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Rush hour at the Museum – Diversification patterns provide new clues for the success of figs (*Ficus* L., Moraceae)

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## ABSTRACT

Tropical rainforests harbour much of the earth's plant diversity but little is still known about how it evolved and why a small number of plant genera account for the majority. Whether this success is due to rapid turnover or constant evolution for these hyper-diverse plant genera is here tested for the species-rich genus *Ficus* L. (figs). The pan-tropical distribution of figs makes it an ideal study group to investigate rainforest hyper-diversification patterns. Using a recently published, dated and comprehensive phylogenetic hypothesis, we infer that figs are an old lineage that gradually accumulated species and exhibits very low extinction rates, which corresponds to the 'museum model' of evolution. Overall, no major significant shifts in evolutionary dynamics are detected, yet two shifts with lower probability are found. Hemi-epiphytism, monoecy, and active pollination are traits that possibly are associated with the hyper-diversity found in figs, making it possible for the plants to occupy new niches followed by extensive radiation over evolutionary time scales. Figs possess unique diversification patterns compared to other typical rainforest genera.

## 1. Introduction

Rainforests harbor the majority of biodiversity on Earth and are viewed as old ecosystems that have been prevalent throughout much of the Cenozoic (65-0 Ma). However, rainforest hyper-diversity is not well understood and it has variously been attributed to be a museum of diversity, showing constant speciation and low extinction (Wallace, 1878; Stebbins, 1974), or a cradle of diversity, referring to more recent and rapid speciation (Pennington et al., 2015; Richardson et al., 2001). Previous phylogenetic studies of diversification patterns in typical rainforest plant families, such as Annonaceae, Arecaceae, and Menispermaceae, have suggested that they are old lineages having experienced a gradual and more or less constant lineage accumulation over time, supporting the museum model (Couvreur et al., 2011a, 2011b; Wang et al., 2012). In contrast, other studies have inferred more recent radiations of rainforest lineages at the genus level for *Inga*, *Costus*, *Guatteria*, and *Renealmia*, supporting the cradle model of recent diversification (Erkens et al., 2007; Kay et al., 2005; Richardson et al., 2001; Särkinen et al., 2007). Further complicating the picture, Koenen et al. (2015) recently documented that despite the Meliaceae family originated already in the Eocene (56-34 Ma), the majority of the rainforest species diversity is recent and associated with higher speciation rates compared to non-rainforest lineages.

In line with Couvreur et al. (2011b) who suggested a mixed model of steady processes and mixed diversification, Koenen et al. (2015) proposed a concept of highly dynamic diversification processes across ecosystems that are linked to environmental changes (Xing et al., 2014) rather than to climatic stability, as suggested by the museum model. This view is, for example, supported by the Miocene (23-5 Ma) radiation of succulents (Arakaki et al., 2011) and grasses (Edwards et al., 2010), which was interpreted as an effect of global cooling and the

subsequent spread of seasonally dry ecosystems. Furthermore, fossil evidence has shown that Eocene rainforests were more diverse than contemporary rainforests but experienced a period of decreasing diversity up to the Early Miocene, implying both ancient rapid diversification and high past extinction rates (Jaramillo et al., 2010; Wilf et al., 2003). More examples are needed to help clarify if there are general patterns explaining rainforest diversification or if individual plant groups exhibit specific patterns.

Figs (*Ficus* L., Moraceae) are an old Cretaceous (75-90 Ma; Cruaud et al., 2012; Rønsted et al., 2005; Zerega et al., 2005) but mega-diverse (?800 species; Berg and Corner, 2005) and a significant component of tropical forests with many species having wide distribution ranges and ubiquitously high alpha-diversity in lowland tropical rainforests (Berg and Corner, 2005; Harrison, 2005). Harrison (2005) argued that no diversity pattern of any other genus resembles that of figs: other diverse genera have either geographically restricted distributions or are especially diverse in only one region. This indicates that figs possess certain traits that make them exceptionally well adapted to a broad range of niches, which has led to their high diversity all over the tropics (Corner, 1961).

A range of different traits have been suggested as possible drivers for fig diversification (Harrison, 2005; Jousset et al., 2003a; Weiblen, 2004). They exhibit a variety of growth forms, including typical rainforest habits like hemi-epiphytes (stranglers and banyans), trees (with/ without buttress roots), and large woody climbers. Furthermore, many species are pioneers of forest succession and possess many pioneer traits, such as small seeds (Harrison, 2005). Furthermore, fig wasps have evolved a unique active pollination behaviour that is very uncommon in most other plants except a few known cases such as in *Yucca*. Fig wasps use coxal combs to collect pollen into pollen pockets and deposit the pollen onto receptive flowers before oviposition. Active pollination is found in two thirds of the species. For the other third of the genus, passive pollination happens when wasps carry pollen dispersed on their bodies without specialized behaviour (Cook and Rasplus, 2003; Kjellberg et al., 2001). Due to their obligate pollination mutualism with short-lived wasps (Agaonidae), crops are available at population level year-round, providing an important food source for over 1200 mammal species globally (Shanahan et al., 2001).

In addition, quick responses to climatic changes and/or the presence of key innovations could promote high diversification (Drummond et al., 2012; Heard and Hauser, 1995; Hodges et al., 1995; Mayhew, 2007; Sanderson and Donoghue, 1994; Silvestro et al., 2014; Vamosi and Vamosi, 2011). The idea of key innovations as a single causal explanation for the rapid diversification of a lineage has largely been abandoned in favour of more complex models developed across angiosperms (Smith et al., 2011) and using more nuanced explanations involving multiple interacting traits assembled step-wise through evolution referred to as synnovation (Donoghue and Sanderson, 2015). Therefore, traits that are shared among species from diverse genera could very well be responsible for the rise of high species richness in general (Lovette et al., 2002). Certain comparative phylogenetic methods allow for testing and comparing the influence of certain traits on diversification patterns. Using those techniques to study the evolutionary history of a pan-tropical diverse genus such as the figs, and to identify diversification rates shifts and/or specific traits linked to higher diversification and survival might provide insights into the evolution of tropical biodiversity across ecosystems and continents in general.

Using a time-calibrated phylogenetic tree of figs, we address the following questions: (1) does the diversification pattern of figs support the museum model of ancient gradual diversification or the cradle model of recent rapid radiations? (2) Do significant diversification shifts within *Ficus* exist and if so, (3) are they correlated with specific traits representing one or more key-innovations?

## **2. Materials and methods**

### **2.1. Taxon sampling**

As input for the different diversification rate analyses, the most recently published dated phylogenetic hypothesis of figs was used (Cruaud et al., 2012). This phylogenetic hypothesis is also the most comprehensive, including 200 species (> 25% of the diversity of the genus) and was constructed based on the 5 low or single copy nuclear markers ITS, ETS, G3pdh, ncpGS, and waxy. Sampling broadly covers the diversity of *Ficus* with section *Oreosycea* and subgenus *Synoecia* being the least inclusive with 12% of the species of these lineages included (Supplementary data S1). Although support and resolution of certain infrageneric relationships within *Ficus* are still low, the phylogenetic tree of Cruaud et al. (2012) represents by far the best hypothesis available to date rooted with four taxa of *Castilleja*, the sister lineage of *Ficus* (Clement and Weiblen, 2009).

### **2.2. Diversification rate analyses**

A lineage through time (LTT) plot for the entire genus was generated with the R package *paleotree* 2.7 (Bapst, 2012). One thousand random post-burnin trees from the BEAST inference analysis by Cruaud et al. (2012) were used as input. A median curve with the 95% confidence interval is displayed.

A Bayesian Analysis of Macro-evolutionary Mixtures (BAMM 2.5) (Rabosky et al., 2014) was used to infer shifts in speciation and extinction rates across the phylogenetic tree. To account for non-random incomplete taxon sampling, total diversity and sampling fractions for all clades (see Supplementary data file S1) within figs were obtained from the literature (Berg and Corner, 2005; Rønsted et al., 2008a). The MCMC analysis was run for 1 million generations with sampling every 1000 generations and, after checking for convergence with the R package *coda* 0.19–1 (Plummer et al., 2006), the first 10% was discarded as burn-in. We used the R package *BAMMtools* 2.1.6 (Rabosky et al., 2014) and *ape* 4.0 (Paradis et al., 2004) to summarize rates over each branch of the phylogenetic tree (visualized in the so-called ‘phylorate’ plot), to plot the 95% credible shift set (CSS) with sampling frequencies of the different shift configurations, and to obtain the shift configuration with the maximum a posteriori (MAP) probability.

Problems with estimating extinction rates have been reported for earlier versions of BAMM (Moore et al., 2016) and although they have been accounted for in the latest version, we decided to include a MEDUSA analysis as a second method to infer diversification rate shifts (Alfaro et al., 2009). MEDUSA requires species richness to be assigned to unresolved clades and we therefore pruned the original dated phylogenetic tree of Cruaud et al. (2012) to section level and assigned diversity to each terminal. The R package *geiger* 2.0.6 (Alfaro et al., 2009) was used to perform the MEDUSA analysis.

### **2.3. State-dependent diversification rate analyses**

State-dependent diversification rate analyses were performed with the Binary-State Speciation and Extinction (BiSSE) model (Maddison et al., 2007) and the MultiState Speciation and Extinction (MuSSE) model, as implemented in the R package *diversitree* 0.9–9 (Fitzjohn, 2012). The influence of two traits on the diversification rates was analysed using the BiSSE model: 1) pollination mode with the states active versus passive pollination, and 2) monoecious versus (gyno)dioecious plants. The influence of habit was analysed using the MuSSE model and four different states were defined: shrub or small tree (< 30 m, understory), climber, large tree (?30 m, canopy), and hemiepiphyte. Information on the trait states for each taxon was extracted from the literature (Fig. 1; Berg and Villavivencio, 2004; Berg, 2012; Berg and Corner, 2005; Berg and Wiebes, 1992; Burrows and Burrows, 2003; Corner, 1967; Zhengyi et al., 2003; supplemented by our own taxonomic knowledge). For each analysis, we corrected for state-specific incomplete taxon sampling. Likelihood ratio tests were performed to test for significant differences between the unconstrained and constrained rate models and these found

the unconstrained model to be the best-fit model for all characters. The MCMC analysis was performed with a standard Cauchy distribution as hyper-prior to avoid zero rates (Burin et al., 2016) and was run for 10,000 generations with sampling every 1000 generations. Chain convergence and effective sampling size (ESS) parameters were inspected with the R package coda 0.19–1 (Plummer et al., 2006). The mean speciation, extinction, and net diversification rates and their respective 95% credibility intervals were calculated for each state of each character. A Cohen's d effect size test was performed to test for differences between these means. The results were visualized in posterior probability distribution plots.

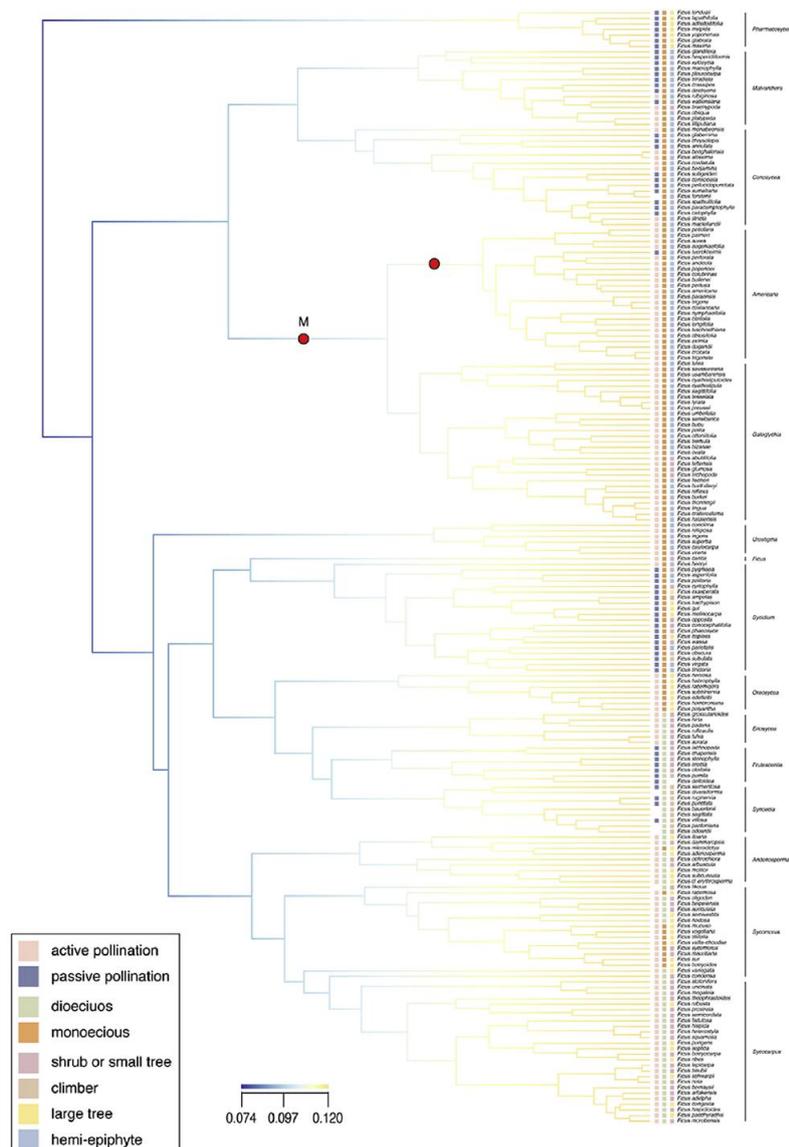


Fig. 1. Phylorate plot of *Ficus* with branches colored according to speciation rate (lineages/Ma), resulting from the Bayesian Analysis of Macro-evolutionary Mixtures (BAMM) analysis. For 70% of the samples in the posterior distribution no shift is observed. However, at a lower probability, a shift in diversification dynamics is observed at the lineage leading to section *Americanae* (20% of the samples in the posterior distribution) and at the lineage containing both section *Americanae* and section *Galoglychia* (3.6% of the samples in the posterior distribution), as indicated with red circles. The M is located on the branch where a rate shift occurs according to the MEDUSA analysis. The scored traits along with the species are indicated on the tips of the tree.

### 3. Results

#### 3.1. Diversification shifts

The BAMM analysis revealed that 70% of the samples in the posterior distribution exhibit no shifts in speciation rates, thus a constant model of evolution is favoured with no sudden increase in diversification rates for any clades (Fig. 1). However, shifts in diversification rates are detected with lower probability at the branch leading to section *Americanae* (20% of the samples in the posterior distribution) and at the branch leading to the clade containing both section *Americanae* and section *Galoglychia* (3.6% of the samples in the posterior distribution) (Fig. 1; red circles & Supplementary data file S3). The detected shifts with a lower probability (20% and 3.6%) are at a lower marginal shift probability and therefore not as well supported and significant as a model of constant evolutionary rate. MEDUSA identified significant acceleration of net speciation rates at one point in the tree where a branch leading to the clade containing both section *Americanae* and section *Galoglychia* (Fig. 1; red circle with an M). Overall net diversification rates inferred by MEDUSA and BAMM are very similar, confirming the robustness of our result.

The LLT plot shows a gradual increase in lineage accumulation through time, meaning that no sudden radiation of lineages is detected at any point (Fig. 2). This demonstrates consistency between the patterns inferred by BAMM, where no strongly supported shifts in rate dynamics is observed either.

#### 3.2. State-dependent diversification rates

Following the methodology of the Cohen *d* effect size test, the differences in diversification rates between traits found in the BiSSE analysis are defined as ‘very small’, ‘small’, ‘large’, ‘very large’, and ‘huge’ and this terminology is used in the description of the results. See supplementary data file S2 for all inferred rates by BiSSE and MuSSE analysis.

**Pollination mode.** The BiSSE analysis inferred a huge difference in net diversification rates between active and passive pollination: species with active pollination ( $r = 0.071$ ) diversify faster than species with passive pollination ( $r = 0.052$ ) – see supplementary data file S2. There is a large difference in extinction and speciation rate between the two traits, with extinction rate being higher for passively pollinated fig species and speciation faster for actively pollinated figs, as also suggested in Kjellberg et al. (2001). The transition rate from passive to active pollination was found to be larger than the reverse.

**Monoecy and dioecy.** When comparing monoecious and dioecious figs, the BiSSE method inferred a huge difference in net diversification rate between monoecious and dioecious fig species. We found that monoecious figs evolve faster ( $r = 0.076$ ) than dioecious species ( $r = 0.055$ ). Extinction rate is similar with a very small difference between the two trait states (thus, less different than for the mode of pollination). The speciation rate is hugely different between dioecious and monoecious species, with monoecious species evolving faster than the dioecious ones (see supplementary data file S2). The transition rate from dioecy to monoecy is also much higher than the reverse.

**Life forms (habits) of Figs.** In order to account for the various life forms of figs, a state-dependent diversification analysis using the MuSSE model was performed and four trait states were defined: shrubs/ small trees, large trees, climbers, and hemi-epiphytes. Net diversification rate of hemi-epiphytes ( $r = 0.076$ ) is much higher than net diversification for the three other life forms (shrubs/small trees, large trees, climbers) which also show very similar rates ( $r$  between 0.049 and 0.057). The speciation and extinction rates for all life forms are somewhat similar, however, the hemi-epiphytic figs show a slightly higher speciation rate and a slightly lower extinction rate, resulting in the generally higher net diversification rate.

**Transition rates between life forms.** The rate of transitions between life forms varies considerably (see Fig. 3). The highest transition rates are inferred for figs transitioning from

large canopy trees (>30 m) to smaller understory trees (< 30 m) or shrubs (mean = 0.033), as well as for the opposite direction (mean = 0.029). The transition rate from either of these life forms as well as climbers to hemi-epiphytic figs is low (from 0.006 up to 0.035). However, the transition rates from hemiepiphytes to any of the other three life forms are much lower – all ranging between 0.001 and 0.003.

#### **4. Discussion**

Our results, which are based on the largest and most recent phylogenetic tree of figs, provide possible explanations for some of the diversification patterns that have been hypothesized up till now. Our aim was to (1) test if the diversification patterns of *Ficus* support a museum model of ancient gradual diversification or a cradle model of recent, rapid radiation. Also, (2) to see if any significant shifts in diversification patterns occur within *Ficus* and (3) if they are linked with specific traits.

##### **4.1. Diversification patterns**

To investigate diversification patterns in figs, we constructed a lineage-through-time (LTT) plot and performed an analysis using both BAMM and MEDUSA to test how lineages evolve and diversify through time. Diversification of figs seems to correspond with a museum model of constant evolution and little extinction, leading to the gradual accumulation of lineages, possibly in response to long-lasting and stable tropical ecosystems (Figs. 1 and 3). However, it is worth noting that other examples of rainforest lineages supporting the museum model of gradual diversification are detected for pan-tropical rainforest tree families (Couvreur et al., 2011a,b; Wang et al., 2012), whereas generic level studies have primarily focused on the Neotropics and largely support the cradle model of recent diversification (Richardson et al., 2001; Kay et al., 2005; Erkens et al., 2007; Särkinen et al., 2007). These patterns could suggest that Neotropical rainforests may be cradles of recent diversity within a pantropical museum model.

Consequently, the diversification patterns we have found lend support to the statement by Harrison (2005) that no other genus compares to the diversity pattern of *Ficus* as other diverse genera have either geographically restricted distributions or are especially diverse in only one region. Furthermore, the overall net diversification rate for the genus ( $r = 0.1$ ) is higher, largely explained by a lower extinction rate ( $\epsilon = 0.009$ ), than the overall net diversification rate inferred across all angiosperms ( $r = 0.07\text{--}0.09$ ) (Magallon and Sanderson, 2001).

Overall, the BAMM analysis inferred no significant rate shifts in most of the samples from the 95% credibility set, but at a lower marginal probability two shifts towards increased speciation rates are found (Fig. 1). The shift with the second highest probability is found at the lineage leading to section *Americanae* and the third rate shift is detected at the branch leading towards the clade containing both section *Americanae* and section *Galoglychia* (Fig. 1; red circles). The latter rate shift was also detected by the MEDUSA analysis on the branch leading towards a clade with both sections. Even though the analysis do detect a shift in rate diversification this is only at a very low probability and the most supported analysis detects no shifts in the genus.

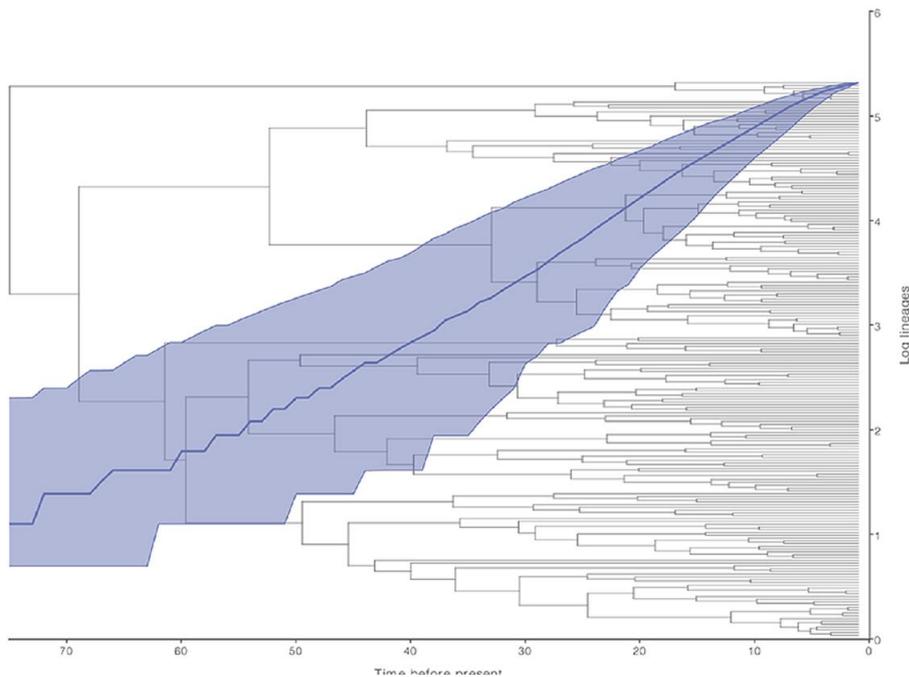


Fig. 2. Lineage-through-time plot depicted on the dated phylogenetic tree from Cruaud et al. (2012). A gradual increase of lineages through time is observed and no sudden bursts of speciation are present within the genus.

#### 4.2. State-dependent diversification patterns

The aim of the diversification analyses was to explore the potential link between traits or key innovations and varying diversification rates. Our separate results show higher diversification rates linked to figs that are actively pollinated, monoecious, and hemi-epiphytes compared to passively pollinated, dioecious figs exhibiting other life forms. Furthermore, these traits all occur in clades associated with higher diversification rates from BAMM and MEDUSA (sections *Americanae* and *Galoglychia*; see Fig. 1). It should also be noted that the traits were analysed separately and are perhaps not necessarily linked together.

Active pollination in fig species is positively linked with higher diversification rates, i.e. species that are actively pollinated evolve faster. It has previously been hypothesized that active pollination could be a driver of speciation, which is in line with our results (e.g. Harrison, 2005; Jousselin et al., 2003b; Kjellberg et al., 2001). It has also been suggested that active pollination might have evolved as a way for wasps to ensure fertilization of the flowers in which they oviposit (Jousselin et al., 2003a). Harrison (2005) suggests that maintaining high levels of heterozygosity due to ensured outcrossing, together with a very high proportion of inflorescences pollinated could also be a driver of faster speciation in actively pollinated figs. Also, active pollination could be maintained over evolutionary time by actively pollinating species being less prone to extinction than passively pollinating ones (Kjellberg et al., 2001), which is confirmed by results exhibiting a lower extinction rate.

The efficiency of active pollination has enabled figs to occupy rare (micro)-niches and it is therefore an important factor for the high alphan diversity in figs, since the ability to outcross at extremely low population densities may also have lowered extinction rates (Harrison, 2005). Our results support these hypotheses by inferring an extinction rate almost twice as low for actively pollinating species (0.007 vs. 0.016) compared to passively pollinated species.

Monoecy or (gyno)-dioecy. Being monoecious is correlated with increased rates of diversification in figs. In contrast to angiosperms in general (Käfer et al., 2014), monoecious fig species have a higher diversification rate and this has also been shown elsewhere for other plant species (Laenen et al., 2016), which has been explained by the longterm advantages of

outcrossing. In figs, however, this does not seem to be the case. It could instead be explained by self-compatible bisexual species being more likely to establish new colonies following long-distance dispersal than unisexual or self-incompatible ones, potentially promoting allopatric speciation and finding new niches (Heilbuth, 2000; Laenen et al., 2016).

Fig. 3. Transitions rates between life forms (habits). The circle size is proportional to the number of species with that trait state and the thickness of the arrows is proportional to the transition rates. Hardly any species evolve from a hemiepiphytic life form to any of the three other states. Life forms. Figs that are hemi-epiphytic have an increased diversification rate compared to other life forms, which all show a somewhat similar net diversification rate (see supplementary data file S2). Around half of the species are hemi-epiphytic, further suggesting that this life form is advantageous for figs (Cruaud et al., 2012; Harrison, 2005). They seem to possess some key innovations or a syndrome of advantageous traits explaining their diversification success. The ability to grow on rocky outcrops using aerial roots has probably been very important in the diversification and evolution of figs. Even though hemiepiphytic figs are present in low population densities, most hemi-epiphytic species have large ranges related to a more diffuse dispersal mechanism as opposed to terrestrial species, which tend to have more locally restricted dispersal abilities (Harrison and Rasplus, 2006). Dispersal range also differs between dioecious figs, which may be more restricted compared to monoecious figs. Whereas pollinators of monoecious figs disperse by ascending above the canopy and drifting in the wind until they reach the fume of receptive fig odour emitted by a tree, the pollinators of dioecious figs disperse more locally and do not use the wind for dispersal (Harrison and Rasplus, 2006).

The hemi-epiphytic life form allows for occupation of niches that most plants do not readily colonize. Hemi-epiphytes are adapted to grow in the canopy layer with low water availability and high light conditions. Adaptive root flexibility may also explain transitioning from forest habitats to similar dry environments expressed by lithophytes in Australia (Harrison, 2005; Harrison et al., 2003; Harrison and Shanahan, 2005; Rønsted et al., 2008b).

Transitioning between life forms. The rate of which the traits tested evolve and transition into each other is an indication of the diversification dynamics of figs and may offer explanations as to how they became so successful. We scored large canopy trees and small understory trees/shrubs as separate life forms, but our results indicate that it is easy to transition between these two states, probably because it does not require large evolutionary sacrifices or changes.

The rate at which figs become hemi-epiphytic is not high but the rate of hemi-epiphytic figs transitioning back towards another life form is very low (Fig. 3). Consequently, the hemi-epiphytic life-form appears to be a more stable state providing an adaptive advantage and explaining why such a high proportion of the figs are hemi-epiphytic (Berg and Corner, 2005).

#### 4.3. What has made figs so successful?

The origin of figs has been dated to the late Cretaceous (75-90 Ma; Cruaud et al., 2012) – which is before the K/Pg boundary (65 Ma) where a lot of plant diversity is hypothesized to have gone extinct (Wilf and Johnson, 2004). For figs, this might have created opportunities to expand into new niches, as they are generally opportunistic species with low competitive abilities (Berg and Corner, 2005; Harrison, 2005). After having established in such new niches, figs would have kept evolving at a constant rate as competition is low in many (micro)-niches (Frenzke et al., 2016; Gentry and Dodson, 1987). Figs do possess many traits typical of pioneer plants – small seeds, high assimilation and growth rates, high fecundity, and flexible rooting habits – that are advantageous in colonising new areas as also expressed by the genus *Piper* and epiphytic Orchids (Harrison, 2005).

Furthermore, the renowned pollination system of figs with its unique fig-pollinating wasps ensuring high pollination success is beneficial when population densities are low. Even though fig species and their pollinators show high levels of co-diversification and specificity (Cruaud

et al., 2012), multiple pollinators for a single fig species are frequently reported (Machado et al., 2005). Hybridization and introgression could also have contributed to the large genetic and species diversity in figs (Bruun-Lund et al., 2016).

## 5. Conclusion

Overall, the diversification rate analyses show that figs generally follow the museum model of evolution with a gradual accumulation of species over time and with very low extinction rates and no significant evolutionary shifts. However, the trait state-dependent analyses show that monoecy, active pollination, and having a flexible root habit (i.e. hemi-epiphytes) are linked with higher diversification rates and this is further underpinned by these character states being expressed by a subclade with higher diversification rate. These trait states are found throughout most of the phylogenetic tree suggesting that they represent key innovations or syndromes, possibly responsible for making the figs so successful in terms of species diversity and accumulating high species diversity over an evolutionary time scale.

**Supplementary data** related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2017.11.001>.

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