Molecular Phylogenetics and Evolution 85 (2015) 161–170

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Bricklebush (*Brickellia*) phylogeny reveals dimensions of the great Asteraceae radiation in Mexico

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ARTICLE INFO

Article history:
Received 28 November 2014
Revised 12 February 2015
Accepted 13 February 2015
Available online 21 February 2015

Keywords:
Rate shifts in net diversification
Sonoran Desert
Time calibrated phylogeny
Mexican biodiversity
Eupatorieae

ABSTRACT

Data from molecular phylogenetics were used to assess aspects of diversity and relationships in *Brickellia*, a large and widespread genus of Eupatorieae. The dataset included sequence data from nuclear ribosomal ITS, ETS, and plastid *psbA–trnH* regions. An initial question was to assess the monophyly of the genus and whether *Barroetea*, *Phanerostylis*, and *Kuhnia* should be recognized as separate from or included in *Brickellia*. The results supported the hypothesis that *Brickellia* is monophyletic, with the small (2–3 species) *Pleurocoronis* as the sister group and showed *Barroetea*, *Phanerostylis*, and *Kuhnia* all embedded within the genus. Results of a time calibrated phylogeny from a BEAST analysis gave an estimated origination time for *Brickellia* at about 9 million years ago (Ma), with the oldest split within the genus dated at about 7.5 Ma. A BAMM analysis based on the time calibrated tree showed that *Brickellia* has one rate shift in diversification associated with its origin in the late Miocene. Some lineages within the genus have had an increase in the rate of diversification over the past 5 Ma, whereas other lineages have had a decrease in net diversification during this period. The results also elucidated nine clades within *Brickellia* which are accepted as taxonomic sections, and that will form logical units for future detailed studies.

1. Introduction

Species diversification varies across the tree of life and the focus of many evolutionary studies is to understand the causes of the resulting clade size imbalances (Alfaro et al., 2009; Rabosky, 2009, 2014; Purvis et al., 2011). Exploration of the dimensions of species level diversification has accelerated as refinements have been made for both data sources and analytical methods (Magallon and Sanderson, 2001; Rabosky, 2006; Ronquist and Sanmartín, 2011). The results have confirmed high rates of diversification in areas of noted biodiversity (e.g. Hughes and Eastwood, 2006), but have also yielded unanticipated results. For instance some European plant groups exhibit relatively high diversification rates (Valente et al., 2010) whereas noted species-rich groups such as grasses (Christin et al., 2014) and sedges (Escudero et al., 2012) do not have particularly high rates of divergence. For plants, diversification rates can be particularly high in montane regions (Schwery et al., 2014; Wen et al., 2014; Hughes and Atchison, 2015). The importance of broad taxonomic sampling for such studies has also been noted (Deng et al., 2015.) Surprisingly, no recent studies have focused on Asteraceae, despite it being one of the most species-rich families of angiosperms.

Mexico, a country noted for its overall high floristic diversity (Rzedowski, 1981) with much of its territory recognized as a world biodiversity hotspot (Mittermeier et al., 2011) has the largest diversity of Asteraceae in the world with more than 3295 species (Llorente-Bousquets and Ocegueda, 2008). In particular, one of the largest tribes of the family, Eupatorieae, has 530 of its approximately 2000 species in Mexico (Turner, 1997). This is notable because despite its clear morphological distinctiveness and high number of species, a relatively young age can be inferred for Eupatorieae based on molecular studies that show it to be an ingroup to the classically defined Heliantheae (Panero et al., 2014). Mexico has a complex geological history with multiple recent events related to volcanism and orogenies (Metcalfe, 2006; Gómez-Tuena et al., 2007), resulting in changes to climate and vegetation types that might favor certain lineages and lead to new species formation. Some widespread groups in the country,

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http://dx.doi.org/10.1016/j.ympev.2015.02.007
1055-7903/

however, have been shown to exhibit patterns of genetic variability without undergoing speciation (Ruiz-Sanchez and Specht, 2013). The presence of extensive and recent montane regions in Mexico might be expected to stimulate increased plant diversification (Hughes and Atchison, 2015).

Brickellia is one of several genera of Eupatorieae in Mexico that exhibit conspicuously high species diversity (Fig. 1), but the timing and patterns behind the richness in species have never been explored. As with many large groups, there are large differences in species richness among genera of Eupatorieae ranging from multiple monotypic ones to several large genera (*Ageratina*, *Brickellia*, *Chromolaena*, *Koanophyllon*, *Mikania*, and *Stevia*) that include 100 species or more (King and Robinson, 1987). Of these, *Brickellia* is notable in having almost all of its species-level diversity within Mexico, as well as lacking any complicating factors such as apomixis or polyploidy, and thus provides a distinctive group to study diversification of Asteraceae within this geographical region. Knowledge of the systematics and relationships of *Brickellia* has potential applications to other studies beyond merely resolving the generic boundaries. The genus offers a particularly useful system for studies of diversification and biogeography because of its large number of species, relatively widespread geographic distribution, and entirely homoploid and sexual breeding system. Based on the high level of morphological similarity among many of its species, it might be expected that the genus has experienced an elevated level of diversification. Other large genera of Eupatorieae such as *Ageratina*, *Eupatorium*, and *Stevia* have the complexity of hybridization, polyploidy, and apomixis (King and Robinson, 1987; Schilling, 2011a; Siripun and Schilling, 2006; Soejima et al., 2001). Species of *Brickellia* that have been studied are self-incompatible, and wide hybridization appears to be unlikely (Powell, 1985); thus the phylogenetic history is unlikely to have

Fig. 1. Floral diversity in *Brickellia*. (A) Section *Barroetea*: *B. subuligera*. (B and C) Section *Brickellia*: *B. cordifolia*, *B. grandiflora*. (D) Section *Coleosanthus*: *B. venosa*. (E) Section *Kuhnia*: B. eupatorioides. (F) Section *Leptanthodium*: *B. coulteri*. (G) and (H) Section *Microphyllae*: *B. veronicifolia*, *B. oblongifolia*. (I) Section *Phanerostylis*: *B. pedunculosa*. (J) Section *Xerobrickellia*: *B. floribunda*. (Photo Credits. (C–F, H, J. Max Licher; A, G, I. Jose L. Panero; B. Edward E. Schilling).