A pollination mutualism over the edge: growth form and fig traits respond differently during niche expansion to arid environments

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Background: It is unclear how climate shifts may interfere with the diversification of tightly associated species interactions. Obligate pollination mutualisms are ideal for investigating the underlying processes of niche evolution by environmental change.

Objectives: Niche evolution that corresponds with phenotype-by-environment interactions that include climate shifts is expected to affect the stability of partner associations of mutualisms. Here, we compare the evolution of fig syconium size and growth form strategies for coping with soil water stress during a range expansion by *Ficus* into arid environments.

Methods: Niche models of 31 *Ficus* taxa were used to define contemporary habitat requirements of each species, which are then incorporated into Bayesian mixed models to examine the response of each trait to the soil water variables, other environmental variables and phylogenetic dependencies.

Results: The results showed that phylogenetic constraints best explained syconium size variation, while environmental lability best characterised growth form variation. Two species adapted to arid environments that exhibited convergence in these traits had significantly different habitat requirements compared to forest and savanna species.

Conclusion: The niche expansions by *Ficus ilicina* and *Ficus cordata* involved distinct historical processes. The findings suggest selection for traits that varied at different temporal scales limit the rate of niche expansions, and potentially destabilise mutualist partnerships and promote host shifts.

Keywords: phenotype-by-environment, habitat selection, ecological niche, water stress, Karoo, phylogenetic constraints, host shift.

Introduction

Abiotic and biotic factors limit the geographical ranges of all species, but also create opportunities for their diversification (Ackerly 2003; Holt 2009; Carscadden et al. 2020; Mestre et al. 2020). However, climate shifts potentially reorganise species phenotypes, the geographic distributions of resources, and drive niche evolution of respective partner species of mutualisms (Joy 2013; Werner et al. 2018). Phenotype-by-environment interactions (Via & Lande 1985) that are critical to the contemporary geographic distribution of mutualisms are rarely linked to their evolutionary histories during niche and climate shifts. Plant growth form responds to changes in the abiotic environment and has consequences for physiological innovations of the plant (Rowe & Speck 2005). Specifically in *Ficus*, syconium morphology influences

the reproductive ecology of the fig–fig wasp mutualism through the availability of female florets used as wasp breeding sites, and the number of seeds that can be produced by the tree (Bronstein 2001). Ecological or evolutionary mismatches in these traits might underlie host shifts and the exceptions to the extraordinary patterns of co-diversification observed in the *Ficus* pollination mutualism.

Species associations that exhibit strong evolutionary constraints (i.e., the observed pattern as generated by prior evolution) may either limit (Bronstein 2001) or facilitate (Joy 2013) processes such as niche expansions by which mutualisms diversify (Gilman et al. 2011; Burkle et al. 2013). Theory predicts that when species interactions of mutualisms are compartmentalised, when there is high interaction specificity, they are susceptible to destabilisation (Thébault & Fontaine 2010; McLeish et al. 2011). Niche expansions may cause phenotypic and phenological mismatches that destabilise interactions between partners and determine avenues of diversification or extinction. Generally, it is uncertain how selective pressures act on respective pairs of a mutualism because each species need not express the same functional associations with the environment (Sachs & Simms 2006; Ibanez et al. 2016). For instance, if phenotype-by-environment interactions are strong, population divergence may occur along resource gradients during environmental change over time, and reorganise underlying genotypes critical to functional aspects of species associations (Bolnick et al. 2011; Newman et al. 2012). Populations experiencing changes to environmental conditions that result in low-density geographic distributions, are expected to alter the ecological niches of respective mutualist partner species (e.g., Gilman et al. 2011). This can potentially lead to other association types or to the extinction of one or both partners (Kiers et al. 2010). Species that are distributed on the range limits, in marginal environments, or are subject to climate shifts may exhibit these demographic processes (Bridle & Vines 2007).

Obligate pollination mutualisms are ideal for investigating the underlying processes of niche evolution when responses to environmental perturbations are expected to be different between free-living and sedentary partner species of insect–plant associations. The spectacular co-diversification pattern inferred between *Ficus* and their pollinator fig wasps (Agaonidae, Chalcidoidea) suggests that their co-evolution has been contributed to by phylogenetic constraints (Van Noort & Compton 1996; Cornille et al. 2011). By phylogenetic constraint, we refer to the importance of ancestry as a strong determinant of the *Ficus* species that a wasp will obligately pollinate (Hawkins & Compton 1992). The growing number of exceptions to these mirrored patterns of diversification are indicative of non-phylogenetic influences (Renoult et al. 2009; Cruaud et al. 2011; McLeish & Van Noort 2012) and suggest environmental

variation may have influenced the reproductive ecology, stability or diversification of the mutualism.

In South Africa, *Ficus* largely occurs as mono-specific patches in savanna or coexists in forest habitats. However, some species have adapted to arid environments and water-stressed habitats. The observation that *Ficus* species occupy arid habitats raises the question of how they evolved to expand out of their pantropical ranges (Cruaud et al. 2012), and how this may have influenced the reproductive ecology of the mutualism. Both growth form and syconium morphology are associated with strategies for coping with water stress and are hypothesised to be sensitive to water availability gradients (Piedra-Malagón et al. 2011). Plant growth form responds to changes in the abiotic environment and has consequences for physiological innovations of the plant (Rowe & Speck 2005). For example, the evolutionary labile expression of growth form in *Ficus* species has a direct influence on the assimilation of water (Hao et al. 2011), and water loss from their syconia (Patiño et al. 1994). For example, Hao and colleague's (2010) work on leaf structure and physiological traits associated with growth form and habitat show trade-offs between leaf water flux and leaf drought tolerance. The correlation between syconium diameter and leaf area has also been shown to respond to environmental variation (Lasky et al. 2014). Variation in physiological tolerances has a critical role in the geographical distributions and associations of host figs and their pollinators (Warren et al. 2010). Syconium morphology influences host and pollinator fitness because of the duality between the availability of female florets in the syconium that are galled and used as breeding sites, and the number of seeds that can be produced by the tree (Bronstein 2001). Additionally, syconium size is critical to maintaining non-lethal internal temperatures within the tolerance thresholds of pollinating fig wasps (Patiño et al. 1994). In tropical habitats, large syconia are critical to the survival of wasps and the regulation of internal temperature that is dependent on transpirational cooling and optimisation of water resources (Krishnan et al. 2014). Thus, growth form and syconia trait adaptations may differ between environments with contrasting water resource availability. Most *Ficus* species in subgenus *Urostigma* have a hemi-epiphyte habit with a growth stage resistant to water deficiencies of the canopy environment before the transition to the terrestrial stage, and are pre-adapted to an epilithic growth form (lithophyte) in drier environments (Berg & Corner 2005; Hao et al. 2010). Hemi-epiphytism has evolved independently on multiple occasions and is expected to have undergone selection for drought tolerant traits (Hao et al. 2011). We expected that soil water gradients influenced contemporary and historical geographical distributions of growth form and syconium size of *Ficus* in South Africa. Changes to the distribution of these traits during niche expansions may have destabilised mutualist associations and resulted

in host shifts evident in many South African lineages (McLeish & Van Noort 2012).

In this study we aim to test whether the geographic distribution of fig traits central to the physiological tolerance thresholds and reproductive biology of the fig pollination mutualism, corresponded to either environmental variation or phylogenetic constraints. Soil water properties have a strong relationship with niche differentiation of species at local and much larger spatial scales (Guo et al. 2017) and were used in conjunction with other environmental variables to connect climate to topographic variation in moisture availability (Larcher 2003). We test the hypotheses that: 1) physiological and reproductive trait responses correspond to environmental variation, or 2) to phylogenetic constraints. We first use habitat selection analyses to describe each *Ficus* species' soil water resource and ecological niche dimensions and use these as predictors of trait variation and test phylogenetic dependencies. Habitat selection in plants is an evolutionary process involving the adjustment of species' geographical ranges by environmental factors (Bazzaz 1991). Second, we examine the relationship between variation in growth form and syconium traits with soil water and environmental variation while correcting for phylogenetic dependencies using Markov chain Monte Carlo generalised linear mixed models (MCMCglmms). We test the hypothesis that the evolution of growth form and syconium size of *Ficus* covaried with soil water and environmental variation. By evaluating habitat requirements of *Ficus* (Moraceae) in South Africa, we investigate whether the evolutionary histories of physiological tolerance and reproductive traits corresponded with each other during niche expansions by ancestral lineages of *F. ilicina* and *F. cordata* from hydric to xeric climates. The findings showed that the occupancy of the Karoo deserts by *F. ilicina* and *F. cordata*, corresponded with convergence in traits but via distinct evolutionary histories. Generally, stronger niche conservatism in syconium size contrasted the environmental lability of growth form and suggested that interdependencies between these traits may limit the rate of niche expansions.

Materials and methods

Species biology

Approximately 500 of the 800 or so *Ficus* species germinate as epiphytes and develop into hemi-epiphytes that rely on a host for physical support (Berg & Corner 2005). Hemi-epiphytic forms of *Ficus* predominate in tropical environments, while free-standing trees (i.e., arborescent) and lithophyte forms are associated with drier environments at higher latitudes at the extents of circum-tropical ranges (Berg & Wiebes 1992; Dixon 2003). The fruit-like structure that *Ficus* species produce, develop as syconia and provide a keystone resource for a rich assemblage of pollinating and non-pollinating wasps, and many other invertebrate and vertebrate species (Compton & Van Noort 1992). Asynchronous production of syconia throughout the year requires continuous cycling of pollinators between patches to maintain viable populations of both mutualistic partners. Heterogeneous host distributions make dispersal of fig wasps among patches risky and exposes them to desiccation especially in dry environments.

Habitat selection analyses

To define the habitat requirements of *Ficus* and conduct habitat selection analyses (Dolédec 2000; Calenge 2006), we extracted environmental variables from raster data that were then associated with presence records of each taxon. The method provides an estimate called marginality, which corresponds to deviations of a species mean resource requirements from the mean conditions of the entire study area. The method was used to generate environmental predictors for use in the prediction of trait variation (see below). The variables used in the habitat selection analysis comprised soil water stress (SWS) that indicates the number of days per year at which soil water content would be critical to plant stress (Schulze et al. 2007). Areas inside the arid west of South Africa are typically exposed to severe soil water stress (SWS) for at least 150 days of the year and can be for periods of more than 300 days. Plant available water (PAW) was also used to indicate variation in the storage of water available from the soil profile (Schulze et al. 2007). Both SWS and PAW depend on soil texture and the soil profile depth (Supplementary material S1). We also included variables that influence soil quality, drainage and evapotranspiration. These comprised elevation (https://srtm.csi.cgiar.org/srtmdata), slope, aspect (calculated from elevation) and biome class (https://bgis.sanbi.org/SpatialDataset/Detail/329). Biomes are classified according to vegetation types defined by contributions of dominant, common and rare species, in conjunction with topographic and climatic features (Dayaram et al. 2017, Mucina & Rutherford 2006). Biome categories generalise about climatic zonation and bio-productivity that potentially constrain each species distribution. We used a modification of the outlying mean index (OMI) approach called canonical OMI (canOMI) in the habitat selection analyses, to evaluate soil water resource requirements and environmental dimensions of each species. The canOMI approach corrects for potential biases created by the presence of strong environmental patterns characteristic of South Africa and transforms the sampling area into resource units.

Presence data of 2 163 localities comprising 1 202 unique records of 31 *Ficus* species and subspecies in South Africa (Supplementary Table S1) were compiled from field

trip collections and the SANBI and PRECIS databases (available at https://posa.sanbi.org/sanbi/Explore). The presence data represented approximately 75% of known South African species. The PRECIS data included records that synonymise *F. petersii* and *F. burkei* as *F. thonningii*. We retained the taxonomy used in these records for consistency and assume that this will result in *F. thonningii* having resource use characteristics similar to the other two species. Species with low sample sizes of < 3 individuals (i.e., *F. natalensis* subsp. *graniticola* and *F. sycomorus* subsp. *gnaphalocarpa*) were retained after pilot analyses indicated their inclusion resulted in negligible changes to niche comparisons and the MCMCglmm outcomes. We treated records with subspecies assignments as separate taxa in the habitat selection analyses and tested the effect of synonymising them in the MCMCglmm analyses. The approach assumes uniform sampling effort and probability of detection among species and is addressed by weighting the sampling units in proportion to their abundance. Each resource unit corresponds to a pixel of a raster map and the soil water variables associated with it. The canOMI analysis was conducted using the R version 3.6.3 (R Core Team 2012) package *adehabitatHS* (Calenge 2006).

Phylogenetic dependencies

To estimate phylogenetic dependencies in the prediction of growth form and syconium size, an ultrametric consensus phylogeny of 37 species (alignment available from authors on request) was pruned to 24 South African species for which there were corresponding presence records. As there were sequences available for taxa identified to species and subspecies level (*F. cordata* and *F. cordata* subsp. *cordata*), both were retained in the interest of inclusivity and sample size. We used MRBAYES 3.1.1 (Huelsenbeck & Ronquist 2001) to evaluate phylogenetic uncertainty and BEAST and BEAUTI v. 1.7.5 (Drummond et al. 2012) to infer an ultrametric consensus tree. Sequence data of up to 767 bp of a ribosomal internal transcribed spacer (*ITS*) and up to 479 bp of external transcribed spacer (*ETS*) were compiled from various sources (Jousselin et al. 2003;

Rønsted et al. 2007; McLeish & Van Noort 2012). All sequence data are available from the GenBank repository (https://www.ncbi.nlm.nih.gov/genbank/). The sequence data was partitioned by *ITS* and *ETS* loci, and a general time reversible DNA substitution model (GTR) with gamma distributed (+G) rates and a proportion of invariant sites (+I) applied for the analysis. Four Markov chains were run for 40 million generations, sampling each chain every 1 000 trees. Posterior probabilities and mean branch lengths were derived from 35 000 post-burnin trees. Convergence and posterior parameter distributions were assessed using the MCMC Tracer Analysis Tool v.1.6 (Rambaut et al. 2014). An inverse relatedness matrix and phylogenetic covariance matrix were generated from the consensus tree using the R package *MCMCglmm* (Hadfield & Nakagawa 2010) and introduced to the MCMCglmms as a random variable (Supplementary material S2).

Trait response models: MCMCglmms

We evaluated the relative strengths of PAW and SWS in predicting growth form and fig size with and without the contributions of the other topological variables (altitude, aspect, slope and biome), to assess the effect of variables on model performance (Table 1). The Bayesian mixed model approach was selected because it allows the analysis of phylogenetic dependencies using categorical (growth form) and continuous (syconium size) response variables. Species-level variation in syconium size was based on diameter measurements sourced from the literature (Berg & Wiebes 1992; Burrows & Burrows 2003). We calculated a mean value of syconium diameter for each species to infer variation across the internal nodes of the phylogeny, as this parameter is appropriate for testing the effects of ancestry on phylogenetic dependencies (e.g. Ackerly et al. 2006). We coded growth form for each species as a multinomial variable for lithophyte, terrestrial tree, hemi-epiphyte or combinations of these categories (Supplementary Table S2). For tests of phylogenetic dependencies, we aggregated each subspecies of (*F. cordata*, *F. natalensis*, *F. polita*, *F. sansibarica*, *F. sycomorus* and *F. tremula*) to a

Table 1. Mixed model (MCMCglmms) designs showing response traits and predictor variables; PAW = plant available water; SWS = soil water stress

Response trait	Predictor variables [random factor]
Syconium size	PAW + SWS + [phylogeny + species]
Syconium size	mean PAW + within-species PAW + mean SWS + within-species SWS + [phylogeny + species]
Syconium size	PAW + SWS + elevation + slope + [phylogeny + species + biome + aspect]
Growth form	PAW + SWS + [phylogeny + species]
Growth form	mean PAW + within-species PAW + mean SWS + within-species SWS + [phylogeny + species]
Growth form	PAW + SWS + elevation + slope + [phylogeny + species + biome + aspect]

single species to correspond with the phylogeny. A random factor (taxon) that distinguished all taxa including subspecies, was used to test the effect of aggregating subspecies in the MCMCglmms. Variables for biome and aspect were treated as categorical random factors. The remaining variables were assessed for normality and treated as continuous normal predictors. Slope was square root transformed and all variables scaled (subtracting the mean and dividing the result by the standard deviation) for the MCMCglmm analyses (R code available from authors on request).

To evaluate the level of species-specificity of the soil water variable, we assessed the proportion of within- and between-species variance using MCMCglmms. Species mean PAW and SWS were included as fixed factors to assess between-species variance, in addition to fixed factors for the individual estimates of PAW and SWS to look at within-species variance. A random factor for species was included in addition to one for phylogeny to accommodate the modelling of between-species contributions. Finally, phylogenetic heritability (the probability associated with an ancestral state), H^2, of growth form and syconium size was calculated as $\sigma^2_a / (\sigma^2_a + \sigma^2_e)$, where σ^2_e is the residual variance (comprising the fixed effects) and σ^2_a is the phylogenetic variance. The MCMCglmms of species-specificity and the heritability analyses were both run for 10.0×10^6 iterations with a thinning interval of 1 000 and burnin of 10 000. We used a G-structure prior of $V = 1$ and $nu = 0.002$, and a R-structure prior of $V = 1$ and $nu = 1$ in the syconium size model. For the growth form model, we used a G-structure prior of $V = 1$, and $nu = 1 000$ for random variables and a fixed R-structure prior ($fix = 1$) at $V = 200$. The growth form data were from a categorical variable distribution, and therefore, residual variance was fixed (i.e., to an arbitrary prior). The posterior distribution of predictor variables (Sol), covariance estimates (VCV), and auto-correlation between posterior values sampled from the Markov chain were assessed in all models to ensure parameter convergence and a reasonable approximation of the true posterior. The Bayesian p-value (pMCMC) is ($2\times$) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support. The estimate is credible if its highest posterior density (HPD) distribution does not span zero. All MCMCglmm analyses were conducted using the R package MCMCglmm.

Results

Habitat selection analyses

The analyses of habitat selection that included all predictor variables shows three main patterns: (i) the

subspecies of *F. cordata* and *F. ilicina* cluster along the soil water variables vectors and with Karoo, Thicket, Fynbos and Grassland biomes (Figure 1, Figure 2a); (ii) most species clustered between the vectors for PAW and Savanna; (iii) and there were three species, *F. bizanae*, *F. natalensis* and *F. polita* that were strongly affiliated with high PAW and the Forest biome (Figure 2a). Kruskal-Wallis rank sum tests indicated that syconium size ($\chi^2_{(15)} = 14.798$, p = 0.046) and growth form ($\chi^2_{(6)} = 18.307$, p < 0.006) were significantly associated with the first axis of the canOMI analysis, and indicated that both traits had a strong relationship with contemporary water resource variables. The first canOMI analyses indicated *F. cordata* and *F. ilicina* occupied biomes that represent atypical distributions of *Ficus* in South Africa, i.e., lithophyte species that have shifted towards south-facing slopes, higher SWS, and lower PAW in the Karoo biomes. A majority of species occupy the Savanna biome, with comparatively few Forest biome species. The results of a second canOMI analysis that comprised PAW and SWS only, differed from the analysis that comprised all variables, as it showed that biome had a strong influence on the forest species (Figure 2b). Otherwise, the same general patterns were maintained between the two analyses. Both showed that the obligate lithophyte species were clearly distinguished from the other species (the second canOMI analysis). For instance, the differences in the mean PAW and SWS resource unit distributions used by and available to *F. cordata* and *F. ilicina* were opposite to the savanna and forest species (Figure 3). *Ficus cordata* and *F. ilicina* belong to distantly related *Ficus* sections yet converged on the same ecological strategies; both had similar moisture requirements, are epilithic and produce small syconia.
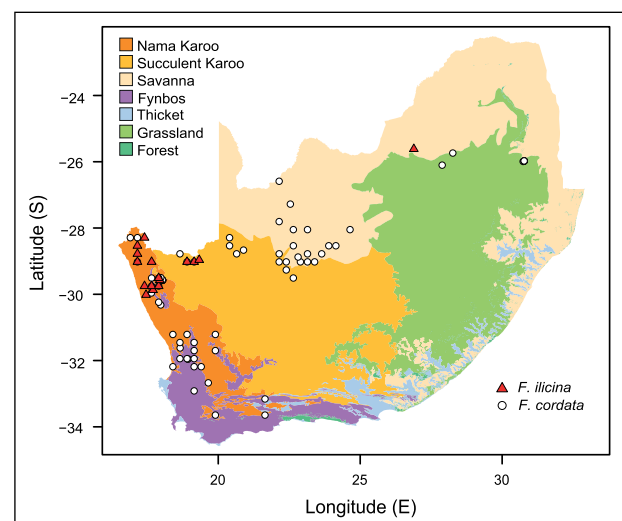

Figure 1. South African biomes and the distributions of *Ficus ilicina* and *Ficus cordata*. Biomes are classified according to vegetation types defined by contributions of dominant, common and rare species, in conjunction with topographic and climatic features.
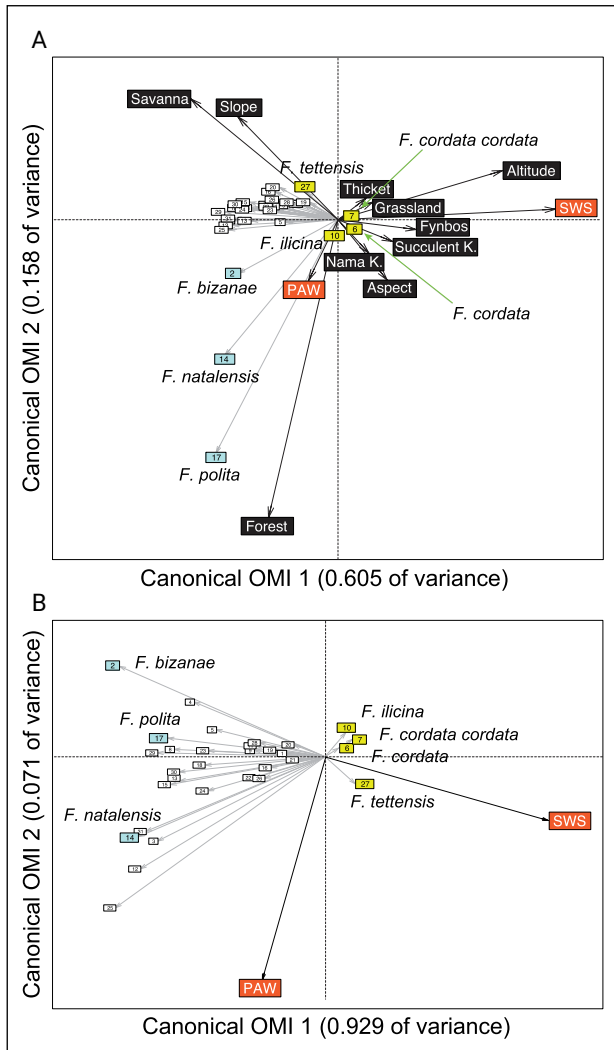
Figure 2. The first two axes of canonical outlying mean index (OMI) analyses including all environmental variables (a) and only soil water stress (SWS) and plant available water (PAW) variables (b). Highlighted are obligate lithophytes *F. cordata*, *F. ilicina*, *F. tettensis* and 'outlier' species. Vectors for each environmental layer are superimposed over the marginal vectors for each species. Numeric species codes are given in Supplementary Table S1.

Consensus phylogeny

To visualise phylogenetic and trait relationships among species caused by shared ancestry, a consensus was inferred. The consensus phylogeny (Figure 4) indicated good stem clade posterior probability support (0.93–1.00) and generally good crown clade support (0.83–1.00) that was consistent with the topology of a recent study (Cruaud et al. 2012). The distribution of growth form across the terminal branches indicated phylogenetic clustering of obligate terrestrial tree species. However, the obligate lithophytes were phylogenetically over-dispersed with *F. tettensis–F. abutilifolia*, *F. salicifolia–F. cordata* and *F. ilicina* belonging to three different *Ficus* subsections and indicated multiple evolutionary origins of this trait. Syconium size was phylogenetically conserved in subsection *Caulocarpae*, *Sycomorus* and

Urostigma, compared to greater variation in *Chlamydodorae* and *Platyphyllae*. The consensus tree inferred that the relationship between the traits tended to be clustered only in sections *Sycomorus* and *Urostigma*, with the large syconia produced by obligate trees, and the small syconia by obligate lithophytes, respectively.

Trait evolution and soil water gradients

We inferred a phylogeny to correct for dependencies among species caused by shared ancestry, using Bayesian trait reconstructions implemented with MCMCglmms. As SWS and PAW were estimated multiple times for each species, we assessed between- and within-species variance. The analyses indicated weak ($pMCMC > 0.962$) species-specific variance compared to strong interspecific differences ($pMCMC < 0.046$) in both growth form and syconium size (Supplementary Table S3), indicating relatively high interspecies variation. We weighted variance priors for the G- (phylogeny) and R- (residual) covariance structures to evaluate phylogenetic dependencies and used the DIC (Deviance Information Criterion) to compare model-fit (Supplementary Table S4). Mean syconium size was best explained when the bias favoured the random factor for phylogeny (Δ-DIC = 3 553.5). By contrast, growth form was best explained when the priors favoured the residual over the phylogenetic variance component (Δ-DIC = -275.7). The variance contributions by phylogeny to syconium size relative to growth form indicated that phylogenetic dependencies were a stronger factor in the evolution of syconium size compared to growth form.

The MCMCglmms of soil water, environmental and trait variation, indicated the effects of SWS ($pMCMC < 0.001$) and PAW ($pMCMC = 0.002$) on growth form were strong relative to the weak effects of SWS ($pMCMC = 0.600$) and PAW ($pMCMC = 0.697$) on syconium size (Table 2). The inclusion of the other environmental predictors (Supplementary Table S5) improved fit in the growth form model (Δ-DIC = 5.72) but reduced fit in the syconium size model (Δ-DIC = -9.9). These contrasts in model-fit indicated that growth form, relative to syconium size, responded better to the other environmental predictors than explained by PAW and SWS alone. The heritability analyses indicated that syconium size had a high probability (i.e., 95% CI = 95% Credible Interval) of being transmitted to descendants (0.980 with 95% CI of 0.966–0.994) compared to growth form (0.005 with 95% CI of 0.005–0.006). Together, the MCMCglmm analyses indicated that the distribution of growth form in South Africa was strongly affected by soil water gradients relative to syconium size that had a much stronger phylogenetic signal.
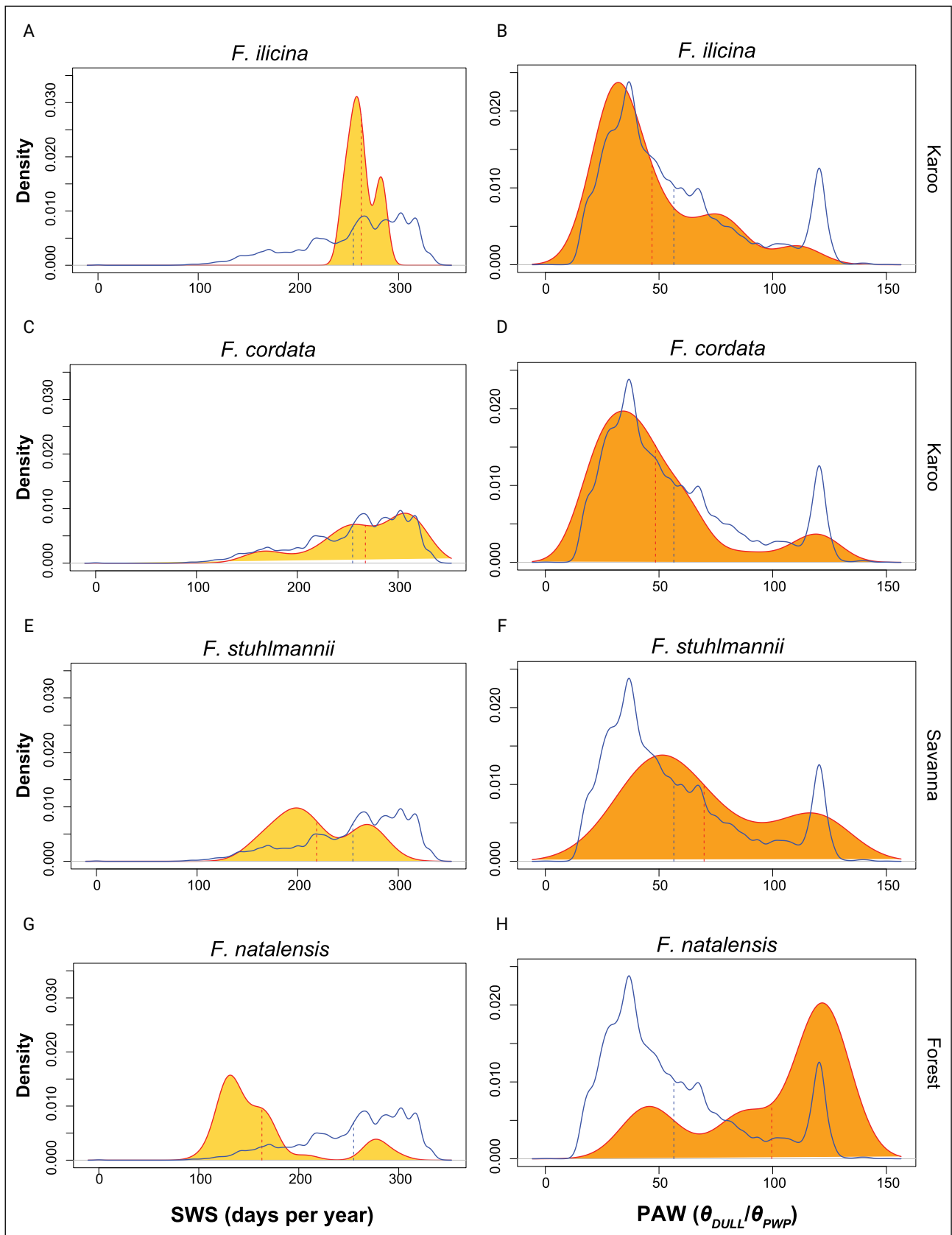
Figure 3. Kernel density estimation of available (smoothed line) and used resource units (filled distribution) of arid, savanna and forest species. The mean of each distribution is indicated by dashed lines. Soil water stress (SWS) indicates the number of days per year at which soil water content would be at critical plant stress. Plant available water (PAW) is the ratio of the drained upper limit of soil water (θ_{DUL}), and the permanent wilting point of soil water (θ_{PWP}). Available units (environment) are sites that correspond to where a species presence is uncertain, but where we consider that it could be present as characterised with the soil water variables.

Figure 4. A Bayesian consensus chronogram of *Ficus* species in Africa. The taxa pruned for the MCMCglmm analyses have grey terminal taxon labels. Circles on terminal branches indicate obligate lithophytes or obligate terrestrial trees with unlabelled terminals as having multiple growth forms (see Supplementary Table S2 for details). Branch weight corresponds to mean syconium size. Posterior probabilities indicated on the branches. The respective associated fig wasp pollinator genera are indicated in the adjacent column to the host fig species. *Ficus* sections and subsections indicated respectively by vertical bars on the right. *Ficus ovata* has become a synonym of *F. laurifolia*. *Sequence data from *F. sycomorus* sampled in the Congo basin.

Table 2. The posterior distribution of the MCMCglmm coefficients for growth form and mean syconium size responses as explained by PAW (plant available water), SWS (soil water stress), and phylogeny. CI = 95% Credible Interval. Strong effects indicated with bold *pMCMC* value. The term *G* describes a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances. The Bayesian p-value (*pMCMC*) is (2×) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support

	Variable	Posterior mean	Lower CI	Upper CI	Effective sample	*pMCMC*
Syconium size						
G-structure	Phylogeny	2.087	1.061	3.559	990	-
	Taxon	0.007	0.000	0.025	990	-
R-structure	Residual	0.029	0.021	0.038	1202	-
Fixed effects	PAW	-0.028	-0.167	0.103	990	0.697
	SWS	-0.063	-0.289	0.162	990	0.600

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	Variable	Posterior mean	Lower CI	Upper CI	Effective sample	*pMCMC*
Growth form						
G-structure	Phylogeny	1.088	0.983	1.197	990	-
	Taxon	1.154	1.051	1.267	990	-
R-structure	Residual	200	200	200	0*	-
Fixed effects	PAW	2.848	0.996	4.798	1092	**0.002**
	SWS	-12.519	-14.235	-10.692	990	**< 0.001**

*Fixed variance prior for categorical response.

Discussion

We linked the soil water requirements of *Ficus* species with the geographic distributions and evolutionary histories of growth form and syconium size. The significant relationships between the water-stress predictors and trait variation agreed with the hypotheses that *Ficus* traits are sensitive to water availability gradients (e.g., Piedra-Malagón et al. 2011). However, the growth form responses to soil water variation were stronger than those of syconium size in explaining the evolution of these traits. The strong phylogenetic signal of syconium size in concert with their consistent spatial positioning on the tree within the respective subsections contrasted with that of growth form, and supported the hypothesis that syconium morphology is crucial to the reproductive biology and stability of the mutualism (Compton & Van Noort 1992). Our findings indicated that constraints on syconium size evolution might have limited the rate of expansion by *Ficus* to arid environments, while the environmental lability of growth form may have facilitated niche evolution. Such performance trade-offs that arise due to complex patterns of covariation among functionally related traits (Pigliucci 2003) might have a role in destabilising mutualistic associations with pollinators.

Figs and soil water gradients

Our findings supported the hypothesis that the contemporary distribution of both traits corresponded to water gradients (i.e., canOMI axis one) in South Africa. For instance, *F. ilicina* and *F. cordata* are two obligate lithophyte species with small syconia, which occupy particularly low PAW and high SWS habitats (Figures 2 and 3) in the Nama and Succulent Karoo deserts (Figure 1). The habitat selection analyses distinguished the contemporary distributions of these species from the majority of the other *Ficus* lineages in South Africa that occupy the Savanna biome. For instance, *F. cordata* and *F. ilicina* were more frequently observed on

southward-facing aspects that presumably resulted in lower exposure to solar radiation. Conversely, evidence of occupation on northward-facing aspects in a large majority of the other species suggests an advantage in increased exposure during colder months in seasonal climates. Climate shifts during the Quaternary caused changes to water availability in southern Africa and resulted in the dominance of arid-adapted vegetation typical of the savanna biomes today (Linder 2014).

A number of processes may have led to the occupation of arid environments by *F. ilicina* and *F. cordata*. For example, covariance among phenotypes might have arisen due to environmental filtering (i.e., ecological sorting) that occurs due to spatial autocorrelation (Freckleton & Jetz 2008). Alternatively, the coexistence of these distantly related species may have arisen as a consequence of allopatric speciation between ecologically similar habitats, with subsequent range shifts into sympatry in their contemporary distributions. Although there was evidence of 'selection' for higher SWS in both the lineages, *F. ilicina* occupied habitats with relatively narrow SWS variation (Figure 3) compared to *F. cordata*, which might indicate alternative routes to adaptation to water stressed habitats. For example, it has been shown that in seasonal semideciduous forest in Brazil, hemi-epiphytes established at much lower height on host trees than in evergreen rainforests (Coelho et al. 2014). The distinctions in environmental niche requirements between the arid-distributed species and the other obligate lithophytes that occupy savanna (*F. abutilifolia*, *F. salicifolia* and *F. tettensis*), suggests a number of unique historical factors influenced the occupation of water-stressed habitats by ancestral lineages of the obligate lithophyte species. Both the arid-adapted species have relatively restricted distributions from southwestern Angola through the Namib Desert into South Africa (Berg & Wiebes 1992). Although the contemporary geographic ranges of *F. cordata* and *F. ilicina* largely overlap, the former species extends a little farther south and eastward in South Africa.

The habitat selection analysis (Figure 2) discriminated biome affiliations between these species, showing *F. ilicina* to be largely associated with the Nama Karoo in its South African range. In South Africa, the Succulent Karoo, Fynbos and Grasslands biomes were also included in the distribution of *F. cordata*. Phylogenetic patterns of closely related species of *F. ilicina* (Figure 4) have disjunct ranges in west-central (*F. pseudomangifera*) and eastern (*F. usambarensis*) Africa, and suggests fragmentation contributed to vicariant speciation across these regions (Jürgens 1997). Conversely, the range of *F. cordata* is parapatric with its sister species, *F. salicifolia*, and suggests differentiation occurred across the savanna-Karoo divide (Figure 1). *Ficus salicifolia* is widely distributed through the eastern parts of Africa into the Arabian Peninsula, whereas the two subspecies of *F. cordata* (the nominate subspecies and *F. cordata* subsp. *lecardii*) have strongly disparate distributions with *F. cordata* subsp. *lecardii* restricted to the savanna belt extending from central Africa (southern Sudan and Central African Republic) to Senegal in west Africa (Berg & Wiebes 1992). All these contemporary distributions have most likely been driven by the fluctuating expansion and contraction of the savanna, woodland and forest biomes over the last 150 000 years (Dupont et al. 2000; Salzmann & Hoelzmann 2005). The evidence of differences in the breadth of soil water resource utilisation between *F. cordata* and *F. ilicina* (Figure 3) also suggests unique processes or timescales were associated with the occupancy of the Karoo deserts by the lineages of these two species.

The Nama and Succulent Karoo biomes have distinct phytogeographical characteristics that are each part of different Palaeo-Kingdoms (Cowling et al. 1999). Generally, the geology and soil characteristics of South Africa's biomes underlie environmental factors limiting the distribution of the vegetation (Guo et al. 2017). Soil fertility has been shown to be a regionally important factor in the distribution of savanna, along with effective rainfall and seasonal variability of rainfall (Lehmann et al. 2011). However, soil nutrient states between savanna and grassland biomes are strikingly similar and suggest other factors besides nutrient limitation drove vegetation changes in these regions (Gray & Bond 2015). Changes in soil characteristics have also been shown to be independent of changes to community structure in these regions, where interactions involving precipitation and fire regimes were determinants of changes to the vegetation (Dougill et al. 2010). For instance, Fynbos and Succulent Karoo are fire refuge areas that are distinct from the C$_4$ grass-rich savanna biome that is prone to annual burning (Linder 2014) and suggests a role for fire in niche evolution of *Ficus*. Additionally, the groundwater availability in rocky terrain of the Karoo ranges from depths of 20 to 100 m (De Vries et al. 2000) and might also be an important factor contributing to *Ficus* occupying the Karoo deserts. Generally, mixed historical processes such as rainfall gradients, fire frequency, seasonal variability and topographic features have produced the biogeographic distributions evident in the contemporary communities. Under changing environmental conditions, local adaptation and niche expansion by *F. cordata* and *F. ilicina* are expected to be slow, with population divergence occurring over long periods (Pyron et al. 2015) and possibly under contrasting mechanisms.

Niche expansion and phenotypic integration

Our findings were consistent with at least two independent niche expansions by *Ficus* from their palaeotropical origins (Cruaud et al. 2012) into arid environments. *Ficus cordata* and *F. ilicina* have occupied similar contemporary geographic ranges in arid biomes. This has resulted in the convergence of obligate lithophyte growth forms (Figure 4) and small syconium size in these distantly related lineages. Therefore, the geographic distribution patterns of these traits largely correspond to contemporary water gradients. However, differences between the heritability of the phenotypic traits and in the phylogenetic signal of SWS and PAW, suggest that the expansion into arid environments depended on phenotypic integration (Pigliucci 2003). Correlations or covariances between syconium size and growth form might be altered by changes in environmental conditions. For example, each trait might respond differently to environmental variation according to discrete spatial and temporal scales (Cornwallis & Uller 2009). The phylogenetic over-dispersion (Figure 4) and low probability of heritability of growth form suggests a labile trait important for habitat specialisation. This result is consistent with previous work that compared traits between hemi-epiphytic and non-hemi-epiphytic fig species and showed that ecophysiological traits exhibit phylogenetic lability (Hao et al. 2011). Over-dispersion of traits implies that closely related species may have differentiated between environmental niches (Cavener-Bares et al. 2009). It is possible that the niche expansions by *Ficus* into arid environments occurred along water availability gradients and resulted in selection for habitat specialisation (e.g., Hoffmann & Parsons 1993). Furthermore, given environmental lability in growth form, the relatively strong phylogenetic signal of syconium size suggests a limiting factor on the rate at which *Ficus* is able to adapt to arid conditions.

Syconium size and growth form may each have had a unique role in niche differentiation either locally or across wider regions. Epiphytism in *Ficus* has a role in α-niche (within-community) differentiation as a consequence of variation in ecological requirements and in habitat specificity among species (Nieder et al. 2001). For example, the negative relationship between syconium size and elevation suggested local niche partitioning in tropical habitats occurred at local scales of less than

3 km (Lasky et al. 2014). The ability to cope with water stress and low nutrient availability has been put forward as a key feature underlying the community composition of epiphytes in general (Zotz & Hietz 2001). The convergence of the lithophyte forms in arid habitats, and divergence between *F. ilicina* and *F. cordata* and the lithophytes *F. abutilifolia*, *F. salicifolia* and *F. tettensis* in savanna habitats, suggests a role for growth form in facilitating β-niche (between-community) differentiation. For example, among-population variation in several traits of *Ficus*, including syconium morphology, has been shown to correlate with latitude and precipitation variation (Piedra-Malagón et al. 2011). Both *F. cordata* and *F. ilicina* have a relatively small syconium size (0.5–1.0 cm and 1.5–2.0 cm diameter respectively), but not exclusively so, as the sister species *F. salicifolia*, which is associated with mesic environments, has similar fig size to the nominate subspecies (Berg & Wiebes 1992). Habitat aridity has been shown to be significantly correlated with tree height but not with fig size (Compton & Hawkins 1992).

The associated wasp fauna species richness is comparatively dramatically reduced in these two arid-adapted species with only four (*F. cordata*) and five (*F. ilicina*) fig wasp species developing within each of the host species (Compton & Hawkins 1992), although *F. salicifolia* supports a richness similar to these. Small fig size in combination with a smaller crop size also has implications for wasp population density, with wasp abundance per fig crop dramatically reduced compared to fig species developing in mesic environments. This may have reproductive implications that reduce the efficacy of pollinator dispersal and hence successful location of other fig crops suitable for pollination and oviposition. The arid-adapted lineages may be increasing the prevalence of apomixis, but any evidence for this is scarce (Firetti 2017). Given the negative implications of arid habitats on successful pollination, reproduction by vegetative means may be more advantageous than sexual reproduction for arid-adapted plants, reducing the genetic load associated with small fig and crop sizes, and also reduced wasp population abundance. Overall, one trait may have limited (e.g. the rate) while the other facilitated (e.g. a niche expansion) niche evolution by *Ficus* into arid habitats, as lineages accommodated climate shifts to drier conditions.

Destabilisation of the mutualism

Evidence that supports niche expansions by figs into arid habitats over long periods, suggests that pollinators had ample time to adapt to the changing conditions (i.e., phenotypic matching; Anderson & Johnson 2008). Additionally, niche expansions may have had consequences for populations experiencing marginal habitat quality at their range limits (Bridle & Vines 2007). Demographic processes at the range limits potentially led to changes in the habitat preferences and ecological

niche of pollinating wasps. For instance, polyphyletic affiliations of the pollinator genera *Elisabethiella* and *Nigeriella* (Figure 4) did not agree with a co-diversification hypothesis (McLeish & Van Noort 2012). Host shift patterns are consistent with changes to mutualist partners of ancestor lineages of *F. ilicina* and other *Ficus* species in this clade (subsection *Chlamydodorae*). One explanation put forward to explain the relatively high incidence of pollinator host shifts in African *Ficus* is the bias many species exhibit towards smaller syconium sizes (Berg & Wiebes 1992; Renoult et al. 2009). However, it is difficult to connect large-scale geographic changes and adaptive responses with phylogenetic patterns (Ackerly 2003) such as these. The relationship between small syconia and host shifts was not always consistent with the phylogenetic patterns. The role geographic distributions of phenotypes have on host shifts and the diversification of mutualisms is unclear as multiple traits influence partner associations.

Theoretically, partner associations of mutualisms are destabilised by limitations to seed and pollen dispersal (Amarasekare 2004), phenological mismatches (Gilman et al. 2011), and changes to interspecific interactions (Aung et al. 2022). *Ficus* species exhibit mixed densities across their range, which are dependent on seasonality and reproductive constraints on the maintenance of viable populations (Zhang et al. 2014). During environmental change, the fitness of fig and wasp pollinators at the range limits may therefore be determined by physiological tolerance thresholds that differ among respective populations. Dispersal that is dependent on physiological or behavioural phenotypic traits may cause individuals to settle in the environmental conditions that best accommodate their own phenotype and create non-random gene flows and spatial heterogeneity among phenotypes (Jacob et al. 2015). For example, connectivity among patches of the Sonoran Desert fig *F. petiolaris*, and the frequency of foundress visitation, decreased at the range limits (Duthie & Nason 2016). Small population sizes at the limit may be subject to the stochastic sampling of phenotypic variation that causes changes to phenotype means and variances of populations, and with it, enhance drift and destabilise species associations (Bolnick et al. 2011). For instance, geographic disassociations between fig and wasp populations may result in pollinator-effectiveness trade-offs (e.g., Armbruster 2017), which occur when plant fitness is either positively or negatively correlated between co-occurring pollinators. Adaptation in changing environments may have resulted in performance trade-offs among reproductive, physiological or other life-history traits of figs or wasps. If environmental lability in growth form was adaptive, it might strongly influence the evolution of reproductive traits and have feedbacks into the ecology of the mutualism. Any trade-off between ecological and evolutionary factors experienced by either fig or pollinator, might have also coincided with changes in mutualistic partners.

Conclusion

The niche expansions by *F. ilicina* and *F. cordata* involved distinct historical processes occurring over long periods and possibly under contrasting mechanisms. Niche expansions by *Ficus* into arid environments occurred along water availability gradients and resulted in selection for habitat specialisation. The environmental lability evident in growth form and the relatively strong phylogenetic signal of syconium size may have limited the rate at which *Ficus* was able to adapt to arid conditions. The selection for traits that limited the rate of niche expansions potentially destabilised mutualist partnerships and promoted host shifts.

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Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

M.J.M and D.G. conducted the data analysis and M.J.M. prepared the first draft of the paper. S.v.N., D.G. and M.J.M. reviewed and edited the paper for final publication. All authors contributed to the development of the study.

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

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Supplementary material

S1. Calculation of soil water variables

Climate variables and parameters interact and combine with each other and with the soil to generate the environment which the plant grows in, and water becomes available to the plant through soil moisture (Schulze et al. 2007). The variables, days of year with severe soil water stress (SWS) and plant available water (PAW), are used to test whether there is a relationship with syconium size. Days of year with severe soil water stress (SWS) indicates the number of days per year at which soil water content would be at critical plant stress. Severe soil water stress refers to the soil water content at which total evaporation is reduced to below 20% of the maximum evaporation: $\theta < 0.2\ E/E_m$. With θ as the actual soil water content, E is the total evaporation of a plant/soil system and E_m is the maximum evaporation that could take place. Plant available water (PAW) is the water in the soil profile that is readily available to plants. In this case PAW $= \theta_{DUL} - \theta_{PWP}$. With PAW as the plant available water, θ_{DUL} as the drained upper limit of soil water, and θ_{PWP} as the permanent wilting point of soil water. The plant available water indicates the storage of water available, and therefore it depends on the soil texture and the soil profile depth and the geological formations (Schulze 2007). The centre-west parts of South Africa have low plant available water and mostly at less than 40 mm deep (Schulze & Horan 2007).

S2. MCMCglmms

Growth form was treated as a multinomial variable with $J - 1$ linear predictors with J categories (Hadfield 2010). The priors passed to the Markov chain Monte Carlo generalised linear mixed model (MCMCglmm) take three parts that specify the R-structure, G-structure, and fixed effects (Hadfield 2010). The term G is used to describe a covariance matrix of the random effects, and R as the covariance matrix of the residual variances that are assumed to follow an inverse-Wishart distribution. The R- and G-structures use the scalar parameters V and *nu* to describe the inverse-Wishart distribution. A third parameter, *fix*, can be specified (i.e. a *fixed* variance component is not estimated) so that the model is free to estimate the other variance components. To test and compare the phylogenetic dependencies of each phenotype, we fixed priors for the R- and G-structure (as either 0.95 or 0.05 of phenotype variance) using an intercept model (with no fixed factors). By conditioning the variance structure of the model in this way to favour either the phylogeny or the residual component, we compared the respective contributions of each component to phenotypic variation. The deviance information criterion (DIC) was used to compare model fit. The DIC is conceptually similar to the Akaike Information Criterion, with lower values indicating better model fit (Spiegelhalter et al. 2002). The Markov chains of the intercept models were run for 5.0×10^6 iterations with a burnin of 10 000 and a thinning interval of 1 000.

Supplementary Table S1

Ficus species used in the canonical outlying mean index (OMI) analyses

Taxon	*n*	OMI code
Ficus abutilifolia	91	1
Ficus bizanae	15	2
Ficus bubu	5	3
Ficus burkei	56	4
Ficus burtt-davyi	51	5
Ficus cordata	10	6
Ficus cordata subsp. *cordata*	61	7
Ficus craterostoma	102	8
Ficus glumosa	83	9
Ficus ilicina	17	10
Ficus ingens	117	11
Ficus lingua	4	12
Ficus lutea	22	13
Ficus natalensis	40	14
Ficus natalensis subsp. *graniticola*	20	15
Ficus petersii	13	16
Ficus polita	5	17
Ficus polita subsp. *polita*	7	18
Ficus salicifolia	72	19
Ficus sansibarica	7	20
Ficus sansibarica subsp. *sansibarica*	16	21
Ficus stuhlmannii	31	22
Ficus sur	131	23
Ficus sycomorus	20	24
Ficus sycomorus subsp. *gnaphalocarpa*	1	25
Ficus sycomorus subsp. *sycomorus*	41	26
Ficus tettensis	21	27
Ficus thonningii	123	28
Ficus tremula	3	29
Ficus tremula subsp. *tremula*	4	30
Ficus trichopoda	18	31

Supplementary Table S2

Growth form categories used to model *Ficus* species in the MCMCglmm analyses; 1 = lithophyte, 2 = tree, 3 = hemi-epiphyte, 4 = lithophyte–hemi-epiphyte, 5 = hemi-epiphyte–tree, 6 = lithophyte–tree, 7 = all forms

	Lithophyte	Hemi-epiphyte	Tree	Code
F. abutilifolia	1	-	-	1
F. bizanae	1	2	-	4
F. bubu	1	2	3	7
F. burkei	1	2	3	7
F. burtt-davyi	1	2	3	7
F. cordata	1	-	-	1
F. cordata subsp. *cordata*	1	-	-	1
F. craterostoma	1	2	-	4
F. glumosa	1	-	3	6
F. ilicina	1	-	-	1
F. ingens	1	-	3	6
F. lingua	-	2	-	3
F. lutea	-	2	3	5
F. natalensis	1	2	3	7
F. natalensis subsp. *natalensis*	1	2	3	7
F. petersii	-	2	3	5
F. polita	1	2	3	7
F. polita subsp. *polita*	1	2	3	7
F. salicifolia	1	-	3	1
F. sansibarica	-	2	-	3
F. sansibarica subsp. *sansibarica*	-	2	-	3
F. stuhlmannii	-	2	3	5
F. sur	-	-	3	2
F. sycomorus	-	-	3	2
F. sycomorus subsp. *gnaphalocarpa*	-	-	3	2
F. sycomorus subsp. *sycomorus*	-	-	3	2
F. tettensis	1	-	-	1
F. tremula	-	2	3	5
F. tremula subsp. *tremula*	-	2	3	5
F. thonningii	-	2	3	5
F. trichopoda	-	-	3	2

Supplementary Table S3

The posterior distributions of MCMCglmm coefficients of mean syconium size and growth form responses explained by within- and between-species variance. CI = 95% credible interval. The term *G* describes a covariance matrix of the random effects and *R* as the covariance matrix of the residual variances. The Bayesian *p*-value (*pMCMC*) is (2×) the proportion of values from the posterior estimate that are of the opposite sign to the parameter calculated from the Monte Carlo sampling and provides a way to assess variable support.t

	Variable	Posterior mean	Lower CI	Upper CI	Effective sample	*pMCMC*
Syconium size						
G-structure	Phylogeny	1.040	0.335	1.962	1146	-
	Taxon	0.015	0.000	0.059	990	-
R-structure	Residual	0.030	0.020	0.039	990	-
	Species mean PAW	-1.051	-1.758	-0.237	844	**0.008**
	Within-species PAW	0.002	-0.136	0.135	1106	0.980
	Species mean SWS	-0.834	-1.607	-0.072	990	**0.046**
	Within-species SWS	-0.005	-0.235	0.250	990	0.962
Growth form						
G-structure	Phylogeny	1.025	0.941	1.116	2095	-
	Taxon	1.036	0.946	1.134	1980	-
R-structure	Residual	200	200	200	0*	-
	Species mean PAW	273.9	219.5	324.8	319	**<0.001**
	Within-species PAW	0.000	-4.071	4.154	1980	0.991
	Species mean SWS	-233.6	-276.0	-192.0	317	**<0.001**
	Within-species SWS	0.047	-7.830	7.370	1980	0.996

*Fixed prior for categorical response

Supplementary Table S4

Intercept models showing the 95% highest posterior density intervals of the distribution of the variance for mean syconium size and growth form responses. The term G describes a covariance matrix of the random effects, and R as the covariance matrix of the residual variances. The table shows models with different prior R- and G-structure variance prior assumptions (as either 0.95 or 0.05 of phenotype variance respectively). CI = Credible Interval; DIC = Deviance Information Criterion

Variance component	Variance prior	Factor	Posterior mean	Lower CI	Upper CI	Effective sample	DIC
Syconium size							
G-structure	0.05	Tree	252.40	120.40	394.90	990	-739.24
		Taxon	0.83	0.21	1.76	990	
R-structure	0.95	Null	0.08	0.08	0.09	990	
G-structure	0.95	Tree	240.40	87.37	424.70	990	-4292.76
		Taxon	11.48	3.85	21.44	990	
R-structure	0.05	Null	0.00	0.00	0.00	990	
Growth form							
G-structure	0.05	Tree	2.85	0.00	6.63	590	3090.20
		Taxon	8.54	4.57	13.22	568	
R-structure	0.95	Null	4.70	4.70	4.70	*0	
G-structure	0.95	Tree	55.85	16.01	90.13	19	3365.89
		Taxon	13.24	0.57	30.02	14	
R-structure	0.05	Null	0.25	0.25	0.25	*0	

*Fixed variance prior for categorical response.

Supplementary Table S5

The posterior distribution of the MCMCglmm coefficients for growth form and mean syconium size responses as explained by geobiological variables (biome, aspect, slope), PAW (plant available water), SWS (soil water stress), and phylogeny. CI = 95% credible interval. A relatively high effective sample indicates that the model is mixing well. Strong effects indicated with bold *pMCMC* value. The term *G* describes a covariance matrix of the random effects, and *R* as the covariance matrix of the residual variances

	Variable	Posterior mean	Lower CI	Upper CI	Effective sample	*pMCMC*	DIC
Syconium size							
G-structure	Phylogeny	2.088	0.931	3.546	990		9117.48
	Taxon	0.008	0.000	0.026	990		
	Biome	0.006	0.000	0.021	990		
	Aspect	0.002	0.000	0.005	990		
R-structure	Residual	0.030	0.020	0.039	961.6		
Fixed effects	PAW	-0.033	-0.159	0.109	990	0.620	
	SWS	-0.072	-0.339	0.187	990	0.606	
	Elevation	0.002	-0.126	0.154	990	0.976	
	Slope	-0.048	-0.215	0.155	990	0.616	
Growth form							
G-structure	Phylogeny	1.083	0.989	1.183	990		735.88
	Taxon	1.144	1.049	1.261	990		
	Biome	1.011	0.920	1.090	896.1		
	Aspect	1.000	0.916	1.095	990		
R-structure	Residual	200	200	200	0		
Fixed effects	PAW	2.540	0.517	4.575	818.5	**0.014**	
	SWS	-13.174	-15.772	-10.532	1127.8	**< 0.001**	
	Elevation	-2.288	-4.217	-0.089	1087.3	**0.040**	
	Slope	2.587	0.309	4.884	990	**0.034**	

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