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

Sam Bruun-Lund^{a,*}, Brecht Verstraete^a, Finn Kjellberg^b, Nina Rønsted^a

^a Natural History Museum of Denmark, University of Copenhagen, Sølvgade 83S, DK-1350 Copenhagen, Denmark

^b CEFE UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, F-34293 Montpellier Cédex 5, France

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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*, *Gutteria*, and *Renalmia*, 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

* Corresponding author. Tel.: +45 35 32 22 22.

E-mail address: sam.bruunlund@snm.ku.dk (S. Bruun-Lund).

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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; Joussein et al., 2003a; Weiblen, 2004). They exhibit a variety of growth forms, including typical rain-forest 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; Vamossi and Vamossi, 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 *Oreosyce* 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 Castilleae, 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 ‘phy-lorate’ 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 hemi-epiphyte. Information on the trait states for each taxon was extracted from the literature (Fig. 1; Berg and Villavencio, 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.

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