests. However, biogeographical mechanisms such as extinctions subsequent to arid paleoclimatic events or dispersal barriers might skew such inference (Morley, 2000; Coiffard *et al.*, 2007).

Alternatively, the ecological distribution of flowering plants which diverged from the lineage leading to most flowering plants (basal angiosperms) has been viewed as reflecting many of the environmental attributes of early angiosperms (Feild *et al.*, 2000, 2004, 2009; Feild and Arens, 2005, 2007). Because the ecological diversification of angiosperms probably parallels the diversification of the main angiosperms clades, as highlighted by fossils (Doyle *et al.*, 2008), the extant members of the basal grade represented by terrestrial woody species might represent the best living models of the ecology of the earliest angiosperms (Feild *et al.*, 2011).

The current image of early angiosperm ecology drawn from extant basal angiosperms is primarily based on analyses of their eco-morphological traits (xylem structure, leaf mesophyll, growth habit and seed size) and eco-physiological performance (photosynthetic rate and stomatal conductance) as well as functional inferences from Early Cretaceous angiosperm fossil leaves. This suite of traits argues for an origin of angiosperms in habitats with conditions similar to what we know today as tropical rain forests (Feild *et al.*, 2000, 2004, 2009; Feild and Arens, 2005, 2007).

Traits were found to be useful to infer the biome distribution of early angiosperms, but the trait-based approach is of limited relevance for a quantitative assessment of the environment *per se*. As various classification schemes of tropical rain forests and other biomes have been proposed in the past on the basis of climatic variables (e.g. Whittaker and Robert, 1962; Bailey, 1983; Walter, 1984; Olson *et al.*, 2001), it remains difficult to delimit the contours of the early angiosperm climatic envelope. The use of innovative and integrative approaches is essential to understand the first steps of angiosperm evolutionary history (Katz, 2017). Several lines of evidence suggest that niche conservatism in climatic tolerance can be observed over a long evolutionary time scale and limit geographical range expansion of extant taxa (Ackerly, 2004, 2009; Crisp 2009; Buckley, 2010). Thus, an environment-focused approach searching for signatures that might remain in plant distributions and preferences that are vestiges of history is likely to complement the view of the ecology of early angiosperms drawn from plant-focused approaches.

Species distribution models (SDMs; niche models or habitat suitability models) have been designed to correlate geographic records of species occurrence with spatially explicit environmental variables (Elith and Leathwick, 2009). By delimiting a region of the environmental hyperspace (hypervolume) that encompasses observed species occurrences, these models have been interpreted to be in compliance with the Hutchinsonian concept of an environmental niche (Warren, 2012).

Basal angiosperms (*Amborella*, Austrobaileyales and Chloranthaceae) are most widespread and often restricted to the tropics (Morley, 2001; Feild *et al.*, 2009). At first sight, this pattern seems not to deviate from the global distribution of species richness where the richest areas are found in tropical regions. An influential idea to explain this pattern has been the tropical conservatism hypothesis. This hypothesis suggests that most extant clades originated in the tropics and, as such, are specialized to tropical climates (Wiens and Donoghue, 2004). As a result, most taxa might have difficulties dispersing out of the tropics because of niche conservatism, and most speciation events might have occurred in the tropics as a consequence of longer presence and greater available area (Kerkhoff *et al.*, 2014).

Another recurrent distributional feature of many extant basal angiosperms is their distribution above 1000 m elevation (e.g. Todzia, 1988; Feild *et al.*, 2009; Pouteau *et al.*, 2015), which tends to support another biogeographical model that could be behind the higher species richness in tropical regions: the mid-domain effect (MDE). According to the MDE hypothesis, random species placement over bounded gradients would predict an increasing niche overlap towards mid-domains (Colwell and Hurtt, 1994). Regarding latitudinal and elevational

gradients, the theory predicts the tropics (mid-domain between the poles) and mid-elevations (mid-domain between sea level and the highest summits) to be the richest areas. Thus, one can argue that the ecological distribution of extant basal angiosperms might simply reflect geometric constraints that might be expected from a simple null model.

In this study, we address the question of whether SDMs applied to modern basal angiosperms can contribute to reconstruct the environmental distribution of early angiosperms. In this respect, we built an individual SDM for the most prevalent terrestrial extant basal angiosperm species on a global scale. We then searched for environmental convergence that might deviate from what would be expected on the basis of a null hypothesis and might mirror environmental requirements of basal angiosperms as a potential witness of early angiosperm ecology.

MATERIALS AND METHODS

Focal extant basal angiosperms

All terrestrial extant basal angiosperm species belonging to the ANA grade and the Chloranthales order were considered (Angiosperm Phylogeny Group IV, 2016; Moore *et al.*, 2010). The root of angiosperm phylogeny is composed of *Amborella*, Nymphaeales and Austrobaileyales. Nymphaeales were discarded because their aquatic habit is thought to be derived rather than ancestral in this clade (Endress *et al.*, 1994; Feild *et al.*, 2003). We included Chloranthales occupying an uncertain position at the base of the phylogeny, often branching immediately above the ANA grade. Congruent phylogenies place Chloranthales as sister to eumagnoliids (magnoliids + eudicots) (Qiu *et al.*, 2000; Soltis *et al.*, 2000; Zanis *et al.*, 2002).

Species occurrence records were extracted from the Global Biodiversity Information Facility (GBIF) database (<http://www.gbif.org/>). We removed invalid entries, occurrences out of the recognized natural range of the species (e.g. in botanical gardens) and occurrences duplicated on the same pixel to avoid spatial autocorrelation. Subspecies and varieties were merged at the species level because many specimens have not been identified at infraspecific ranks in the GBIF.

Within each genus, the third of all species with the highest number of occurrence records were used in the subsequent analyses and the remaining two-thirds of species were discarded. The most widespread extant basal angiosperm species were expected to reflect the ecological diversification of the group and to have a distribution shaped by ecological rather than geographical boundaries (e.g. small island endemics) while maximizing the accuracy of SDMs (Stockwell and Peterson, 2002). For monospecific genera (*Amborella*, *Austrobaileya* and *Sarcandra*), we used the only species available. This method led to the selection of 51 basal angiosperm species belonging to ten genera and five families (Supplementary data Appendix 1). The number of occurrences ranged from 256 for *Chloranthus serratus* (Chloranthaceae) to four for *Illicium verum* and *Kadsura philippinensis* (Schisandraceae) with a mean of 75 occurrences per species. To ensure that unbalanced numbers of species within genera did not bias the following analyses, they were computed at two taxonomic levels: the species level and the genus level.

Niche fitting

Species' niche was described in an environmental space with two dimensions: annual mean temperature (°C) and annual rainfall (mm) to enable correspondence with the well-known biome-type classification scheme of Whittaker (Whittaker and Robert, 1962). Using a higher number of environmental dimensions would also have decreased our chance of finding a common niche pattern with, ultimately, no niche intersection. Current climate variables (averaged for the period 1960–1990) were downloaded from the WorldClim website (Hijmans *et al.*, 2005; <http://www.worldclim.org/>) at 2.5 arcminute resolution, i.e. 4.75 km at the equator, 3.25 km at 45° (BIO1 and BIO12).

Species presences projected in the 2-D environmental space were fitted using support vector machines (SVMs), a next-generation machine learning algorithm presenting numerous computational advantages including non-linearity, no assumption on the statistical distribution of training data, ability to be trained on presence-only data (i.e. without absences or pseudo-absences) and good performance when trained on few occurrence records (Guo *et al.*, 2005; Drake *et al.*, 2006; Pouteau *et al.*, 2012). SVMs model the support of the statistical distribution of environments from which the species presence observations are drawn, i.e. an environmental hyperspace, which is consistent with the classical definition of a niche as a multidimensional environmental space (Hutchinson 1965). In contrast, logistic regression (Keating and Cherry, 2004), MAXENT (Phillips *et al.*, 2006), ecological niche factor analysis (ENFA; Hirzel *et al.*, 2002) and other models based on probability densities represent the relative frequency of habitat use and are related rather to the idea of resource utilization or resource selection (Drake *et al.*, 2006).

We used the one-class SVM implementation found in the package 'e1071' (Meyer *et al.*, 2019) of the R software (R Development Core Team, 2019). SVM fitting depends on a regularization parameter, C , which controls niche breadth and a kernel function that manages the shape of the niche. We chose the Gaussian radial basis function as kernel which relies on tuning only one kernel-specific hyperparameter, γ , while outputting accurate results (Hsu *et al.*, 2010). The 'tune.svm' function was used to search for the optimal couple of C and γ in the range $[2^{-10}, 2^{-9}, \dots, 2^{10}]$ after 4-fold cross-validation in order to maximize model accuracy while preventing overfitting.

Niche overlap

Once fitted, individual species niches were stacked so that they expressed the local potential richness of basal angiosperms over each site of the combined map or each region of the environmental space (Guisan *et al.*, 1999). We then computed a niche overlap index (NO) as the proportion of co-occurring basal angiosperm species or genera. At the genus level, niches were defined by merging species-based models rather than by building new models from merged species occurrences because it was easier to manage species' unbalanced occurrences and this procedure was more consistent with the species-specific concept of environmental niche. Thereafter, we focused our attention on regions of maximum niche overlap at the species

and genus ranks, denoted as 'species NO_{\max} region' and 'genus NO_{\max} region', respectively.

Phylogenetic reconstruction

The term 'basal', used to describe the phylogenetic position of early diverging lineages of angiosperms, is often incorrectly interpreted as a synonymous for 'primitive', yet one cannot assume that a basal group retains more ancestral features and most of basal taxa bear many derived features (Crisp and Cook, 2005). Ancestral character states might nevertheless be captured by being mapped on a phylogeny so that any character that is shared by successively branching lineages can reasonably be posited as putatively ancestral (Felsenstein, 1985). To distinguish whether occupation of a biome stemmed from a convergent evolution in angiosperms towards a derived environment (niche evolution) or from a legacy of a common primitive niche (niche conservatism), we assembled a composite phylogenetic tree of extant basal angiosperms using as a backbone the phylogenetic relationships available in Smith and Brown (2018), including the branch length calibration proposed in Magallón *et al.* (2015). These relationships coincide with the topology proposed by Doyle and Endress (2000), who presented complete and fully resolved relationships of the sampled genera. We mapped NO_{\max} at the species and genus ranks. We used Brownian motion-based maximum likelihood estimations of ancestral states considering NO_{\max} as a continuous variable. We used the packages 'ape' (Paradis and Schliep, 2018) and 'phytools' (Revell, 2012) for the production of phylogenetic trees, to perform ancestral state reconstructions and to visualize ancestral states on the phylogeny.

Testing for a mid-domain effect

We built a null model to test whether NO_{\max} regions mirrored ecological preferences of basal angiosperms or a purely stochastic MDE according to which species ranges thrown randomly within a bounded range are expected to overlap more in the centre of the domain (mid-latitudes and elevations) than at the borders (low and high latitudes and elevations) (Colwell and Lees, 2000).

First, we corrected the area effect according to which differences in land area along the global latitudinal gradient can influence the pool of species found in each latitudinal band or according to which the schematically conical shape of mountains provides smaller habitats for species as elevation increases. This phenomenon is a direct consequence of the basic species richness–habitat size relationship equated by Arrhenius (1921):

$$S = cA^z \quad (1)$$

where S is the empirical species richness, c a constant that equals the number of species that the latitudinal or elevational band would support if it was confined to a one square unit, A is the regional area of the elevational zone and z is a constant describing the slope in a double-log species–area plot (McCain, 2007).

We used eqn (1) to account for the area effect on the global latitudinal and elevational patterns of basal angiosperm richness. S , the area-dependent basal angiosperm richness, was estimated using the range overlap of species within bands of 2° latitude and 100 m elevation. A was the planar area occupied by 2° latitudinal and 100 m elevational zones. Elevation was derived from a Shuttle Radar Topographic Mission digital elevation model (DEM) aggregated to 2.5 arcminutes resolution using the nearest-neighbour resampling method. We empirically determined z as the slope of the linear regression of the species richness (S)–area (A) plot on a log–log scale, and subsequently calculated c , the area-independent basal angiosperm richness, by solving the power model $c = SA^z$ (see McCain, 2007 for further details). For visual interpretation, c was multiplied by a constant so that the maximal empirical richness matched the maximal area-corrected richness.

In order to test whether the MDE explains the richness pattern of basal angiosperms within latitudinal and elevational boundaries of their distribution, area-corrected values of richness were compared with the average of 10 000 Monte Carlo simulations of a null model (McCain, 2007). Simulations of species richness were obtained using the software RangeModel 5.0 (Colwell, 2008) with empirical range size of species and random range mid-points. We assumed that basal angiosperm latitudinal and elevational distribution reflected an MDE if richness simulations were significantly correlated to area-corrected observations.

RESULTS

Widespread terrestrial basal angiosperms occurred in a large climatic envelope where annual mean temperature ranged from -3°C to 30°C and within a rainfall interval of 700 to 7500 mm (Fig. 1A). This climatic envelope covered all Whittaker's biomes with the only exception of sub-tropical desert and tundra (Fig. 1C). The niche of 39 species out of the 51 (77 %) overlapped in a most occupied region of the environmental hyper-space (species NO_{\max} region) described by an annual mean

temperature of 17°C and annual precipitation in the range 2300–2400 mm year $^{-1}$. The species NO_{\max} region was located in the biome Whittaker referred to as 'temperate rain forest' (Fig. 1C). The ten basal angiosperm genera converged into a larger region (genus NO_{\max} region) characterized by annual mean temperature in the range of 17 – 22°C and annual rainfall in the range of 2000–2800 mm (Fig. 1B). The genus NO_{\max} region intersected four biomes: 'tropical rain forest', 'tropical seasonal forest', 'temperate rain forest' and 'temperate deciduous forest' (Fig. 1C).

This pattern in which more than three-quarters of the selected basal angiosperm species and all genera intersected in a similar environmental space was unexpected regarding the fact that all genera never co-occur (poor geographic overlap) and occupy altogether different biogeographical regions (Fig. 2). Two genera occur exclusively in the tropics (*Amborella* and *Austrobaileya*), five genera were represented by species occurring in both tropical and temperate regions (*Ascarina*, *Chloranthus*, *Hedyosmum*, *Sarcandra* and *Trimenia*) and the three genera belonging to the Schisandraceae were represented by species only occurring in temperate regions (*Illicium*, *Kadsura* and *Schisandra*). *Illicium* and *Schisandra* are distributed in the Northern hemisphere, *Chloranthus*, *Kadsura* and *Sarcandra* in Eastern Asia and in the Pacific, *Hedyosmum* in the Neotropics, *Ascarina* and *Trimenia* in the South Pacific, *Amborella* is endemic to New Caledonia and *Austrobaileya* is endemic to Queensland, Australia.

The number of species per genus explained little of the variation in the proportion of species within each genus whose niche intersected the species and genus NO_{\max} regions ($r^2 = 0.02$ for the species NO_{\max} region and $r^2 = 0.20$ for the genus NO_{\max} region; P -value = 0.73 and 0.20, respectively). The niche of the monospecific genera *Amborella* and *Austrobaileya* as well as those of a high percentage of species in the Chloranthales (*Sarcandra*, *Chloranthus* and *Ascarina*) crossed both NO_{\max} regions (5–100 %) (Fig. 3), the two exceptions being *Ascarina lucida*, endemic to New Zealand, and the Andean *Hedyosmum angustifolium*. In contrast, Austrobaileyales (*Illicium*, *Kadsura*,

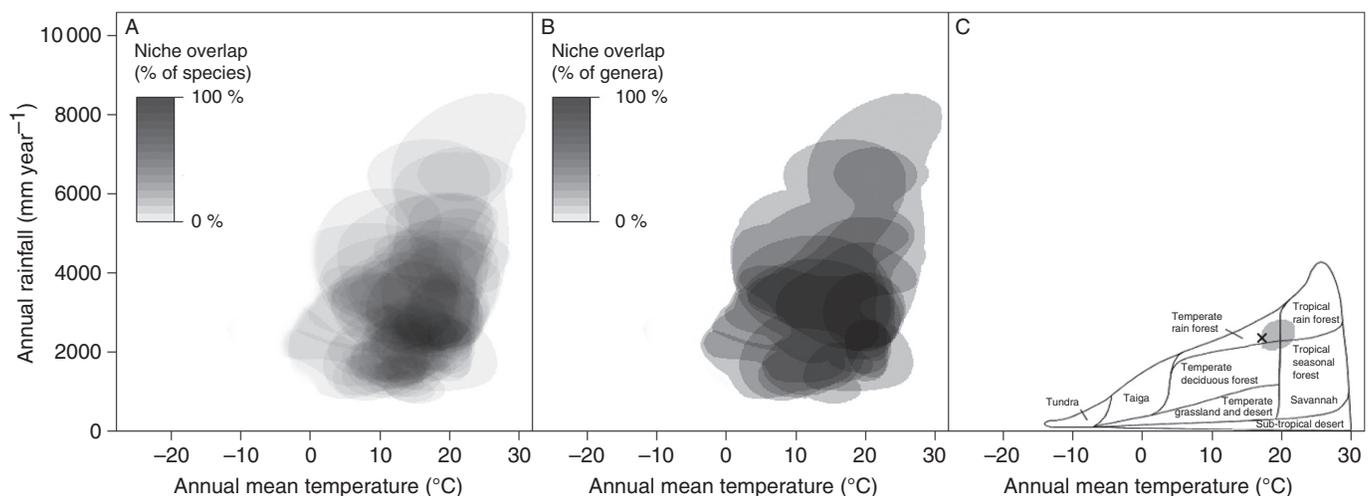


FIG. 1. (A) Niche overlap of 51 widespread terrestrial basal angiosperm species. (B) Niche overlap of the ten corresponding genera (see the Materials and methods for computational details). (C) Black lines represent contours of Whittaker's biome-type classification scheme. The centre of the black cross indicates the region of maximum species niche overlap (species NO_{\max} region) occupied by 39 species (77 %). The grey-shaded area indicates the region of maximum genus niche overlap (genus NO_{\max} region) where all genera (ten) co-occur.

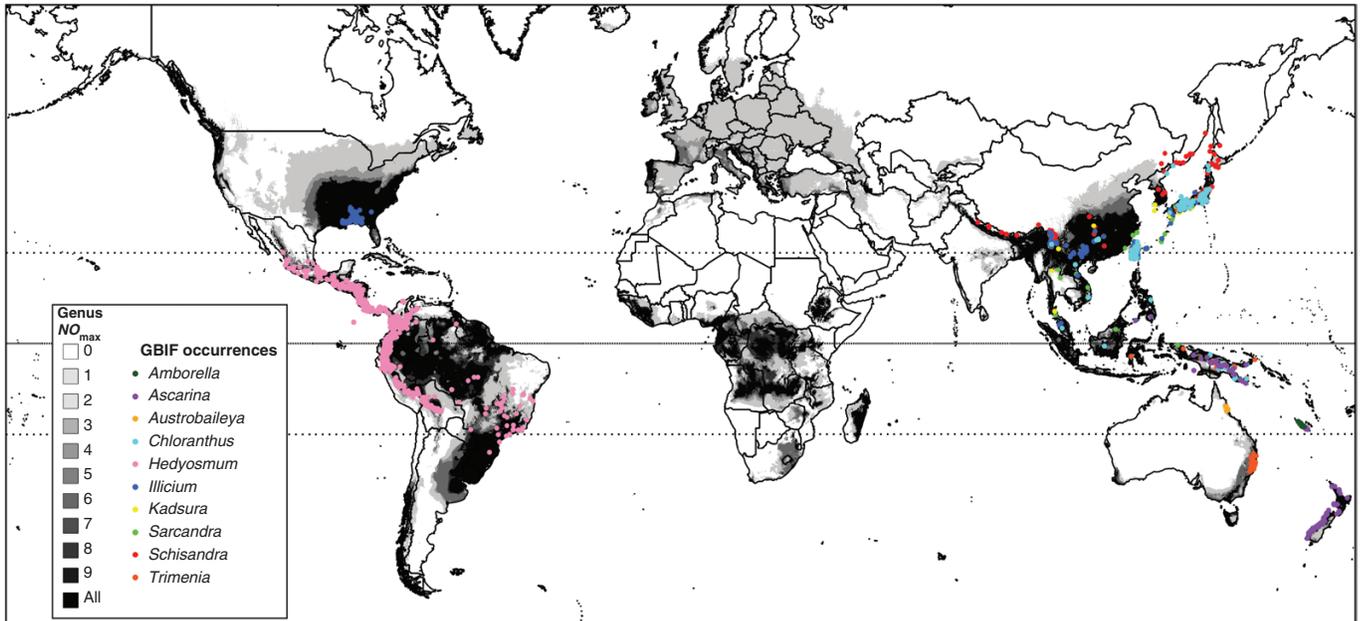


FIG. 2. Distribution of the ten terrestrial basal angiosperm genera according to herbarium records from the GBIF database. Genera are represented by the most prevalent third of all species found in each genus (or the only species available for monospecific genera). Grey levels denote the proportion of basal angiosperm genera whose climate envelopes overlap in a given region.

Schisandra and *Trimenia*) less frequently occupied the species NO_{max} region (40–80 %). Within this group, both *Trimenia* species *T. moorei* and *T. papuana*, however, intersected the genus NO_{max} region, while Schisandraceae (*Illicium*, *Kadsura* and *Schisandra*) were found to be less prevalent in that region (63–80 %) and to occur more frequently under cooler and drier temperate climates (Fig. 3). Coincidentally, maximum likelihood phylogenetic reconstructions indicated that the putative common ancestor of the sampled basal angiosperms had a species NO_{max} value of 0.85, and a genus NO_{max} value of 0.93 (Fig. 3). Therefore, both reconstructions suggested high probability for a high niche overlap in the putative common ancestor of the sampled basal angiosperms.

At a global scale, the latitudinal pattern of basal angiosperm richness was poorly affected by the area effect as empirical and area-corrected patterns were highly correlated ($r^2 = 0.89$ at the species level and $r^2 = 0.90$ at the genus level; P -value < 0.05 in both cases) and culminated in the tropics between 10° south and 30° north (Fig. 4A, C). However, correction of the area on the global elevational pattern of basal angiosperm richness revealed a humpback curve peaking between 2000 and 3500 m (Fig. 4B, D). At all taxonomic levels, area-corrected patterns along both latitudinal and elevational gradients fell within the prediction curve of the MDE model ($r^2 > 0.55$; P -value < 0.05).

DISCUSSION

Most widespread extant basal angiosperms appeared limited in their latitudinal distribution by temperature and precipitation: areas with mean annual temperature below -3°C and annual rainfall below 700 mm are never occupied. This limited distribution could be explained by their ecophysiological requirements. For instance, basal angiosperms might have a restricted

distribution due to their sensitivity to hydraulic failure derived from xylem embolisms (Trueba et al., 2017), which result from the very high xylem tensions experienced under drought stress. Moreover, they also present low hydraulic competitiveness compared with vessel-bearing eudicot angiosperms with greater hydraulic efficiency (Sperry et al., 2007), which might have restricted basal angiosperms to more hydraulically permissive environments.

Many basal angiosperms bear tracheids or vessels composed of vessel elements with long scalariform perforation plates and various degrees of pit membrane remnants (Carlquist and Schneider, 2002). Vessels with scalariform perforation plates exhibit hydraulic performances similar to those of tracheids, driving low hydraulic conductance and high vulnerability to drought-induced embolisms (Sperry et al., 2007; Trueba et al., 2019). Because of the physiological impact of anatomical traits such as a tracheid-based wood or vessels with long scalariform perforation plates, hydraulically permissive habitats with low evapotranspirative demands are expected to be particularly suitable for many basal angiosperm taxa (Feild and Wilson, 2012; Pouteau et al. 2015; Trueba et al., 2017). Given that these types of vascular conduits seem to be maintained in most basal angiosperms (ANA and Chloranthaceae), they are considered as a plesiomorphic state in angiosperms, and therefore basal taxa have been suggested to occupy mesic to wet environments since their origin (Carlquist, 2012).

We noticed a discernible preference of extant basal angiosperms for intermediate mesic to moist and cool environments located in the tropics at mid-elevation (2000–3500 m). This most occupied environment is typical of tropical montane cloud forests (TMCFs) that do not appear *per se* in the bidimensional biome classification of Whittaker (Whittaker and Robert, 1962), probably because they cover a marginal proportion of the Earth's terrestrial area (1.4 % of tropical forest area;

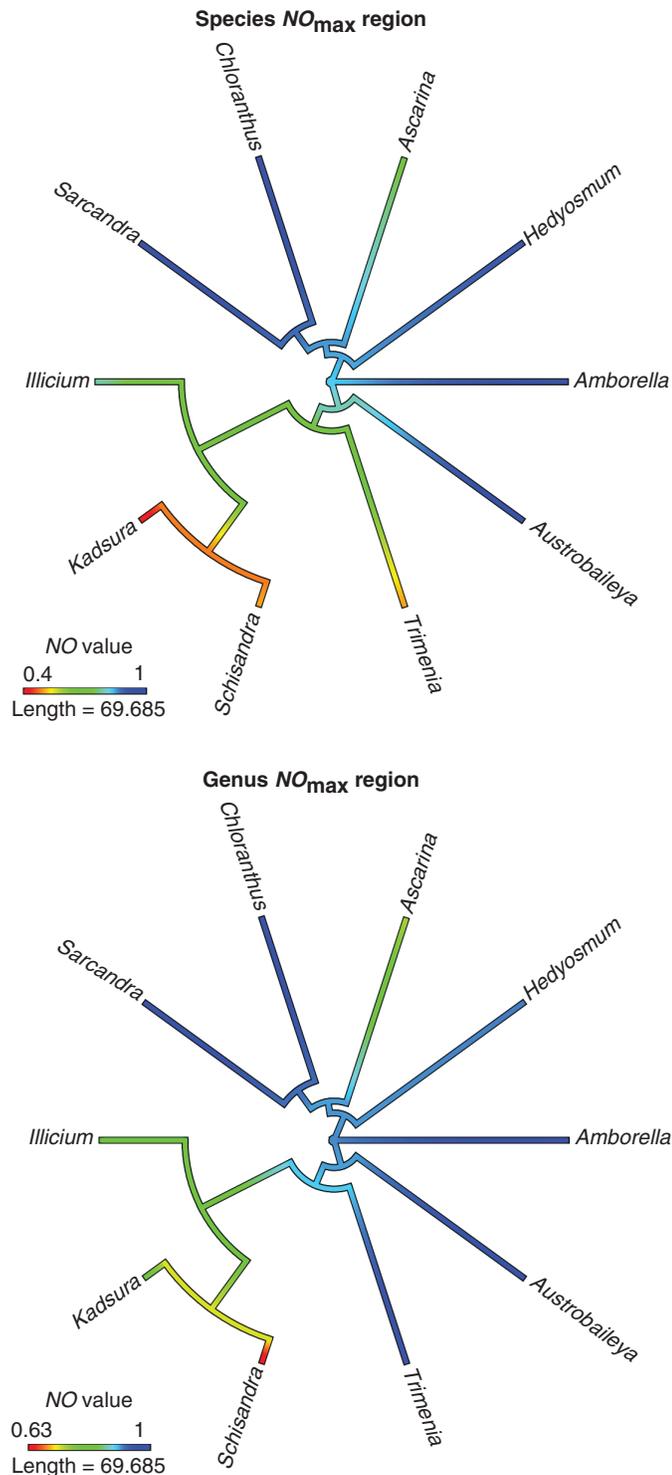


FIG. 3. Maximum likelihood estimation of ancestral states occupying NO_{max} regions at the species and genus levels. The continuous colour gradient shows the most probable NO_{max} values across the basal angiosperm phylogeny.

Bruijnzeel et al., 2011). TMCFs are characterized by frequent cloud presence, low light transmittance, cool temperature, reduced vapour pressure deficit, and thus a low evaporative demand (Bruijnzeel et al., 2011). The elevation of TMCFs shows considerable variation as it depends on many meteorological

(moisture content of the air, velocity and direction of the wind) and oro-topographical effects (mountain size, distance to the sea). However, a typical elevation for TMCFs on large, inland mountains is between 2000 and 3500 m while on coastal and isolated mountains, as on oceanic islands, the cloud forests is found at much lower elevations (e.g. 1000 m in Hawaii) (Hamilton et al., 1995). The question then arises as to whether the occupancy of TMCFs reflects a random distribution or a legacy of a common ancestral niche.

The global latitudinal and elevational distribution of richness in extant basal angiosperms converging in TMCFs was statistically correlated with predictions of the MDE within the ecological limits of basal angiosperms imposed by their requirements for hydraulically permissive habitats. Thus, at first glance, the abundance of extant basal angiosperms in TMCFs appears not better explained by a deterministic niche perspective than by a purely null model within these boundaries. However, phylogenetic mapping of biome occupation revealed that the occupation of TMCFs is likely to have been shared with a common ancestor. This finding stems from the fact that the most basal taxa tend to occupy TMCFs more frequently than the least basal taxa, which is not predicted by the MDE. The convergence towards TMCFs of the environmental niche of the basal-most terrestrial woody angiosperms such as that of the monospecific genera *Amborella* and *Austrobaileya* indicates a legacy of an ancestral mesic to moist and cool ecological niche that might have been conserved over time. Nevertheless, less basal genera such as *Kadsura*, *Schisandra* and *Illicium* have both higher species and ecological diversification as they tend to comprise more species and to diverge from this ancestral niche following a random pattern under physiological and geometric constraints.

The Austrobaileya indeed decreased the probability that the common ancestor would have occupied the species NO_{max} region. However, this may arise from the poor sampling of certain genera such as *Trimenia* in which many less widespread species, not sampled in this study, are known to be restricted to TMCFs. This is the case of the two *Trimenia* endemic to the Marquesas archipelago, *T. nukuhivensis* found above 760 m on the islands of Nuku Hiva and Ua Pou, *T. marquesensis* found above 790 m on Hiva Oa and Tahuata (Wagner and Lorence, 2002), of *T. weinmanniifolia* found above 700 m in Fiji and Samoa, of *T. bougainvilleensis* found above 1500 m in the Solomon Islands (Rodenburg, 1971) and of *T. neocaledonica* occurring above 700 m in New Caledonia (Morat and MacKee, 1977). It is perhaps not surprising that many basal angiosperms have persisted on islands over time as island TMCFs have been shown to be much less sensitive to climate change than mainland TMCFs (Pouteau et al., 2018). These findings support the idea that TMCFs is the biome with the highest probability to have hosted early angiosperms.

Our niche reconstruction therefore challenges the assumption built from fossil records that early angiosperms emerged in arid to semi-arid biomes (Stebbins, 1974; Doyle and Hickey, 1976; Hickey and Doyle, 1977) and tends to support the idea developed from biogeographical patterns (Takhtajan, 1969; Thorne, 1976) and eco-morphological traits of extant basal angiosperms (Feild et al., 2000, 2004, 2009; Feild and Arens, 2005, 2007) suggesting that the origin of angiosperms would be in tropical rain forests. However, our approach tells

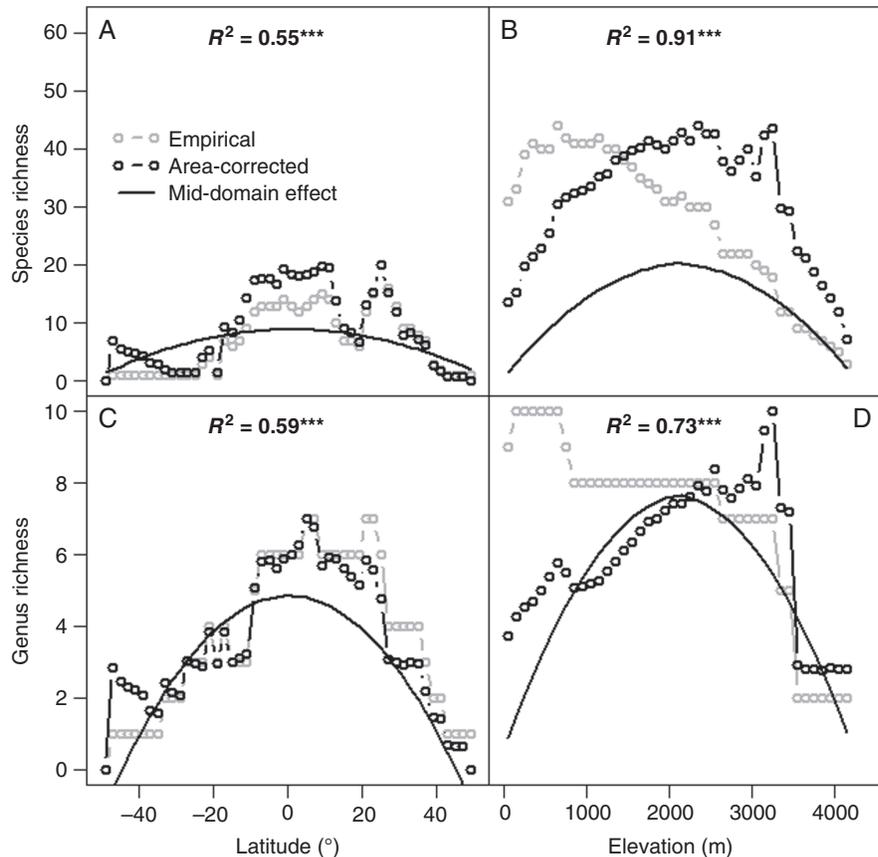


FIG. 4. Comparison of basal angiosperm richness patterns with a null mid-domain effect (MDE) model along latitudinal (A, C) and elevational gradients (B, D) at the species (A, B) and genus levels (C, D). R^2 are determination coefficients between area-corrected species richness (dashed black line) and MDE simulations (continuous black line).

a slightly different story as it identified tropical temperate-like rain forests (approx. 17 °C mean annual temperature and approx. 2300–2400 mm year⁻¹) as the most likely ancestral habitat, which is typically represented by TMCFs. If former approaches based on extant basal angiosperms were shown to be useful to draw an overall picture of the early angiosperm biome, our direct assessment of the environmental distribution of extant basal angiosperms enabled a more detailed delimitation of the contours of the early angiosperm environmental niche.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of Appendix 1: list of basal angiosperm species belonging to the ANA grade and the Chloranthales order used in this study.

ACKNOWLEDGEMENTS

We thank Taylor S. Feild (University of Florida, USA), Greg Jordan (University of Tasmania, Australia), Sébastien Lavergne (UMR LECA/CNRS, France), Yohan Pillon (UMR LSTM/IRD, France) and two anonymous reviewers for their helpful comments and suggestions.

LITERATURE CITED

- Ackerly DD. 2004. Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. *The American Naturalist* **163**: 654–671.
- Ackerly DD. 2009. Evolution, origin and age of lineages in the Californian and Mediterranean floras. *Journal of Biogeography* **36**: 1221–1233.
- Arrhenius O. 1921. Species and area. *Journal of Ecology* **9**: 95–99.
- Angiosperm Phylogeny Group IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**: 1–20.
- Bailey RG. 1983. Delineation of ecosystem regions. *Environmental Management* **7**: 365–373.
- Brujinzeel LA, Scatena FN, Hamilton LS. 2010. *Tropical montane cloud forests*. Cambridge: Cambridge University Press.
- Buckley LB, Davies TJ, Ackerly DD, et al. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences* **277**: 2131–2138.
- Carlquist S. 2012. How wood evolves: a new synthesis. *Botanique* **90**: 901–940.
- Coiffard C, Gomez B, Thévenard F. 2007. Early Cretaceous angiosperm invasion of Western Europe and major environmental changes. *Annals of Botany* **100**: 545–553.
- Colwell RK, Hurtt GC. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist* **144**: 570–595.
- Colwell RK, Rahbek C, Gotelli NJ. 2004. The mid-domain effect and species richness patterns: what we have learned so far? *The American Naturalist* **163**: E1–E23.
- Crisp MD, Cook LG. 2005. Do early branching lineages signify ancestral traits? *Trends in Ecology and Evolution* **20**: 122–128.
- Crisp MD, Arroyo MTK, Cook LG, et al. 2009. Phylogenetic biome conservatism on a global scale. *Nature* **458**: 754–756.

- Darwin F, Seward AC. 1903. *More letters of Charles Darwin. A record of his work in a series of hitherto unpublished letters*. London: John Murray.
- Doyle JA, Endress PK. 2000. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *International Journal of Plant Sciences* **161**: 121–153.
- Doyle JA, Hickey LJ. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In: Beck CB, ed. *Origin and early evolution of angiosperms*. New York: Columbia University Press, 139–206.
- Doyle JA, Endress PK, Upchurch GR. 2008. Early Cretaceous monocots: a phylogenetic evaluation. *Acta Musei Nationalis Pragae Series B Historia Naturalis* **64**: 59–87.
- Drake JM, Randin C, Guisan A. 2006. Modelling ecological niches with support vector machines. *Journal of Applied Ecology* **43**: 424–432.
- Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**: 677–697.
- Endress PK. 1994. Evolutionary aspects of the floral structure in *Ceratophyllum*. *Plant Systematics and Evolution* **8**: 175–183.
- Feild TS, Arens NC. 2005. Form, function and environments of the early angiosperms: merging extant phylogeny and ecophysiology with fossils. *New Phytologist* **166**: 383–408.
- Feild TS, Arens NC. 2007. The ecophysiology of early angiosperms. *Plant, Cell & Environment* **30**: 291–309.
- Feild TS, Wilson JP. 2012. Evolutionary voyage of angiosperm vessel structure—function and its significance for early angiosperm success. *International Journal of Plant Sciences* **173**: 596–609.
- Feild TS, Zwienecki MA, Brodribb T, Jaffré T, Donoghue MJ, Holbrook NM. 2000. Structure and function of tracheary elements in *Amborella trichopoda*. *International Journal of Plant Sciences* **161**: 705–712.
- Feild TS, Arens NC, Dawson TE. 2003. The ancestral ecology of angiosperms: emerging perspectives from basal lineages. *International Journal of Plant Science* **164**: S129–S142.
- Feild TS, Arens NC, Doyle JA, Dawson TE, Donoghue MJ. 2004. Dark and disturb: a new image of early angiosperm ecology. *Paleobiology* **30**: 82–107.
- Feild TS, Chatelet DS, Brodribb TJ. 2009. Ancestral xerophobia: a hypothesis on the whole plant ecophysiology of early angiosperms. *Geobiology* **7**: 237–264.
- Feild TS, Upchurch GR, Chatelet DS, et al. 2011. Fossil evidence for low gas exchange capacities for Early Cretaceous angiosperm leaves. *Paleobiology* **37**: 195–213.
- Felsenstein J. 1985. Phylogenies and the comparative method. *The American Naturalist* **125**: 1–15.
- Friedman WE. 2009. The meaning of Darwin's 'abominable mystery'. *American Journal of Botany* **96**: 5–21.
- Guisan A, Weiss SB, Weiss AD. 1999. GLM versus CCA spatial modelling of plant distribution. *Plant Ecology* **143**: 107–122.
- Guo Q, Kelly M, Graham CH. 2005. Support vector machines for predicting distribution of Sudden Oak Death in California. *Ecological Modelling* **182**: 75–90.
- Hamilton LS, Juvik JO, Scatena FN. 1994. *Tropical montane cloud forests*. New York: Springer-Verlag.
- Hickey LJ, Doyle JA. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review* **43**: 538–589.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- Hirzel AH, Hausser J, Chessel D, Perrin N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* **83**: 2027–2036.
- Hsu C-W, Chang C-C, Lin C-J. 2010. *A practical guide to support vector classification*. Technical note from the Department of Computer Science and Information Engineering, National Taiwan University, Taiwan. Available at: <http://www.csie.ntu.edu.tw/~cjlin/papers/guide/guide.pdf>
- Hutchinson GE. 1965. *Ecological theatre and the evolutionary play*. New Haven, CT: Yale University Press.
- Katz O. 2017. Extending the scope of Darwin's 'abominable mystery': integrative approaches to understanding angiosperm origins and species richness. *Annals of Botany* **121**: 1–8.
- Keating KA, Cherry S. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* **68**: 774–789.
- Kerckhoff AJ, Moriarty PE, Weiser MD. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences, USA* **111**: 8125–8130.
- Magallón S, Gómez-Acevedo S, Sánchez-Reyes LL, Hernández-Hernández T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* **207**: 437–453.
- McCain C. 2007. Area and mammalian elevational diversity. *Ecology* **88**: 76–86.
- Meyer D, Dimitriadou E, Hornik K, Weingessel A, Leisch F. 2019. *Misc functions of the Department of Statistics (e1071), TU Wien. R package version 1.7-0.1*. Available at: <http://cran.r-project.org/web/packages/e1071/>
- Moore MJ, Soltis PS, Bell CD, Burleigh JG, Soltis DE. 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proceedings of the National Academy of Sciences, USA* **107**: 4623–4628.
- Morat P, MacKee HS. 1977. Quelques précisions sur le *Trimenia neocaledonica* Bak. f. et la famille des Triméniacées en Nouvelle-Calédonie. *Adansonia* **17**: 205–213.
- Morley RJ. 2000. *Origin and evolution of tropical rain forests*. Chichester, UK: Wiley.
- Morley RJ. 2001. Why are there so many primitive angiosperms in the rain forests of Asia–Australasia? In: Metcalfe I, Smith JMB, Morwood M, Davidson I, eds. *Faunal and floral migrations and evolution in the SE Asia–Australia*. Tokyo: Balkema, 185–199.
- Olson DM, Dinnerstein E, Wikramanayake ED, et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* **51**: 933–938.
- Paradis E, Schliep K. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**: 526–528.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**: 231–259.
- Pouteau R, Meyer J-Y, Taputuarai R, Stoll B. 2012. Support vector machines to map rare and endangered native plants in Pacific islands forests. *Ecological Informatics* **9**: 37–46.
- Pouteau R, Trueba S, Feild TS, Isnard S. 2015. New Caledonia: a Pleistocene refugium for rain forest lineages of relict angiosperms. *Journal of Biogeography* **42**: 2062–2077.
- Pouteau R, Giambelluca T, Ah-Peng C, Meyer J-Y. 2018. Will climate change shift the lower ecotone of tropical montane cloud forests upwards on islands? *Journal of Biogeography* **45**: 1326–1333.
- Qiu YL, Lee JH, Bernasconi-Quadroni F, et al. 2000. Phylogeny of basal angiosperms: analyses of five genes from three genomes. *International Journal of Plant Sciences* **161**: S3–S27.
- R Development Core Team. 2019. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Retallack GJ, Dilcher DL. 1986. Cretaceous angiosperm invasion of North America. *Cretaceous Research* **7**: 227–252.
- Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Rodenburg WF. 1971. A revision of the genus *Trimenia* (Trimeniaceae). *Blumea* **19**: 3–15.
- Smith SA, Brown JW. 2018. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* **105**: 302–314.
- Soltis DE, Soltis PS, Chase MW, et al. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society* **133**: 381–461.
- Sperry JS, Hacke UG, Feild TS, Sano Y, Sikkema EH. 2007. Hydraulic consequences of vessel evolution in angiosperms. *International Journal of Plant Sciences* **168**: 1127–1139.
- Stebbins GL. 1974. The probable growth habit of the earliest flowering plants. *Annals of the Missouri Botanical Garden* **52**: 457–468.
- Stockwell DRB, Peterson AT. 2002. Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**: 1–13.
- Takhtajan AL. 1969. *Flowering plants: origin and dispersal*. Washington, DC: Smithsonian Institution.
- Thorne RF. 1976. A phylogenetic classification of the Angiospermae. *Evolutionary Biology* **9**: 35–106.
- Todzia CA. 1988. Chloranthaceae: *Hedyosmum*. *Flora Neotropica* **48**: 1–138.
- Trueba S, Pouteau R, Lens F, et al. 2017. Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical island. *Plant, Cell & Environment* **40**: 277–289.

- Trueba S, Delzon S, Isnard S, Lens F. 2019.** Similar hydraulic efficiency and safety across vesselless angiosperms and vessel-bearing species with scalariform perforation plates. *Journal of Experimental Botany* **70**: 3227–3240.
- Wagner WL, Lorence DH. 2002.** *Flora of the Marquesas Islands website*. Available at: <http://botany.si.edu/pacificislandbiodiversity/marquesasflora/index.htm>
- Warren DL. 2012.** In defense of ‘niche modeling’. *Trends in Ecology and Evolution* **27**: 497–500.
- Whittaker RH. 1962.** Classification of natural communities. *Botanical Review* **28**: 1–239.
- Walter H. 1984.** *Vegetation of the earth and ecological systems of the geobiosphere*. New York: Springer-Verlag.
- Wiens JJ, Donoghue MJ. 2004.** Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* **19**: 639–644.
- Zanis MJ, Soltis DE, Soltis PS, Mathews S, Donoghue MJ. 2002.** *Proceedings of the National Academy of Sciences, USA* **99**: 6848–6853.

CORRIGENDUM

Retracing the contours of the early angiosperm environmental niche

Robin Pouteau, Santiago Trueba and Sandrine Isnard

Annals of Botany doi:10.1093/aob/mcz131

In the originally published version of this article a mistake was made in the first sentence of the discussion section on page 5. This sentence should read: 'Most widespread extant basal angiosperms appeared limited in their latitudinal distribution

by temperature and precipitation: areas with mean annual temperature below $-3\text{ }^{\circ}\text{C}$ and annual rainfall below 700 mm are never occupied' and not '700 m are never occupied'. This has now been corrected.