



Exploring the tempo of species diversification in legumes

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ABSTRACT

Whatever criteria are used to measure evolutionary success – species numbers, geographic range, ecological abundance, ecological and life history diversity, background diversification rates, or the presence of rapidly evolving clades – the legume family is one of the most successful lineages of flowering plants. Despite this, we still know rather little about the dynamics of lineage and species diversification across the family through the Cenozoic, or about the underlying drivers of diversification. There have been few attempts to estimate net species diversification rates or underlying speciation and extinction rates for legume clades, to test whether among-lineage variation in diversification rates deviates from null expectations, or to locate species diversification rate shifts on specific branches of the legume phylogenetic tree. In this study, time-calibrated phylogenetic trees for a set of species-rich legume clades – *Calliandra*, Indigofereae, *Lupinus*, *Mimosa* and Robinieae – and for the legume family as a whole, are used to explore how we might approach these questions. These clades are analysed using recently developed maximum likelihood and Bayesian methods to detect species diversification rate shifts and test for among-lineage variation in speciation, extinction and net diversification rates. Possible explanations for rate shifts in terms of extrinsic factors and/or intrinsic trait evolution are discussed. In addition, several methodological issues and limitations associated with these analyses are highlighted emphasizing the potential to improve our understanding of the evolutionary dynamics of legume diversification by using much more densely sampled phylogenetic trees that integrate information across broad taxonomic, geographical and temporal levels.

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1. Introduction

The legume family (Leguminosae) is one of the most evolutionarily successful lineages of flowering plants. With c. 19,500 species and 750 genera (Lewis et al., 2005 and additions), it is the third largest plant family; it occupies a global distribution spanning all major biomes (temperate, Mediterranean, dry and wet tropical forest, savanna) (Schrire et al., 2005); it presents spectacular morphological and life history diversity, from giant rainforest trees and woody lianas, to desert shrubs, ephemeral herbs, herbaceous twining climbers, aquatics and fire-adapted savanna species (Doyle and Luckow, 2003); it shows a significantly higher than average species diversification rate over the last 60 Ma than angiosperms as a whole, despite the relatively old age of the family (Magallón and Sanderson, 2001); it forms a high proportion of overall vegetation both

in the fraction of overall species composition and abundance of individuals, especially in tropical biomes (Pennington et al., 2006, 2009); finally, it harbours the largest genus of flowering plants, *Astragalus* (Sanderson and Wojciechowski, 1996), and some of the most rapidly evolving plant clades (Hughes and Eastwood, 2006; Richardson et al., 2001; Scherson et al., 2008). Despite this, we still know rather little about the dynamics of lineage and species diversification across the family through the Cenozoic, or about the underlying drivers of diversification.

As for any large plant clade, there are numerous factors, intrinsic and extrinsic, that could be contributing to the evolutionary success of the legumes. For example, plant–animal and plant–microbe interactions (e.g. Kursar et al., 2009; Marazzi and Sanderson, 2010; McKey, 1989; Sprent, 2001), diversity of habit and other life history traits (e.g. Drummond et al., 2012), ecological adaptability, nitrogen fixation (Doyle, 2011; Sprent, 2001), diversity of sexual reproductive systems, and propensity for polyploidy and hybridization (Goldblatt, 1981; Cannon et al., 2010), have all been implicated in diversification of particular legume clades. However, no attempts have been made to estimate diversification rates across legumes, to correlate these with geography, ecology and other traits, or to compare patterns of diversification across the numerous radiations apparent within the family. Indeed, perhaps

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surprisingly, there have been no attempts to assess the factors that might explain the extraordinary diversity of legumes, including nodulation, perhaps the most obvious candidate key evolutionary innovation in the family (Doyle, 2011).

Estimating species diversification rates and locating diversification rate shifts depend on knowledge of phylogenetic relationships, divergence time estimates and the distribution of species richness across the phylogeny. For legumes, knowledge in all three of these areas has reached a point where exploration of the dynamics of species diversification is possible. First, several family-wide phylogenies (Lavin et al., 2005; Legume Phylogeny Working Group, 2013; Simon et al., 2009; Wojciechowski et al., 2004) and species-level phylogenies for important species-rich clades (e.g. Drummond et al., 2012; Lavin et al., 2003; Schrire et al., 2009; Simon et al., 2011; Souza et al., submitted for publication) are now available. Second, the rich legume fossil record (Herendeen and Dilcher, 1992) affords exceptional opportunities for robustly cross-validated divergence time estimation using multiple, stringently selected fossil constraints (Bruneau et al., 2008; Lavin et al., 2005; Simon et al., 2009). Third, documentation of taxonomic diversity has advanced, most notably with a generic encyclopaedia of the family (Lewis et al., 2005), providing a first approximation of the spectacular variation in species richness across legume lineages, with genus sizes ranging from monospecific (192), 2–10 species (304), 11–99 species (190), 100–499 species (36), and >500 species (5 genera), presenting a classical example of the hollow curve (Scotland and Sanderson, 2004). Thus, in many respects legumes provide an ideal study group for investigating the macroevolutionary dynamics of plant diversification.

At the same time, there have been rapid advances in methods for estimating the extent of among-lineage variation in species diversification rates and detecting the phylogenetic location of shifts in rates of diversification (Stadler, 2013). Early attempts to test for differences in species diversity among lineages relied on sister group comparisons (Sanderson and Wojciechowski, 1996; Slowinski and Guyer, 1989). These methods were used in legumes to test whether the genus *Astragalus*, the largest genus of flowering plants with c. 2500 species, is in fact exceptionally species-rich (Sanderson and Wojciechowski, 1996). However, such methods have limited statistical power and cannot compare rates across a phylogeny. More sophisticated likelihood approaches test whether clade species richness is greater than expected against background diversification rates while incorporating effects of extinction rates (Magallón and Sanderson, 2001). These methods are derived from 'birth-death' models that assume constant rates of speciation and extinction among lineages, and through time (Nee et al., 1994). For example, Marazzi and Sanderson (2010) showed that the extrafloral nectary clade in the species-rich caesalpinoid genus *Senna* is more species-rich than expected and suggested that extrafloral nectaries could have acted as a key evolutionary innovation facilitating rapid species diversification in this group. Lineage Through Time (LTT) plots provide a simple graphical method to project and compare temporal trajectories of lineage diversification across whole clades or particular subclades, but again, with some notable exceptions, these have been little investigated within legumes. LTT plots compiled for the large Mirbelieae/Bossieae clade and for Podalyrieae (Crisp and Cook, 2009; Schnitzler et al., 2011) revealed repeated time-coincident antisigmoidal LTT curves indicative of either mass-extinction events, concurrent shifts to increased rates of diversification (Crisp and Cook, 2009), or high species-turnover throughout the history of clades, with similar results apparent for the genus *Prosopis* (Catalano et al., 2008), and within North American *Pediomelum* (Egan and Crandall, 2008). More recent likelihood methods and Bayesian implementations thereof relax the assumption of constant diversification across the phylogeny providing greater power to both discover possible rate shifts without any a priori hypothesis as to where they may lie on the tree (Alfaro et al., 2009; Santini et al., 2009) and to test their significance (Silvestro et al., 2011). In legumes these methods have so far only been applied to the genus *Lupinus* (Silvestro et al., 2011; Drummond et al., 2012).

In this study we test the hypothesis that there is significant among-lineage diversification rate variation across the Leguminosae. Analyses of diversification rates for a sparsely sampled higher-level phylogeny of legumes as a whole, and a series of five more densely sampled species-level phylogenies of individual legume clades are presented, in order to gain preliminary insights into the extent of among-lineage variation in diversification rates across the family. Models that allow different diversification rates in different parts of the tree are used to identify putative phylogenetic locations of diversification rate shifts. Despite the early stage of these analyses, initial ideas about the dynamics of legume diversification as well as the potential of such studies to shed light on the underlying factors that may have driven the evolutionary success of legumes are highlighted.

2. Methods and study groups

2.1. Estimating diversification rates

In this study a top-down approach using a sparsely sampled higher level legume-wide phylogeny is combined with a bottom-up approach that relies on a set of five more densely sampled species-level phylogenies of specific clades: *Calliandra*, Indigofereae, *Lupinus*, *Mimosa* and Robinieae. For each clade the following analytical approach was used: (i) previously published time-calibrated phylogenies (Drummond et al., 2012; Simon et al., 2009, 2011; Särkinen et al., 2012; Souza et al., submitted for publication) that were estimated under an uncorrelated lognormal relaxed molecular clock model in BEAST (Drummond and Rambaut, 2007) were gathered, and for Indigofereae, BEAST was run specifically for this study using the original dataset of Schrire et al. (2009); (ii) testing for constancy of birth and death rates across the phylogeny, by evaluating at each branch of the phylogeny whether the assumption of a rate shift improves the likelihood of observing the branching times in the phylogeny using MEDUSA (Modeling Stepwise Diversification Using Stepwise AIC) (Alfaro et al., 2009; Santini et al., 2009) to assess among-lineage variation in diversification rates and discover putative diversification rate shifts in one or more phylogenetic positions; (iii) estimation of diversification rates in a Bayesian framework using BayesRate (Silvestro et al., 2011) to evaluate the statistical support for differences in net diversification and underlying speciation and extinction rates among clades or tree partitions delimited by the rate shifts in the best fitting model found by MEDUSA.

Given that current phylogenies rarely contain all extant species in a clade, accounting for incomplete taxon sampling is an important issue and a potentially challenging hurdle in estimating species diversification rates (Cusimano et al., 2012; Marazzi and Sanderson, 2010), especially for sparsely sampled phylogenies or phylogenies for which taxon sampling is not representative of clade species richness (for instance when each genus of a family is sampled, but the proportion of species sampled per genus varies significantly). Objective assignment of unsampled taxa to a set of terminal clades (e.g. based on taxonomy), as implemented in MEDUSA, provides a solution to this problem (Alfaro et al., 2009; Drummond et al., 2012; Santini et al., 2009; Stadler and Bokma, 2012). The disadvantages of this approach are that in some cases there is no satisfactory objective (e.g. taxonomic) basis for assignment of unsampled taxa, and/or that the number of terminal clades needs to be reduced with the consequence of losing statistical power in the analysis. Furthermore, by restricting diversification rate analyses to backbone trees made up of a reduced number of terminal clades, it is possible that a nested subclade within one of those terminal clades is actually diversifying faster rather than the whole clade. Potential additional diversification rate shifts nested within these clades cannot be modelled. Another way of accounting for missing taxa, implemented in BayesRate, is by specifying the proportion of extant taxa sampled (Stadler, 2009; Yang and Rannala, 1997). The advantage is that all nodes in the tree are retained, but it assumes that missing taxa are located randomly across the tree, an assumption that is often

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