Evolving the structure: Climatic and developmental constraints on the evolution of plant architecture. A case study in Euphorbia

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Evolving the structure: Climatic and developmental constraints on the evolution of plant architecture. A case study in *Euphorbia*.

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Summary

- Plant architecture strongly influences ecological performance, yet its role in plant evolution has been weakly explored. By testing both phylogenetic and environmental signals, it is possible to separate architectural traits into four categories: development constraints (phylogenetic signal only); convergences (environmental dependency only); key confluences to the environmental driver (both); unknown (neither).
- We analysed the evolutionary history of the genus *Euphorbia*, a model clade with both high architectural diversity and a wide environmental range. We conducted comparative analyses of 193 *Euphorbia* species worldwide using 73 architectural traits, a dated phylogeny, and climate data.
- We identified 14 architectural types in *Euphorbia* based on trait combinations. We found 22 traits and three types representing convergences under climate groups; 21 traits and four types showing phylogenetic signal but no relation to climate; and 16 traits and five types with both climate and phylogenetic signals.
- Major drivers of architectural trait evolution likely include water stress in deserts (selected for succulence, continuous branching), frost disturbance in temperate systems (selected for simple, prostrate, short-lived shoots) and light competition (selected for arborescence). Simple architectures allowed resilience to disturbance, and frequent transitions into new forms. Complex architectures with functional specialisation developed under stable climates but have low evolvability.

Key words

Desert, *Euphorbia*, evolution, ecology, phylogenetic tree, plant architecture, temperate, tropical

Introduction

The plant body is composed of a few large roots and stems that are responsible for the number and placement of acquisitive (leaves and fine roots) and reproductive organs. These large organs are also involved in many additional functions essential to the plant, such as reserve storage, structural support, and transport of water and nutrients. The ecological performance of plants (i.e., ability to compete for resources and overcome disturbances) largely depends upon how these large organs are spatially and topologically arranged, which is commonly called their architecture (see a more exhaustive definition in Barthélémy & Caraglio, 2007). Plant architecture holds many of the keys to understand species ecological performance as resources (e.g., water, light, nutrients) are spatially variable, and disturbances (e.g., frost, fire, and herbivory) also impact plants spatially (Raunkiaer 1934; Bond & Keeley, 2005; Hoffmann *et al*., 2012, Charles-Dominique *et al*., 2017a).

Plant morphology has usually been analysed separately for two different objectives: Plant morphologists study morphology to understand how plants are organized, disclose taxonomically informative traits, or how the elementary units of the plant body provide information about their function (Nozeran, 1955; Corner, 1958, Emberger, 1964); Plant ecologists study morphology to understand which plant attributes are related to their distribution and ecological performance (Warming, 1909; Raunkiaer, 1934). Plant morphology gained considerable momentum as a tool for taxonomic work and many of the morphological characters currently available for a large number of species are those recorded in floras and taxonomic monographs. Keddy (2005), among others, advocated using readily available characters, such as canopy height or vegetative spread capacity, to analyse the ecological behaviour of species as a pragmatic approach benefiting from the large amount of data already at hand. However, these datasets ignore many branching parameters that can only be observed at the whole plant level, and therefore cannot be inferred from herbarium specimens, floras, taxonomic revisions or monographs.

Research on plant architecture emerged with the aim to understand the organization of the whole plant across space (branching rules, identification of elementary units) and through time (ontogeny). The pioneering work of Hallé *et al*. (1978) demonstrated that all known vascular plants can be categorized into 23 architectural models based on only three structural traits (growth direction, sexual organ position, and branching mode). The study of plant architecture was further refined by the observation that most plant species possess several types of stems, called “axis categories”, with distinct morphological characteristics and functions (Edelin 1984, 1990). Analysing the properties of these axis categories, their organisation in relation to each other (in what is called the architectural unit), their ontogeny, and their repetition in the plant body (termed ‘reiteration’), has promoted a deeper understanding of plant form and function (Barthélémy & Caraglio, 2007). Although conceptual tools for describing plant architecture are now advanced, and it is well understood that architecture affects ecological performance, the evolutionary trajectories of plant architecture in relation to environmental and biotic variables remain poorly understood. Using architectural traits, Coudert *et al*. (2017) identified key innovations responsible for structural diversification in Bryophytes. Bruy *et al*. (2018) showed that the acquisition or loss of side branches were important steps in the evolution of *Atractocarpus* (Schltr. & K.Krause (*Rubiaceae* Juss.) leading to the reinforcement of the reproductive function. The few attempts to analyse the evolution of plant architecture have shown that variation in just a few architectural parameters can inform on the evolutionary trajectories of fossil plants, and that some architectural traits are more labile than others (Chomicki *et al*., 2017), with evolutionarily conserved architectures potentially representing key innovations that contributed to major plant radiations. Substantial work remains to be done to reveal the evolutionary drivers responsible for the vast range of architectural models observed in vascular plants.

In this study we combine phylogenetic analyses with regression modelling to separate architectural traits into four evolutionary categories (Fig. 1):

(1) Traits that are independent to the tested environmental driver but which show significant phylogenetic signal; these traits are associated with specific clades and are likely to be phylogenetically constrained, here designated as developmental constraints on plant architecture.

(2) Traits that show significant dependency with the tested environmental driver but which lack phylogenetic signal suggesting convergent evolution multiple times across the phylogeny with low developmental constraints.

(3) Traits that show significant dependency with the tested environmental driver and significant phylogenetic signal; these traits have evolved under developmental constraint and are restricted to certain sub-clades, and could be key confluences, i.e., innovations followed or preceded by

climate change, potentially driving diversification in those clades (Donoghue & Sanderson, 2005; Bouchenak-Khelladi *et al.,* 2015).

(4) Traits that are independent from the tested environmental driver and lack significant phylogenetic signal; these traits may simply be non-adaptive or could be convergences to environmental drivers not included in our analyses.

The framework used in this paper is based on three assumptions: convergent traits (2) are likely to show some phylogenetic signal but to a lesser degree than developmental constraints and key confluences. While phylogenetic signal of architectural traits can also result from other processes such as stabilizing selection, low rates of evolution or competition (Revell *et al.*, 2008), it offers a convenient tool to identify potential developmental constraints as defined in (1). Finally, coincidence of strong phylogenetic and environment signals for a given trait could constitute evolutionary confluences *sensu* Donoghue & Sanderson (2015) (3), i.e., a combination of intrinsic trait innovations and extrinsic ecological opportunities associated e.g., with a shift in climate regime subtending clades occupying particular climate regimes that can show elevated diversification rates.

The genus *Euphorbia* L. is well suited as a model group to study the evolution of architecture as it has high growth form diversity comprising single stemmed short-statured plants, rosettes, shrubs and trees. It occupies a wide range of biomes including deserts, savannas, tropical forests (rainforests and seasonally dry forests) and temperate meadows, and occurs across all vegetated continents (Dorsey *et al.*, 2013; Riina *et al.*, 2013). With about 2000 accepted taxa (POWO, 2019), the genus *Euphorbia* is one of the biggest among the Angiosperms. It comprises four subgenera named *Esula*, *Athymalus*, *Chamaesyce*, and *Euphorbia* which are well supported taxonomically, have distinct morphological characteristics and distributions (Peirson *et al.*, 2013 Dorsey *et al.*, 2018; Riina *et al.*, 2018; Yang *et al.*, 2018). Several authors noticed this high diversity and used this genus as a model group for the study of the evolution of structure (Park & Jansen, 2007; Zimmermann *et al.*, 2010; Bruyns *et al.*, 2006, 2011; Aubriot, 2012, Evans *et al.*, 2014). Horn *et al.* (2012, 2014) used morphological traits from floras to demonstrate the convergence of *Euphorbia* morphology in arid habitats and the constraints that succulence exerts on growth form evolution. Cremers (1977), in a study restricted to Madagascan *Euphorbia*, showed that architectural traits are very promising tools to support taxonomy. Since these studies were conducted, phylogenetic data for *Euphorbia* have expanded and global environmental datasets are now available, allowing us to consider plant architectural evolution across a wide range of habitats.

We investigate how architectural traits can explain the structural evolution of *Euphorbia*. We specifically test whether climate has been a major evolutionary driver of architecture in the clade. To do so, we 1) built a phylogeny of *Euphorbia* including 193 species and dated it using three fossils, then 2) described architectural traits for each species, mostly from photographic records, using 14 architectural descriptors, 3) assembled species occurrence data and inferred corresponding environmental bioclimatic niches, 4) estimated phylogenetic signal for architectural traits and trait-environment relationship using phylogenetic regressions, 5) reconstructed the ancestral states for each trait and and mapped them onto the dated phylogeny to estimate trait shifts, assess the evolution of architectural trait innovations and their timing. The approach we adopt here can be easily and rapidly applied to a much larger range of plant clades where architectural diversity is apparent.

Materials and Methods

Taxa sampling

A total of 312 taxa of Euphorbiaceae including 297 species of *Euphorbia* (Table S1, Supporting Information) were selected representing all four subgenera (respectively 26.9%, 17.5%, 25.6% and 29.9% of the taxa sampling) and growth forms. DNA sequence data from previous phylogenetic studies of *Euphorbia* (Steinmann, 2001; Steinmann & Porter, 2002; Haevermans *et al*., 2004; N. Zimmerman *et al*., 2010; Barres *et al*., 2011; Yang & Berry, 2011; Aubriot, 2012; Horn *et al*., 2012, 2014; Yang *et al*., 2012; Dorsey *et al*., 2013; Peirson *et al*., 2013; Riina *et al*., 2013, Ernst *et al*., 2016) were downloaded from GenBank. Sampling was completed using closely-related genera (*Anthostema*, *Dichostemma*, *Calycopeplus*, *Neoguillauminia*) as well as ten members of the *Euphorbioideae* subfamily tribe *Hippomaneae* as outgroups. The tree was rooted using the genus *Nealchornea* (*Euphorbioideae* tribe *Stomatocalyceae*).

Phylogenetic tree inference and molecular clock dating

Sequence data were retrieved from GenBank for both chloroplast and nuclear ribosomal DNA: NADH dehydrogenase F (ndhF); the Ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit-like (rbcL) gene including partial sequences; rbcL-accD intergenic spacer, complete sequence and the acetyl-CoA carboxylase beta subunit-like (accD) gene (rbcL+accD); the ribosomal protein L16 (rpl16); the tRNA-Leu (trnL) gene and trnL-trnF intergenic spacer; the NADH dehydrogenase subunit 1 (nad1) gene, intron 2; ribosomal protein S3 (rps3); the internal transcribed spacer 1, partial sequence; 5.8S ribosomal RNA gene, complete sequence; and internal transcribed spacer 2 (ITS); the embryo defective 2765 (EMB2765) gene, exon 9; the embryo defective 2765 (EMB2765) gene, exon 12.Scientific names, authorities, voucher details and GenBank numbers for accessions are listed in Table S1. Sequence alignments were performed by using Transalign (Bininda-Emonds, 2005), with minor manual adjustment and include 36.28 % missing data and 27.89% phylogenetically informative sites. A maximum likelihood (ML) analysis was performed on the combined dataset using RAxML-HPC2 v.7.2.6 (Stamatakis *et al*., 2008) on the CIPRES cluster (M. Miller *et al*., 2009) using the default settings and 1000 bootstrap replicates. Branch lengths were then calibrated in millions of years using a Bayesian Markov chain Monte Carlo (MCMC) approach implemented in BEAST v.1.4.8 (Drummond & Rambaut, 2007). We performed divergence time estimation using two calibration points. The first is the fossil *Hippomanoidea warmanensis* (Crepet & Daghlian, 1982) was assigned to the crown node of the clade comprising genera *Senefelderopsis* and *Mabea*, with an exponential distribution (minimum age of 43 Ma, mean of 2.5). The second is a secondary calibration for the *Euphorbioideae* subfamily clade (excluding tribe *Stomatocalyceae*) obtained from Xi *et al*. (2012), with a mean of 52.79 Ma and a sigma value of 8.03. We performed four independent MCMC runs, each one billion generations, sampling every 1000 generations (to ensure all four runs converged on the same optimum), under Yule model and lognormal relaxed clock with an estimated clock rate of one as starting value. We assessed the MCMC log files for convergence using the effective sample size (ESS) statistics in Tracer v.1.5 (Drummond & Rambaut, 2007). The BEAST analysis reported ESS values > 200, indicating that the posterior estimates were not unduly influenced by autocorrelation. We combined the resulting tree files from the four runs in LogCombiner v.1.7.5 (Drummond & Rambaut, 2007), downsampling 1 in 20,000 trees, and discarding the first 25% trees as burn-in. The maximum clade consensus tree, with means and 95% highest posterior density (HPD) intervals, was generated with TreeAnnotator v.1.7.5 (Drummond & Rambaut, 2007).

Trait description

To process all the data analyses, we chose to keep only the species available in gene databases, having a complete architectural description and available environmental data (see below), for a total of 193 *Euphorbia* species out of the 297 species initially sampled. We analysed the architecture of *Euphorbia* species using photos linked to herbarium vouchers and literature citations from GBIF, FloraZimbabwe, EuphorbiaPBI, and Euphorbia.de project websites. A minimum of three different photographs were used, except for three species described from fieldwork (*E. exigua* L. in France, *E. hirta* L. in India, *E. ingens* E.Mey. ex Boiss. in China). We retained *Euphorbia* species for which we were able to obtain pictures that were taken in natural habitats and were informative enough to allow us to describe all 14 selected architectural descriptors commonly used in the analysis of plant architecture (*sensu* Hallé, *et al*., 1978; Barthélémy & Caraglio, 2007). Following the classification of Barthélémy & Caraglio (2007), we selected the descriptors from three categories I) morphological traits at the axis scale; these traits distinguish the different axis categories composing the plant (e.g., trunk, branches and short shoots) and their contribution to function (e.g., some species only have flowers on short shoots) (1-6); II) traits describing the composition of the architectural unit: number of axis categories and extreme differentiation of a category e.g., into a spine (7-11); III) traits related to the whole plant scale, including reiteration (duplication of the structure) in development sequence or following a disturbance event (12-14) (Fig. 2):

I) Traits at the axis category scale comprise 1) Growth direction of each axis category (orthotropy/plagiotropy/ageotropy); 2) Phyllotaxis of the primary stem (spiral/opposite); 3) Development of each category (monopodial/sympodial); 4) Flowering of each category (lateral/terminal/absent); 5) Meristem functioning of each category (determinate/indeterminate); 6) Branching mode of each category (rhythmic/continuous/diffuse/absent).

II) Traits at the architectural unit scale comprise 7) Short shoots (present/absent); 8) Type of specialised shoots (floral/photosynthetic/spiny/young photosynthetic and old spiny/absent); 9) Presence and type of spines (absent/stipular/petiolar/apical/axial);10) Number of axis categories (from one to four); 11) Above-ground succulence (total/sub-succulent/partial/absent.

III) Traits at the whole plant scale comprise 12) Multistemmedness (yes/no); 13) Reiteration location (no reiteration/sub-apical/distal/basal); 14) Reiteration type (sequential/delayed).

A detailed definition of these descriptors is provided in Table S2. They have also been exhaustively described in Barthelemy & Caraglio (2007) and Bell & Bryan (2008).

Whole-plant architectural types

We identified unique combinations of the architectural traits and defined these as architectural types for *Euphorbia*. This categorisation allowed us to summarise the main events of the evolution of plant architecture in *Euphorbia.* For this classification we ignored the following descriptors that only described variations on major architectural forms: phyllotaxis (2), presence or absence of short shoots (7), type of specialised shoots (8), and presence and type of spines (9). These variants on the major architectural types are described in Notes S1 to S14, Fig. S1 to S14.

We performed pairwise comparisons with PERMANOVA, "pairwise.perm.manova" function ("RVAideMemoire" package; Oksanen *et al*., 2017), using all traits to test whether each architectural type was distinct from all others, to ensure that the variants described above were still associated with their assigned architectural type (Table S3). While a full description of plant architecture requires a description of ontogenetic changes (Barthélémy & Caraglio, 2007), we did not include this part in our descriptions as it is difficult to separate each ontogenetic stage using photographs.

Environmental data and climate group clustering

All environmental data analysis was conducted in R (R Core Team, 2019). We extracted occurrence data for all species represented in GBIF (GBIF.org: http://www.gbif.org/occurrence; accessed on 19 December 2019) using the package "rgbif" (Chamberlain *et al*., 2019), removed duplicated values within species and used the "CoordinateCleaner" package (Zizka *et al.*, 2019) to remove problematic records and outliers (excluding zero coordinates, country capitals, country centroids, biodiversity institutions) with 4913 out of 300665 records excluded. For each retained occurrence, we extracted Worldclim (Fick & Hijmans, 2017) bioclimatic variables and the Koppen-Geiger classes (Kottek *et al*., 2006**)** using the package "raster" (Hijmans, 2020). We simplified Koppen-Geiger categories into cold desert (BWk), dry continental (Dsa, Dsb, Dsc), hot continental (Dfa, Dfb), hot continental monsoon (Dwa, Dwb), hot desert (BWh, BSh), hot Mediterranean (Csa, Csb), mild subtropical (Cwa, Cwb), monsoon tropical (Am), rainforest (Af), savanna (Aw, As), sub-arctic (Cfc, Cwc, Dfc, Dwc, ET, EF), subtropical (BSk, Cfa) and temperate oceanic (Cfb). We excluded species with five or fewer occurrence records from the analysis. We analysed the similarities of climate types for *Euphorbia* species by considering that similar climate types have greater chances to share species: We used Ward agglomerative clustering on Bray-Curtis distance calculated from a [Köppen-Geiger climates x species] matrix. The matrix was scaled to 1 to give equal weight to all species in the analysis and reduce excessive contribution from overrepresented European species. We further used a principal component analysis on the [occurrences x bioclim variables] matrix and Ward agglomerative clustering on Euclidian distance, to delete environmental variables providing redundant information. This identified mean annual temperature (BIO1), annual precipitation (BIO12), annual variation of temperature (BIO4) and precipitation seasonality (BIO15) as sufficient to interpret main differences between the climatic clusters identified previously. We reported the climatic clusters structuring the current distribution of *Euphorbia* species (Fig. 3), highlighted the main contributors to each cluster following the method in Kleyer *et al*. (2012), together with their values for the four BIOCLIM variables. We checked whether the species clusters were coherent with existing descriptions for the species in floras.

Categorisation of traits

To categorise each trait and each architectural type into one of the four information categories described in the Introduction and Fig. 1 (developmental constraint, convergence, key confluence, unknown), we evaluated the phylogenetic signal and the climate group association of each trait and each architectural type.

We evaluated the phylogenetic signal for each of the 73 traits and the identified architectural types using Pagel's Lambda (λ) statistic (Pagel, 1999; Freckleton *et al*., 2002). We computed Pagel's λ using the "fitDiscrete" function ("geiger" package; Harmon *et al.*, 2008) using all-rates-different (ARD), symmetric (SYM) and equal-rates (ER) models on residuals of each trait~climate function according to Revell (2008) and selecting the models giving the best AIC for each trait.

We tested whether each trait and architectural types differed across identified climate groups using the binaryPGLMM function ("ape" package; Paradis, *et al.,* 2015) which includes phylogenetic correction, and logistic regression ("glm" function of R), retaining models with the best-fitting AICs.

We used Tukey HSD tests (R.G. Miller, 1981; Yandell, 1997) for pairwise comparisons of traits across climatic groups. The p-values from the tests between traits and climate groups were reported together with their phylogenetic signal to disclose traits with significant phylogenetic signal (for Pagel's $\lambda > 0.90$) and/or environmental affinities (p-value < 0.05) or none.

Ancestral character reconstruction

We reconstructed the ancestral states for each trait, using the "make.simmap" function ("phytools" package; Revell, 2012) performing stochastic mapping and summarizing character state probabilities at each node. We processed the reconstructions using models giving the lowest AICs (Table S4). We computed 60,000 simulations for each trait and architectural type. That allowed us to understand how the overall plant architecture changed via switches in combinations of several trait modalities in successive steps during the evolution of *Euphorbia*. We reconstructed the ancestral geographic range using DEC models ("BioGeoBEARS" package, Matzke, 2013) and retained the model with the best-fitting AIC.

We performed Multiple State Speciation and Extinction (MuSSE) analyses with the package "diversitree" (FitzJohn, 2012) to evaluate transition rates of number of axis categories following Onstein *et al.* (2017). As we aimed to test evolvability of the number of axis categories rather the rate of trait evolution, we focused on transition rates (q) for model selection, excluding extinction rates (μ) and speciation rates (λ). We ran 10,000 MCMC steps based on the selected model (keeping the 95% credible interval) using "an exponential prior with a mean set to twice the state-independent diversification rate" according to FitzJohn (2012), and a sampling proportion of 0.08.

Results

Architectural types

Using the entire set of 73 architectural traits, we identified fourteen different architectural types in *Euphorbia* (Table 1 and Table S5). Detailed descriptions of these types are in Notes S1 to S14, Fig. S15.

The architectural types have different levels of complexity:

1) The simplest architectural types comprise a single axis category (stem), and can be unbranched

(monocaulous, type 2), or a single kind of axis that is reiterated (types 3, 4, 7, 8, 9, 10, and 11). All have low stature (less than one meter high), but differ by whether they have perennial above-ground structures (living more than two years, such as types 2, 3, 4, 7, 8, 10) or not (types 9 and 11). They also differ by the growth direction of their stems that may be orthotopic (types 2, 3, 4, 8, 9, 10) or plagiotropic (types 7 and 11). Most of these architectural types (except type 2) abundantly reiterate from the base and have shrubby growth forms. Finally, they may be herbaceous (types 9, 11 which also comprise annual species), slightly woody (types 4, 7, 8, 10), or woody (3).

2) A second group of three architectural types (types 5, 6, and 14) comprises two axis categories (stem; branches). These types all show strong differentiation between the stem and branches, conferring either mainly a reproductive function by increasing the number of flowers (types 5 and 14) or a reproductive and assimilative function (type 6). All these types are shrubby, abundantly reiterate from the base, are medium-statured (< 2 m), have perennial above-ground parts, and are slightly woody. They differ in branching mode that may be rhythmic (type 5), continuous (type 6) or diffuse (type 14).

3) A third group of architectural types (types 1 and 12) comprises three axis categories (stem; branches; branchlets) In this group functions are also strongly partitioned between the trunk (stem) which allows vertical expansion, and the branches which allow exploration of the lateral space around the trunk and bear the branchlets which have both assimilative and reproductive functions. These two types are both arborescent and woody, but differ in development of the trunk (monopodial in type 1, and sympodial in type 12) and the meristematic functioning of each category (indeterminate in type 1, determinate in type 12).

4) Finally, architectural type 13 is the most complex, being composed of four axis categories: woody stem, branches, branchlets and twigs, each differing in function, the trunk allowing vertical expansion, the branches lateral expansion around the trunk, the branchlets assimilative function, bearing twigs with reproductive and/or defence functions.

The architectural types we identified could be affiliated to seven of the architectural models proposed by Hallé *et al.* (1978): Rauh (type 1, 13); Attims (type 6); Corner (type 2), Troll (types 7, 11), Leeuwenberg (types 3, 10, 12), Tomlinson (type 4, 5, 8, 9), and Chamberlain (type 14). From their architecture only, we might expect frequent transitions between species from types 2, 4, 7, 8, 9, 11, which are all monocaulous species having lateral flowering; This group is distinguished from the group composed of types 1 and 5 with species having orthotropic stems that are rhythmically branched, and also from a group with modular species having terminal flowering (types 3, 10, 12, 14).

Climate groups and climate-traits relationships

The clustering analysis showed that *Euphorbia* species can be separated into three climatic groups differing in mean temperature, precipitation and seasonality (Fig. 3).

A: desert group, composed mainly by hot deserts and to a lower degree by cold deserts, is characterized by a very low mean annual precipitation and a strong seasonality for precipitation.

B: temperate group, composed mostly of extra-tropical and oceanic island archipelagos is associated with low mean annual temperature and high temperature seasonality, defining a freezing season.

C: wet tropical group, mainly composed of climates hosting savannas, monsoon tropical vegetation and rainforest, characterized by high temperature and precipitation with low temperature seasonality.

We found 22 traits and three architectures lacking phylogenetic signal showing a significant dependency with the climatic groups (Fig. 4 bottom-right quadrants, Table S5, S6). Our results show that in arid environments (group A) architectural types 10 and 14, and continuous branching, are significantly more common. In temperate environments (group B), species with two axis categories are significantly less common. Finally, in tropical environments (group C), the sequential basal and delayed distal reiteration are more common. Pairwise comparisons of traits across climatic groups are reported in Fig. S16 and traits-relationship according to each climatic variable in Fig. S17.

Phylogenetic tree and trait evolution

The four robustly supported major lineages correspond to the subgenera *Esula*, *Athymalus*, *Chamaesyce*, and *Euphorbia* (Figs. 5 & S15a, c). The crown age *Euphorbia* is estimated to be (64.4-)48.2(-35.27) Mya (Figs. 5 & S15b), and the crown ages of the subgenera *Esula*, *Chamaesyce*, *Euphorbia* and *Athymalus* estimated to be (52.4-)41.0(-29.2), (48.5-)37.1(-24.9), (40.9-)31.6(-24.8) and (43.9-)27.9(-18.4) Mya (Figs. 5 & S15). The overall phylogeny is robustly supported, albeit with several areas of poor support which collapse as polytomies in the consensus tree (Fig. S18a).

We found 21 traits and four architectural types without dependency to climate showing a strong phylogenetic signal (Pagel's λ > 0.90) (Fig. 4 top-left quadrants Table S5), suggesting developmental constraints on several lineages, including architectural types 2, 7, 8 and 11, and the growth direction of the primary stem (orthotropic or plagiotropic).

We found 16 traits and five architectural types with strong phylogenetic signal (Pagel's λ > 0.90) and a significant dependency with the climatic groups (Fig. 4 top-right quadrants, Table S5), suggesting key evolutionary confluences of traits and climates that could potentially have triggered radiations in several lineages in the three climatic groups, i.e., architectural types 5 and 6 are significantly more common in arid environments (group A). Architectural type 9 and sequential basal reiteration are significantly more common in temperate environments (group B) but all types of succulence are significantly less frequent in this climate. Finally, two arborescent architectural types (1 and 13) are significantly more common in tropical environments (group C).

We found that single axis category species have the highest transition rates (Fig. 6) and that rates decrease as the number of axis categories increase. This is supported by the pairwise comparisons, showing the three groups are significantly different from each other (Fig. 6). The highest transition rates correspond to transition from one to two axis categories, and the lowest corresponds to transitions from three and four to one axis category, Table S7, Fig. S19).

Character reconstruction

Model selection (Table S8) suggests all transitions occurring at equal rates (ER) are rare (3 descriptors), symmetric transitions (SYM) are more commonly observed (9 descriptors), and each rate having separate parameters (ARD) are most commonly best-fitting (12 descriptors).

Ancestral range inferences show the DEC+J model is best-fitting (Table S9), an ancestral area for *Euphorbia* in Africa (Fig. 5, Fig. S20) and with range shifts along branches subtending *Esula* and *Chamaescyce*, respectively to Eurasia and America. From both Eurasia and the Americas a few lineages re-colonized Africa. Some lineages changed their climatic preferences during their history, most frequently from arid to temperate and from arid to tropical.

Architectural type and trait by trait inferences suggest that *Euphorbia*'s ancestor likely conformed to architectural type 9 (Fig. 5). Three architectural types (10, 3 and 11) likely evolved from this type: they respectively acquired succulence and sub-apical reiteration (type 10), loss of basal reiteration and perennial above-ground parts (type 3), and the plagiotropic growth direction (type 11). From architectural type 2 – derived from architectural type 10 – two ancestral structures similar to the type 2 evolved: one was the ancestor of the types 4 and 6 that both are totally succulent, and a second was likely the ancestor of the types 7 and 8 that both are sub-succulent, as well as the type 2. Detail of inferences for each trait are available in Fig. S21 and S22.

Discussion

In this study, we analysed evolution of plant architecture across the genus *Euphorbia* in relation to colonization of new environments. Using a large phylogeny with 193 *Euphorbia* species, we screened a total of 73 structural traits, and identified 14 architectural types with different structural properties and levels of complexity. We found that plant architecture in *Euphorbia* is strongly associated with three main climatic groups, namely deserts where water is limiting (cold and hot deserts grouped together), temperate zones subject to freezing winter temperatures, and tropical systems that are frost-free and include aseasonal wet systems to seasonally dry systems (Fig. 6). This first attempt to classify *Euphorbia* traits according to their architecture is not exhaustive, considering we only described 10% of this species-rich genus, and additional types may still need to be accounted for.

Our results provide insights into the colonization of arid and temperate systems, the evolution of complex plant architecture, and how the elaboration of structure can allow the emergence of new functions. We summarize the main evolutionary transitions in *Euphorbia*, discuss the effect of drought and frost on plant architecture, the key characters involved in the evolution of arborescence, and structural evolution by complexification. Finally, we summarize focal points for further research on the evolution of the plant architecture.

Key steps in the evolution of architecture in Euphorbia

Our phylogeny confirms monophyly of subgenera *Esula*, *Athymalus*, *Chamaesyce* and *Euphorbia* consistent with previous reconstructions (Bruyns *et al.*, 2011; Horn *et al.*, 2012, 2014) and estimates the crown age of *Euphorbia* to be around (64.4-)48.2(-35.27) Mya with a likely ancestral area in Africa (Fig. 5). Trait reconstruction suggests the most likely ancestral plant architecture was a non-lignified multi-stemmed forb that occupied deserts. While architectural type inference shows crown state ambiguity (majority for type 9), trait by trait inferences strongly support an ancestral architecture similar to type 9 (Fig. S22), suggesting a higher sample size may help to improve resolution. However, the sister species to *Euphorbia*, *Neoguillauminia cleopatra* (Baill.) Croizat also has a type 9 architecture, giving support to our ancestral state reconstruction and independent reconstruction from Horn *et al.* (2012) is also consistent with our suggestion.

Along the branch subtending *Esula,* our model inferences suggest a range shift to Eurasia about (52.4-)41.0(-29.2) Mya with no shift in plant architecture, mostly below-ground perennial and a lack of above-ground perennial structures, suggesting a strong and recurrent disturbance constraining the above-ground architecture, most likely frost. Along the branch subtending subgenus *Chamaesyce* our model suggested a range shift to America around (48.5-)37.1(-24.9) Mya into another system subject to frost, and generally shares similar architecture with *Esula*, with the exception of the section *Anisophyllum* that developed a prostrate habit (plagiotropic growth direction). The two African subgenera *Athymalus* and *Euphorbia* show high architectural diversity derived from simple ancestral types (types 10 and 2).

Our results suggest that species with simple architectures are more likely to evolve into new architectures than architectures with greater structural complexity (Figs. 6, 7). We show that gradual acquisition of succulence was likely prominent in the colonization of deserts in Africa (Eggli & Nyffeler, 2009; Arakaki *et al*., 2011), occurred both *in situ* in deserts in subgenus *Athymalus* and *ex situ* in tropical wet environments in subgenus *Euphorbia*, from whence it recolonised desert systems.

Impacts of drought, frost, and light on plant architecture evolution

Our analyses suggest that the main observable adaptions to drought are the progressive acquisition of continuous branching, and modularity. Continuous branching is probably why species with a succulent rosette architecture (type 6) colonised and radiated in arid African habitats, as having a very short primary stem with continuous branching allows assimilative function transfer from leaves to stem photosynthetic branches (Nozeran, 1955; Corner, 1958) thereby reducing water loss to respiration. Structural adaptations that led to the rosette growth form in dry environments have also been observed in *Cactaceae* (Hernández-Hernández *et al*., 2011) and *Montiaceae* (Hershkovitz, 2019).

Secondly, the modularity of shrubby architectures (types 10 and 14) suggests that the ability to sacrifice individual modules under extreme drought conditions may ensure survival of the genet, as observed in twelve desert shrubs species (Jones & Lord, 1982; Jones, 1984; Schenk *et al*., 2008) and cushion species of Andean deserts (Anthelme *et al*., 2017). Interestingly, although succulence clearly supports water storage, in our analysis the presence of succulence did not differ between arid and tropical climates but was significantly rarer in temperate climates. This may mean that the absence of frost is a prerequisite for the evolution of above-ground succulence, and that succulence is beneficial both in arid desert systems and in semi-arid systems such as savannas and thickets (which are both included under the tropical climate group). As suspected by Evans *et al.* (2014), microenvironmental specialization might explain the presence of drought-related traits, such as succulence in the tropical climate group, which might be locally adaptive on porous substrates that do not retain water, such as rock outcrops, where free-fire succulent biome enclaves occur within savanna landscapes (Ringelberg *et al.*, 2020). Temperate *Euphorbia* species, both from Eurasia and America (respectively subgenera *Esula* and *Chamaesyce*) have distinct architectures from their congeneric species from the tropics. The distinctive characters of *Euphorbia* species living in temperate systems are: 1) short-lived above-ground structures (less than two years), while below-ground cauline structures can be varied (Klimešová *et al*., 2019); 2) simple above-ground architecture that can develop and flower very rapidly; 3) low to extremely low (in prostrate American architectures) investment in mechanical support; 4) absence of succulent species. All these traits point to frost as a strong selection factor in these systems as 1) above-ground structures of spurges are frequently killed by winter frost, which is widely considered to be the 'enemy of succulence' as demonstrated by detrimental effects on succulents in experiments and succulent biomes usually occupying frost-free environments (Vatrican, 1956; Stuart-Hill, 1992; Moolman & Cowling, 1994), 2) plants which need to complete their growth and reach reproductive phase during a single growing season, 3) these architectures, and especially prostrate habit, are likely selected in highly disturbed open (non-forest) environments. Frost being the likely selective agent is consistent with the environmental niche of these two clades that is distinguished from other clades by their high temperature seasonality and low average temperature (Fig. 3). Strategies to store resources below-ground in perennial storage organs are often prevalent in open-canopied ecosystems maintained by some form of above-ground disturbance such as frost, fire, herbivory or seasonal drought (Millan, 2016), as predicted by Raunkiaer (1934).

Carlquist (1970) found that all subgenera in *Euphorbia* have evolved woody shrubs or trees with perennial stems from herbaceous ancestors, a hypothesis consistent with our results. From the architectural perspective, we found that all subgenera have species with traits typically involved in the acquisition of the tree habit, with the presence of 1) a monopodial or pseudo-monopodial trunk (linear trunk composed of a succession of modules with sub-apical branching), and 2) an orthotropic primary stem with a strong dominance over lateral branches. While the developmental conditions are met in all subgenera, the environment of *Euphorbia* evolution seems to have mostly favoured short-statured species. The few exceptions to the short-statured *Euphorbia* are found in less constraining environments such as warm islands (Carlquist 1970) and in the hot and wet Tropics with seasonal drought in Africa (this study). Nürk *et al.* (2019) suggested derived woodiness as a prerequisite for trait acquisition allowing plant growth form diversification, which is consistent with our results suggesting arborescent architectures evolved from slightly woody ancestors. Woodiness might have been a prerequisite for architectural traits involved in woody shrubs (type 3) and arborescent development (types 1, 13), specifically on islands and island-like systems (Lens *et al*., 2013; Nürk et *al*., 2019) such as succulent biome enclaves where their high stature may indicate the need to be competitive in the canopy of tall thickets (Ringelberg *et al*., 2020).

Progressive structural complexification

The genus *Euphorbia* includes species with a wide array of architectures ranging from short rosettes composed of a single leafed stem, to highly complex structures with four different types of stems (arborescent forms). Of the four subgenera, the African subg. *Athymalus* and subg. *Euphorbia* show greatest architectural diversity with height and thirteen architectural types respectively. In both subgenera, ancestral states are very simple architectures composed of a single stem (monocaulous, type 2) or the repetition of the same axis category (e.g. type 3, 4 and 10). Further, our results suggest that species with simple architectures have greater evolvability, here defined as the ability of each architectural type to evolve into new architectures (Fig. 6, 7). On the other hand, species with greater structural complexity (with greater number of axis categories) which acquired stems with specialised functions, have only evolved into one new architecture or remained the same. Thus, there appears to be a trade-off between evolvability of structures and functional specialisation. While having the disadvantage of making the whole structure more difficult to evolve, each new differentiated axis category is an opportunity to reinforce the expression of an existing function or to develop a new function. The reinforcement of an existing function can be exemplified by acquisition of short shoots that exponentially increase foliage or number of fruiting sites at low direct cost (Dörken & Stützel, 2009, 2012; Dörken *et al.*, 2010). Cage architectures against mammalian herbivores also depend on the number of axis categories that increase their defence effectiveness exponentially (Charles-Dominique *et al.*, 2017a). The evolution of functional spines as a specialised category further increases defensive efficiency. The number of categories could therefore probably be used to position species on an evolvability-specialisation trade-off axis, but this would benefit from further investigation in other clades to confirm the evolutionary advantages of complexity versus simplicity. We suggest that simple architectures could be favoured in ecosystems subject to frequent disturbances as developing complex structures takes time that requires long disturbance-free intervals; frequent disturbances such as mechanical mowing have been shown to filter out species with complex architectures and select for short stature species in the Mediterranean system (Millan, 2016). This interpretation is also consistent with our finding that simple above-ground architectures are favoured in temperate climates experiencing regular frost.

Further steps

Our study provides evidence that the evolution of plant architecture in new habitats might be associated to major events of plant diversification. Mapping traits using their phylogenetic signal and environmental affinities helped summarizing important evolutionary steps in *Euphorbia*. This provided a support for classifying traits, but we did not conduct an exhaustive screening of trait-environment relationships. Traits classified as neutral here are not responsive to environmental variables considered in this analysis but may well be responsive to other environmental drivers. This point can be exemplified by the presence of spines in many species of *Euphorbia*. Spines are thought to predominantly function as a defence against vertebrate herbivores (Cooper & Owen-Smith, 1986; Burns, 2014; Wigley *et al.*, 2015; Charles-Dominique *et al.*, 2016; Tomlinson *et al.*, 2016, Armani *et* *al*., 2020). The latter is identified as a neutral trait in our analysis, indicating that it is not aligned with the climate groups we tested here. Some neutral or developmentally constrained traits in our analysis potentially evolved in response to environmental drivers not included in our analysis. Nevertheless, our analysis provides a first step towards identifying architectural traits that potentially represent key evolutionary confluences associated with particular climates. Further works using diversification analysis are needed to ascertain whether these traits are real climate-related key evolutionary confluences (*sensu* Donoghue & Sanderson, 2015) or if other factors explain the apparent relationships among environment, phylogeny and architecture. We believe that future studies will greatly benefit by testing the roles of biotic drivers, such as pollination, herbivory, fire, on the evolution of plant architecture. Lastly, we hope that our study will motivate further experimental work investigating the mechanisms responsible for our observed patterns: specifically, 1) whether simple architectures are favoured in environments with higher disturbance regimes; 2) whether species with simple architecture are outcompeted by more complex species in the absence of disturbance; 3) whether an evolvability-specialisation trade-off is present at the Angiosperm scale.

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Author Contribution

AA, CE and TC-D planned and designed the research. AA conducted data collection and processing. AA, TC-D, OM, and KWT analysed data. AA, CE, and MM wrote architectural descriptions. AA, KWT, TC-D, OM and MM wrote the manuscript.

Data availability statement

Data associated with this article, corresponding to the description of the 193 *Euphorbia* species has been deposited in Figshare: doi.org/10.6084/m9.figshare.12629045.

Concatenated matrix, RAxML output, Beast matrix and Chronogram are available open access at the following DOI: 10.5281/zenodo.4264714

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Accession numbers and voucher data used to build the phylogenetic tree of genus *Euphorbia*.

Table S2: Modalities described for all the 14 descriptors used for the architectural analysis.

Table S3: Results of pairwise comparisons between the 14 architectural types, according to the 73 described traits.

Table S4. Model selection for environment dependency.

Table S5. Trait affiliation to each category (developmental constraint, convergence, key confluence or unknown).

Table S6. Model selection for Pagel's λ estimates.

Table S7. Model selection for Multiple State Speciation and Extinction (MuSSE) analysis.

Table S8. Model selection for ancestral state reconstructions of each trait according to best fitting AIC.

Table S9. Model selection for ancestral range reconstruction. The following models have been tested: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J.

Note S1. Architectural type 1 description.

Fig. S1. Scheme of Architectural type 1.

Note S2. Architectural type 2 description.

Fig. S2. Scheme of Architectural type 2.

Note S3. Architectural type 3 description.

Fig. S3. Scheme of Architectural type 3.

Note S4. Architectural type 4 description.

Fig. S4. Scheme of Architectural type 4.

Note S5. Architectural type 5 description.

Fig. S5. Scheme of Architectural type 5.

Note S6. Architectural type 6 description.

Fig. S6. Scheme of Architectural type 6.

Note S7. Architectural type 7 description.

Fig. S7. Scheme of Architectural type 7.

Note S8. Architectural type 8 description.

Fig. S8. Scheme of Architectural type 8.

Note S9. Architectural type 9 description.

Fig. S9. Scheme of Architectural type 9.

Note S10. Architectural type 10 description.

Fig. S10. Scheme of Architectural type 10.

Note S11. Architectural type 11 description.

Fig. S11. Scheme of Architectural type 11.

Note S12. Architectural type 12 description.

Fig. S12. Scheme of Architectural type 12.

Note S13. Architectural type 13 description.

Fig. S13. Scheme of Architectural type 13.

Note S14. Architectural type 14 description.

Fig. S14. Scheme of Architectural type 14.

Fig. S15. Reiteration strategies described in *Euphorbia*.

Fig. S16. Pairwise comparisons for each trait according to the three climatic groups.

Fig. S17. Trait according to each selected climatic variable, glm significance and R^2.

Fig. S18. Phylogenetic trees of the *Euphorbia* species including majority-rule consensus tree, dated complete tree and tree of the 193 species described.

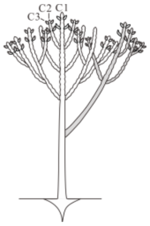
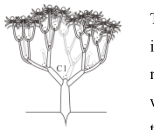
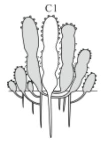
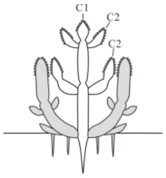
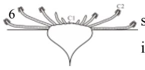
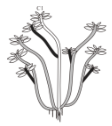
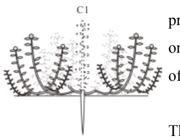
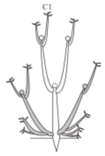
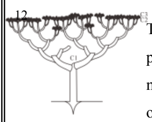
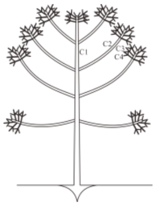
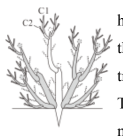
Fig. S19. Transition rate for the number of axis categories to each number of category (forward and backward) using the MuSSE analysis according the best fitting model and pairwise comparisons.

Fig. S20. Ancestral range inference according to the best fitting model (DEC+J model).

Fig. S21. Ancestral state reconstruction of climatic groups.

Fig. S22. All traits' ancestral state reconstruction.

Table 1: Architectural types identified in *Euphorbia*.

Architectural types	Definition	Architectural types	Definition
1 	This type represents totally succulent species having an arborescent habit and displaying: 1) an orthotropic monopodial stem having a rhythmic branching and an indeterminate growth (C1), 2) orthotropic monopodial branches having a rhythmic branching and an indeterminate growth (C2) and lastly 3) orthotropic branchlets having a determinate growth (C3). All three axis categories (maximum observed number for this type) produce inflorescences laterally. Species growing according to this type may present distal sequential reiteration when mature (Notes S1).	2 	This type represents sub-succulent monocaulous species, having an orthotropic monopodial unbranched stem (C1) with an indeterminate development and producing inflorescences laterally Notes S2)
3 	This type describes non-succulent sympodial species, whose body is made of monocaulous modules (one axis category, C1). Their modules are orthotropic monopodial, have a determinate growth with terminal inflorescences, and follow one another by sub-terminal branching to form a branched complex. Branched complexes are repeated at the basis of branched complexes by total sequential reiteration (Notes S3).	4 	This type refers to totally succulent species having an orthotropic monopodial stem (C1) with indeterminate growth and producing inflorescences laterally. This axis produces total sequential reiteration in basal, giving to these organisms a shrubby habit (Notes S4).
5 	This type groups totally succulent species, displaying an orthotropic monopodial stem with indeterminate growth and a branching with a rhythmic pattern, thus setting up tiers of orthotropic monopodial branches with indeterminate growth and usually unbranched. All axis categories produce inflorescences in lateral position. The main stem produces total delayed reiteration, giving this type its shrubby shape (Notes S5).	6 	This type describes totally succulent species growing in a rosette habit. The main stem (C1) is a thick succulent orthotropic monopodial axis with indeterminate growth that never flowers. It has very short internodes and continuous branching. Branches (C2) are thin, succulent orthotropic monopodial axes having a determinate growth and producing inflorescences laterally (Notes S6).
7 	This type describes creeping sub-succulent species having a single axis category. This axis (C1) is a plagiotropic monopodial stem, it has an indeterminate growth and flowering laterally. This axis produces total sequential reiteration on its basal parts. During the ontogeny, the secondary growth of each axis induces the formation of a caudex at the base of the plant (Notes S7).	8 	This type describes sub-succulent species having only one axis category (C1) growing as a long monocaulous orthotropic monopodial stem. This axis has a indeterminate growth, flowers laterally and produces sequential reiteration at its basis, thus giving the organism its shrubby habit (Notes S8).
9 	This type represents non-succulent species having only one axis category (C1) growing with an orthotropic growth direction, having a monopodial development and a determinate growth. It flowers terminally and produces immediate total sequential reiteration at their base (Notes S9).	10 	This type describes sympodial sub-succulent species whose body is made of monocaulous modules (one axis category, C1). Their modules are orthotropic, monopodial, have a determinate growth with terminal inflorescences, and follow one another by sub-terminal branching to form a branched complex. Branched complexes are repeated at the basis of older branched complexes by total sequential reiteration (Notes S10).
11 	This type describes creeping non-succulent species having a single axis category. This axis (C1) is a plagiotropic monopodial stem having a determinate growth and a terminal flowering. This axis produces total sequential reiteration on its basal parts. Each reiterated axis may also reiterate then producing a densely branched crown (Notes S11).	12 	This type represents sympodial arborescent and partially succulent species whose body is made of modules having three axis categories displaying: 1) an orthotropic monopodial stem with rhythmic branching and determinate growth (C1); 2) orthotropic monopodial branches (C2) with rhythmic branching, determinate growth and terminal flowering. 3) succulent orthotropic branchlets (C3) having a determinate growth and terminal flowering. These modules follow on another by sequential reiteration happening via the process of dedifferentiation. One to three C2 axis located in the sub-apical zone of the trunk, change their development to function as trunk. This polychasial succession of modules give this model his short statured arborescent habit (Notes S12).
13 	This type represents arborescent partially succulent species displaying: 1) an orthotropic monopodial stem with rhythmic branching and indeterminate growth (C1). It has an important secondary growth, giving the stem its conical shape and is covered with bark; 2) orthotropic monopodial branches with rhythmic branching (C2) and indeterminate growth. They have a moderated secondary growth, giving the branches a cylindrical shape and is covered with thin bark; 3) orthotropic monopodial branchlets (C3) having a determinate growth, terminal flowering, and a rhythmic	14 	This type represents sympodial sub-succulent species whose body is made of modules having two axis

	branching. They have a quasi-absent secondary growth and are photosynthetic; 4) orthotropic monopodial twigs (C4) having a determinate growth and terminal flowering. They are unbranched, have a quasi-absent secondary growth and are photosynthetic. Species growing according to this type often present distal sequential reiteration (Notes S13).		categories. Each module displays:1) an orthotropic monopodial stem (C1), having a determinate development and produce short branches following a diffuse pattern; 2) orthotropic monopodial branches (C2), having a determinate development. Inflorescences are produced terminally on both axis categories. The modules follow one another by sub-terminal branching to form a branched complex. Branched complexes are sequentially repeated at the basis of older branched complexes by total sequential reiteration (Notes S14).

We report only the most discriminant characters defining the types in this table. For a complete description, see Supporting Information Notes S1 to S14.

Figure legends

Fig. 1: Conceptual framework for extracting the information associated with each trait for a plant clade. The measurements for each trait of both phylogenetic signal and environmental relationship can be divided into four different affiliation quadrants: (1) the top left quadrant (in blue) indicates traits with strong phylogenetic signal only, representative of strong developmental constraints; (2) the bottom right quadrant (in yellow) indicates traits with significant environmental dependency only, representative of convergences under the tested environmental driver; (3) the top right quadrant (in green) indicates traits with strong phylogenetic signal and significant environmental dependency, potentially representing "key evolutionary confluences" *sensu* Donoghue & Sanderson (2005), i.e. trait innovations followed or preceded by evolutionary shifts in climate regime which together could have triggered evolutionary radiations; and (4) the bottom left quadrant (in grey) indicates traits with no phylogenetic signal and no dependency with the tested environmental driver, which may be convergent under other environmental drivers not tested here or be non-adaptive.

Fig. 2: Architectural descriptors (1-14) used to characterize *Euphorbia* species according to Barthélémy and Caraglio (2007).

Fig. 3: Climate group clustering according to structuring of the distribution data of 193 *Euphorbia* species; (a) Clustering of climate types; the position and size of white circles indicate the relative number of species growing in each system and their relative climatic group. Length of axis indicated by unit d: d(Species) = 1, d(Climates) = 0.2. (b) Relative contribution of each Koppen-Geiger class to the climate groups: Cold desert (Bwk); Dry continental (Csc, Dsa, Dsb, Dsc); Hot continental (Dfa, Dfb); Hot continental(m) (Dwa, Dwb); Hot desert (Bwh, Bsh); Hot mediterranean (Csa, Csb); Mild subtropical (Cwa, Cwb); Monsoon tropical (Am); Rainforest (Af); Savanna (Aw, As) ; (Sub-)arctic (Cfc,Cwc,Dfc,DWc,Et); Subtropical (Bsk,Cfa); Temperate oceanic (Cfb). (c) Major climatic variables from Worldclim, identified as the main differences between the climatic groups in (a): temperature (mean annual temperature, BIO1), precipitation (BIO12) , temperature seasonality (annual variation of temperature as standard deviation x 100, BIO4) and precipitation seasonality (coefficient of variation, BIO15). Lower case letters each boxplot panel indicate pairwise comparisons (Tukey HSD

tests).

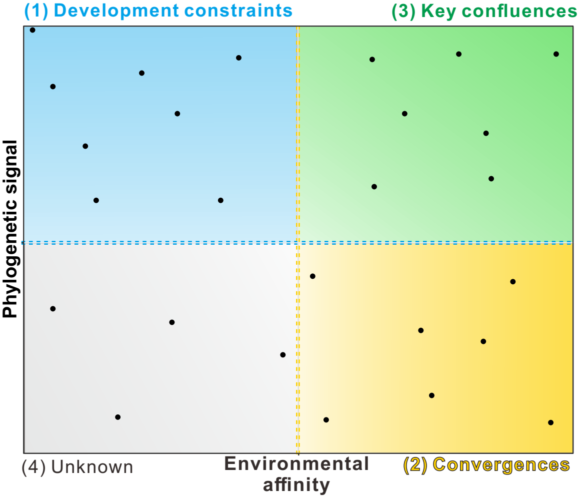
Fig. 4: All traits (panel (a)) and architectural types (panel (b)) described in *Euphorbia* arranged according to their phylogenetic signal (Pagel's λ) and p-value given by the regression model (glm), following the scheme described in Figure 1. Top left quadrants (in blue) show traits and architectural types with Pagel's $\lambda > 0.90$, representative of strong developmental constraints; bottom right quadrants (in yellow) show traits and architectural types with p-value < 0.05, representative of convergences in their relative climate affinity; top right quadrants (in green) show traits and architectural types with Pagel's $\lambda > 0.90$ and a p-value < 0.05, representative of "key confluences" that likely led to adaptive radiations; bottom left quadrants (in grey) show traits or architectural types with no phylogenetic signal and no dependency with the climate drivers tested in this analysis. The climatic affinities of each trait and architectural type are represented using coloured and styled boxes: red solid outline box, more present in temperate; black solid outline box, more present in deserts; light green solid outline box, more present in tropical; red dotted outline box, less present in temperate; light green dotted outline box, less present in tropical; grey solid outline box, no climate relationship.

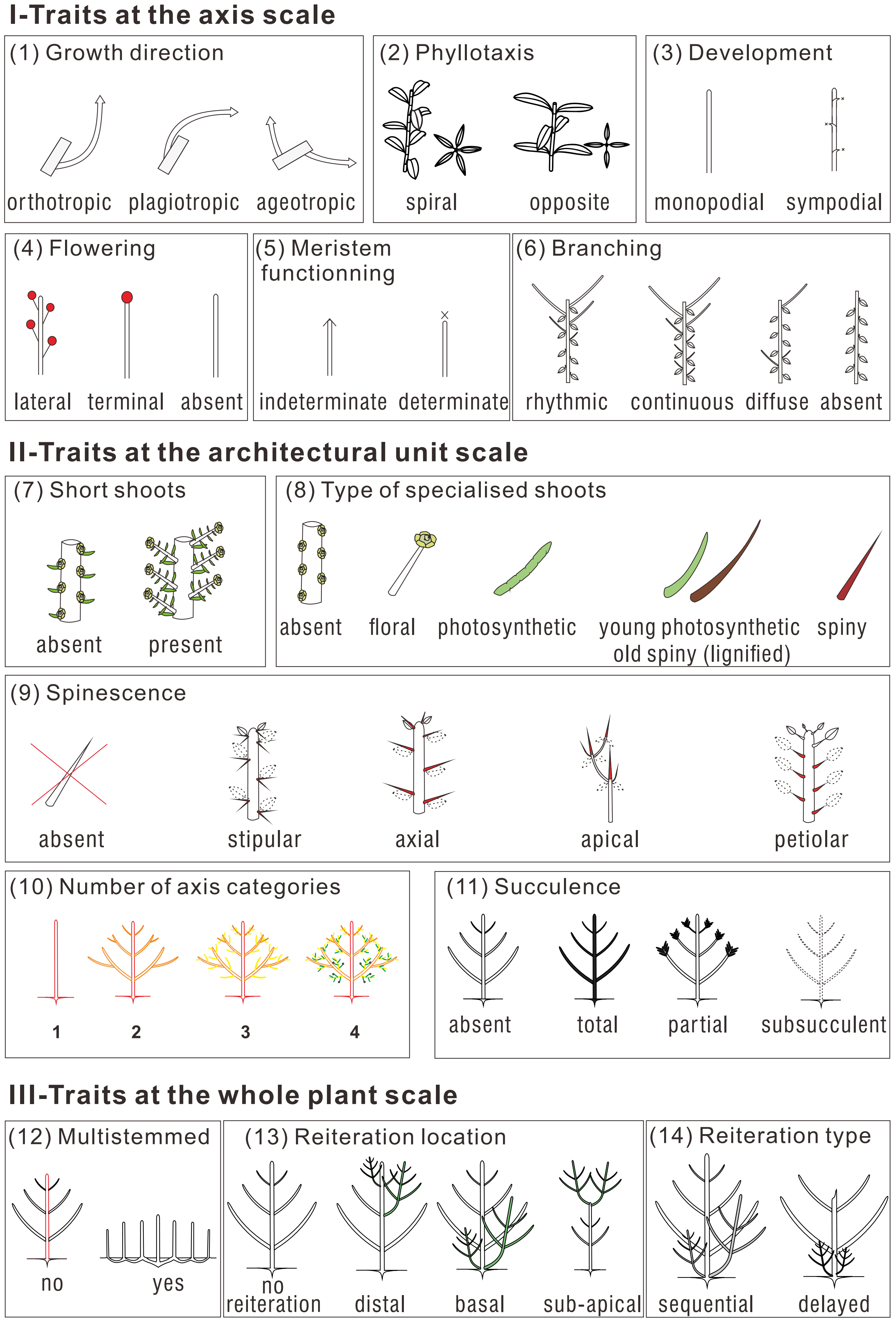
Fig. 5: Reconstruction of ancestral states for the architectural types, each trait, climatic group, and native continent based on 60,000 simulations. Reconstructions have been performed independently trait by trait. This figure represents a synthesis of main transitions at nodes having a probability > 0.9 except for the first node.

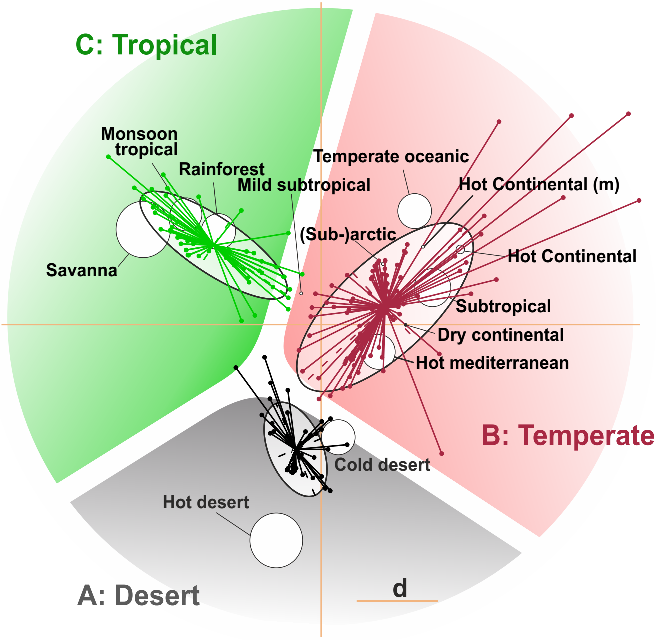
Fig. 6. Transition rate (square root transformed) for the number of axis categories using the MuSSE (Multiple State Speciation and Extinction) analysis according the best fitting model (Supporting Information Table S9). Pairwise comparisons (using Tukey's 'Honest Significant Difference' method, R.G. Miller, 1981; Yandell, 1997) are indicated. Black filled circles within boxplots indicate the means.

Fig. 7: Synthetic scheme of architectural type evolution filtered by climate and under developmental constraints in the genus *Euphorbia*. Type 12 is not shown here as it is poorly represented in our sample (2 species) and the transition states remain unresolved. Type 9, which is the ancestral architecture of *Euphorbia*, is shown in its ancestral environment (desert) and also in temperate regions

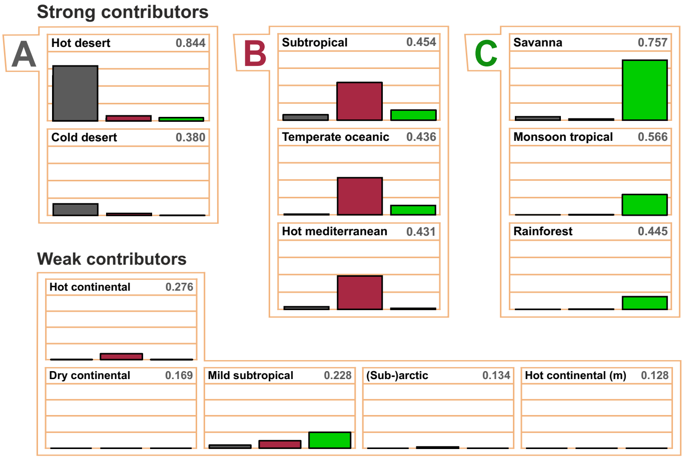
where it migrated to. Text colours: black text indicates climate dependency only (p-value < 0.05); blue text indicates developmental constraints only (Pagel's $\lambda > 0.9$); red text indicates both climate dependency (p-value < 0.05) and developmental constraint (Pagel's $\lambda > 0.9$); grey text indicates no climatic dependency (p-value > 0.05) and no strong phylogenetic signal (Pagel's $\lambda < 0.9$).


(1) Development constraints
(3) Key confluences
Phylogenetic signal
(4) Unknown
Environmental affinity
(2) Convergences

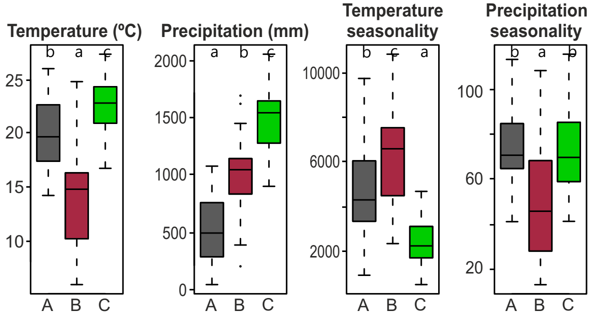

I-Traits at the axis scale
(1) Growth direction
orthotropic
plagiotropic
ageotropic
(2) Phyllotaxis
spiral
opposite
(3) Development
monopodial
sympodial
(4) Flowering
lateral
terminal
absent
(5) Meristem functionning
indeterminate
determinate
(6) Branching
rhythmic
continuous
diffuse
absent
II-Traits at the architectural unit scale
(7) Short shoots
absent
present
(8) Type of specialised shoots
absent
floral
photosynthetic
young photosynthetic old spiny (lignified)
spiny
(9) Spinescence
absent
stipular
axial
apical
petiolar
(10) Number of axis categories
1
2
3
4
(11) Succulence
absent
total
partial
subsucculent
III-Traits at the whole plant scale
(12) Multistemmed
no
yes
(13) Reiteration location
no reiteration
distal
basal
sub-apical
(14) Reiteration type
sequential
delayed



(a) Climatic niches of *Euphorbia* species

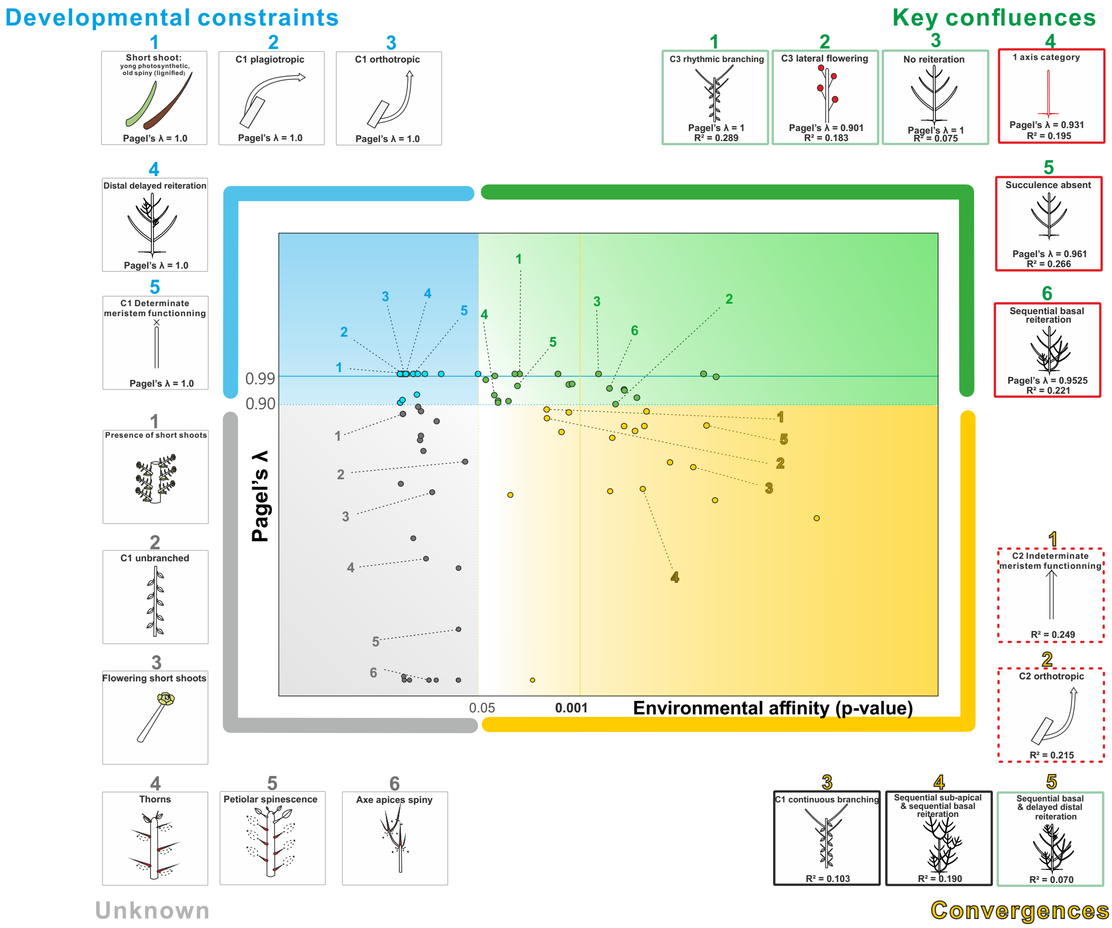


(b) Relative contributions to clusters

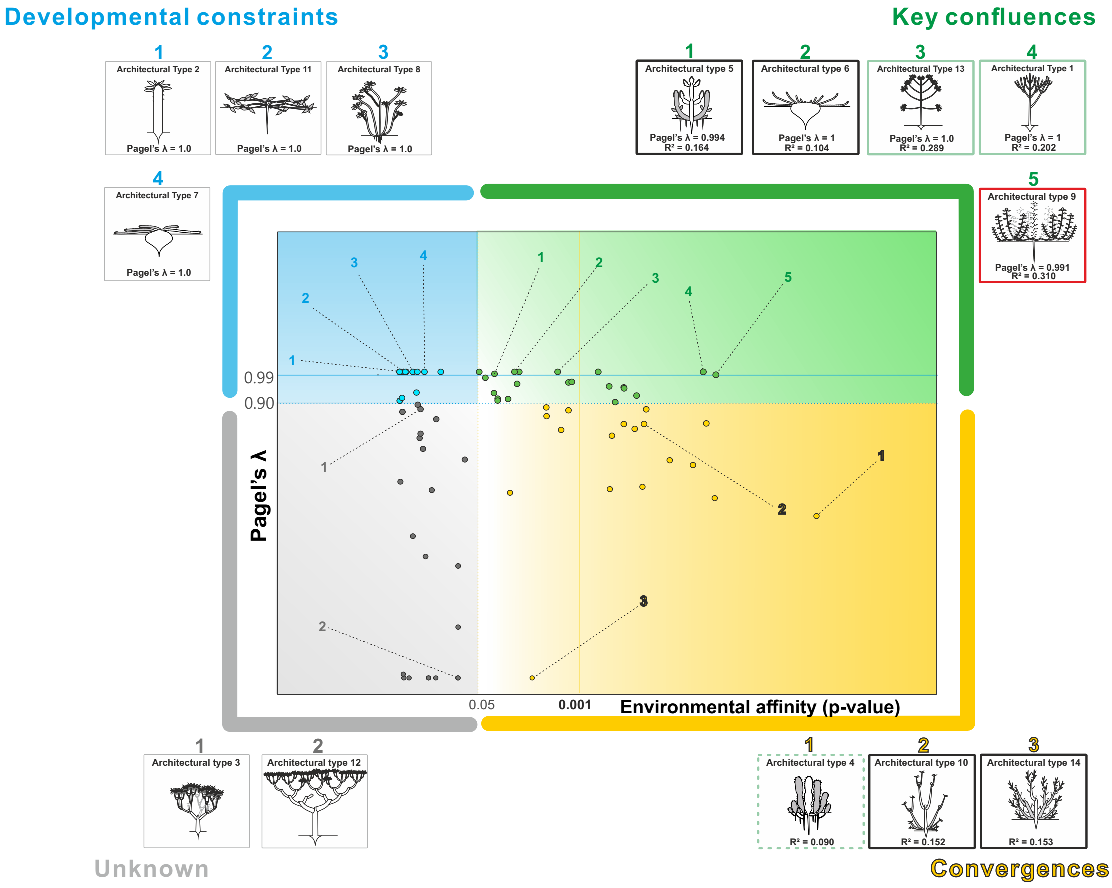


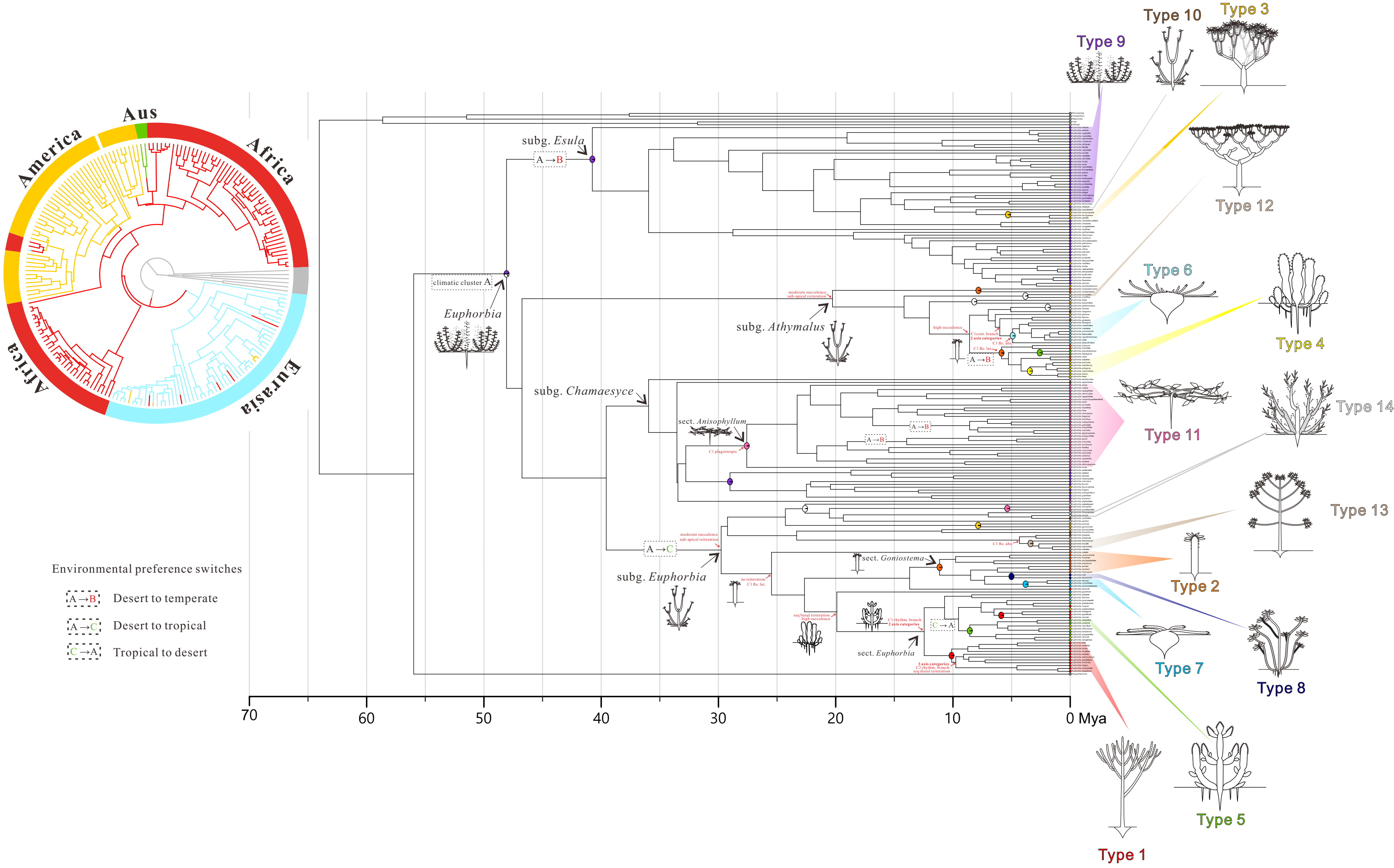
(c) Climatic variables

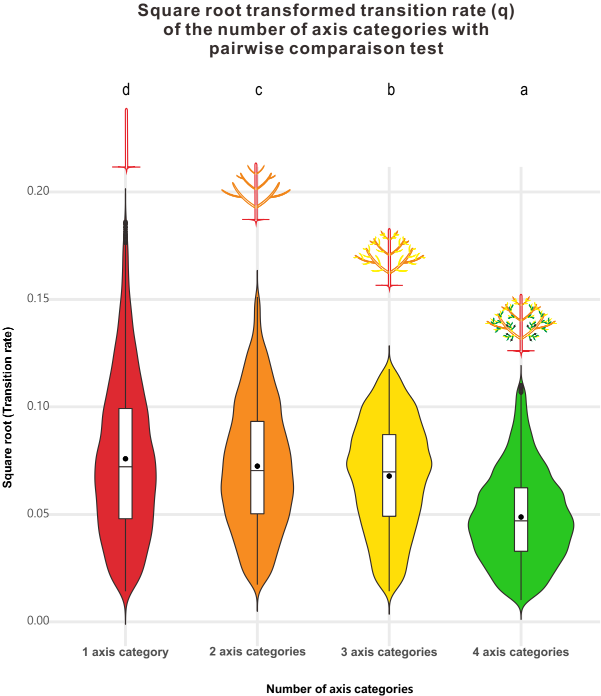
(a) Traits

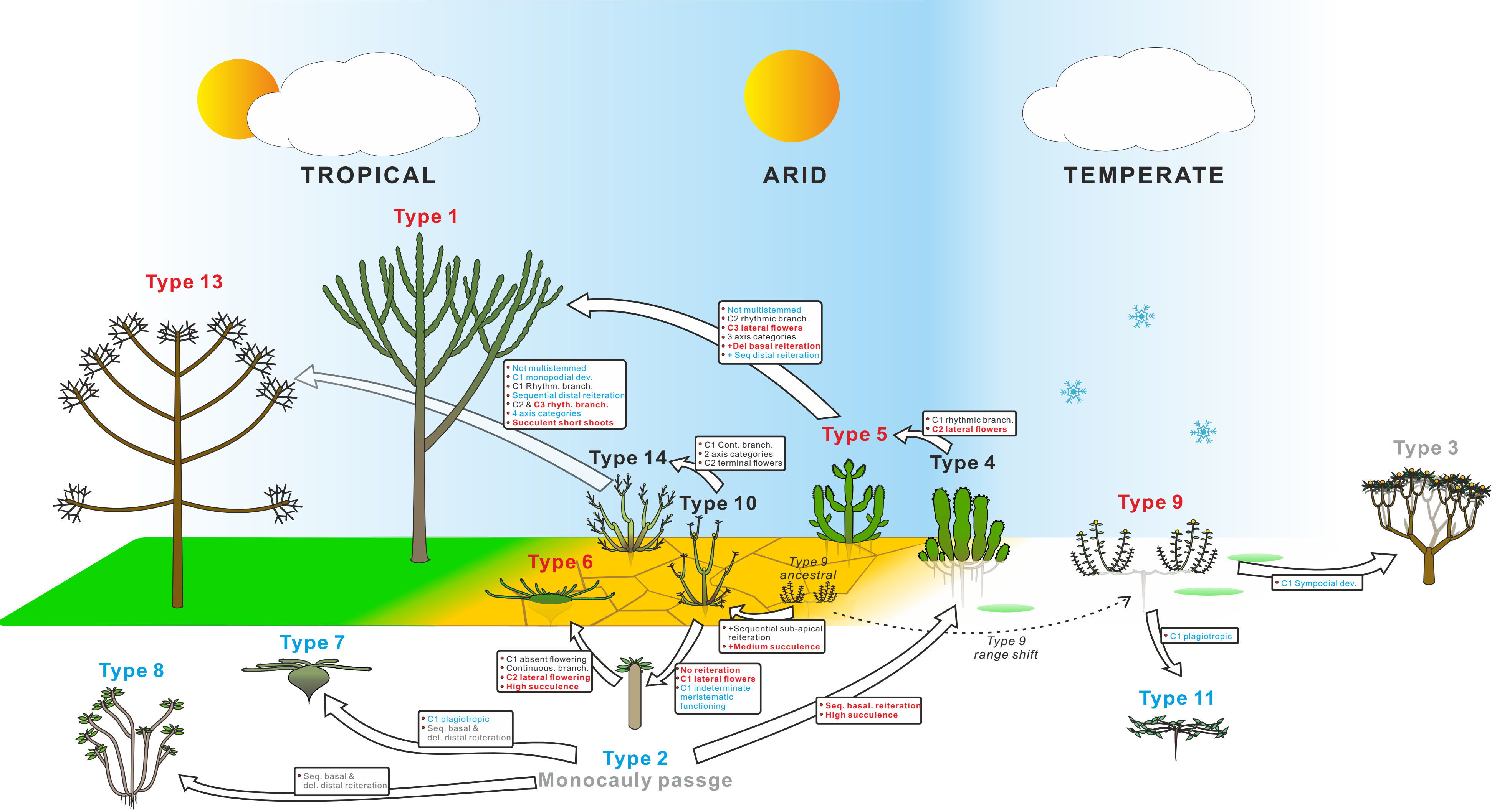


(b) Architectural types




Type 9
Type 10
Type 3
Type 12
Type 6
Type 4
Type 11
Type 14
Type 13
Type 2
Type 7
Type 8
Type 5
Type 1
Aus
America
Africa
Africa
Eurasia
subg. Esula
A→B
climatic cluster A
Euphorbia
moderate succulence
sub-apical reiteration
subg. Athymalus
high succulence
C1 cont. branch
2 axis categories
C1 flo. abs.
C1 flo. lat.
A→B
subg. Chamaesyce
sect. Anisophyllum
C1 plagiotropic
A→B
A→B
A→C
moderate succulence
sub-apical reiteration
subg. Euphorbia
no reiteration
C1 flo. lat.
C1 flo. abs.
sect. Goniostema
seq basal reiteration
high succulence
C1 rhythm. branch.
2 axis categories
C→A
sect. Euphorbia
3 axis categories
C2 rhythm. branch.
seq distal reiteration
Environmental preference switches
A→B Desert to temperate
A→C Desert to tropical
C→A Tropical to desert
70
60
50
40
30
20
10
0 Mya


Square root transformed transition rate (q)
of the number of axis categories with
pairwise comparaison test
d
c
b
a
0.20
0.15
0.10
0.05
0.00
Square root (Transition rate)
1 axis category
2 axis categories
3 axis categories
4 axis categories
Number of axis categories


TROPICAL
ARID
TEMPERATE
Type 1
Type 13
Not multistemmed
C2 rhythmic branch.
C3 lateral flowers
3 axis categories
+Del basal reiteration
+ Seq distal reiteration
Not multistemmed
C1 monopodial dev.
C1 Rhythm. branch.
Sequential distal reiteration
C2 & C3 rhyth. branch.
4 axis categories
Succulent short shoots
C1 rhythmic branch.
C2 lateral flowers
Type 5
Type 4
C1 Cont. branch.
2 axis categories
C2 terminal flowers
Type 14
Type 10
Type 3
Type 9
Type 6
Type 9
ancestral
C1 Sympodial dev.
+Sequential sub-apical reiteration
+Medium succulence
Type 9
range shift
C1 plagiotropic
Type 7
Type 8
C1 absent flowering
Continuous. branch.
C2 lateral flowering
High succulence
No reiteration
C1 lateral flowers
C1 indeterminate meristematic functioning
Type 11
Seq. basal. reiteration
High succulence
C1 plagiotropic
Seq. basal &
del. distal reiteration
Seq. basal &
del. distal reiteration
Type 2
Monocauly passge