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Speciation within *Columnea* section *Angustiflora* (Gesneriaceae): Islands, pollinators and climate

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ABSTRACT

Despite many advances in evolutionary biology, understanding the proximate mechanisms that lead to speciation for many taxonomic groups remains elusive. Phylogenetic analyses provide a means to generate well-supported estimates of species relationships. Understanding how genetic isolation (restricted gene flow) occurred in the past requires not only a well-supported molecular phylogenetic analysis, but also an understanding of when character states that define species may have changed. In this study, phylogenetic trees resolve species level relationships for fourteen of the fifteen species within *Columnea* section *Angustiflorae* (Gesneriaceae). The distributions of sister species pairs are compared and ancestral character states are reconstructed using Bayesian stochastic mapping. Climate variables were also assessed and shifts in ancestral climate conditions were mapped using SEEVA. The relationships between morphological character states and climate variables were assessed with correlation analyses. These results indicate that species in section *Angustiflorae* have likely diverged as a result of allopatric, parapatric, and sympatric speciation, with both biotic and abiotic forces driving morphological and phenological divergence.

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1. Introduction

Darwin (1859) elegantly identified natural selection as a major means of generating biological diversity. Yet, over 150 years later the specific historical processes that drive evolutionary divergence remain unknown for most organisms. Physical (geographic) isolation is an important component in initiating the speciation process and allopatric speciation is widely accepted as a means by which populations diverge (Bush, 1975b). However, populations can diverge even when gene flow is maintained (Bush, 1975a; Feder, 1998; Savolainen et al., 2006). Divergence can result from selection by the environment or through interactions with other organisms (Givnish, 1997; Schluter, 2000), or even through stochastic processes (e.g., genetic drift) that result in species which may or may not be adaptive (Gittenberger, 2008). All of these scenarios create challenges when trying to infer forces that are currently involved in the speciation process, and they become amplified when trying to uncover the processes that generated species diversity in the past.

Advances in obtaining large amounts of sequence data and the methodology to interpret those data have greatly enhanced phylogenetic analyses such that species level evolutionary relationships can be estimated and the confidence of those relationships can be assessed (Swofford, 2002; Huelsenbeck and Ronquist, 2003; Rambaut and Drummond, 2005; Stamatakis, 2006; Zwickl, 2006; Drummond and Rambaut, 2006; Stamatakis et al., 2008). However, understanding the relationships of species only reveals the pattern of speciation. To interpret the processes that led to divergence, various factors can be evaluated across the evolutionary history of the species and deep divergences can be evaluated using molecular dating and paleoclimatic history (Graham, 1997; Symmank et al., 2011). Ideally specific historical events can be examined against evolutionary history (Lemmon et al., 2007), but more often multiple factors are examined across an evolutionary tree to determine where shifts in climatic tolerance or morphological changes have occurred (Kay et al., 2005; Drummond, 2008; Symmank et al., 2011; Valente et al., 2012; De Vos et al., 2014). Identifying biotic or abiotic factors involved in the diversification of extant species is not a direct observation of events; instead the products of selection (adaptations) are examined as proxies for natural selection. While this poses some limits on our ability to assess past speciation processes, the effects of selective agents on extant species with similar adaptations can corroborate that the shifts in character states across a phylogenetic tree are likely the result of similar selective processes in the past.

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Tropical forests provide numerous opportunities to study the forces driving speciation (Martén-Rodríguez et al., 2010; Viljanen et al., 2010; Tolley et al., 2011). Over half the world's plant and animal species are found in tropical forests, which cover only a small portion of the Earth's surface, resulting in a high concentration of biodiversity (Wills et al., 2006; Mittelbach et al., 2007). Although tropical forests have less striking seasonal temperature variation, compared to temperate regions, their climate varies depending upon latitude, elevation, and physiogeographic features, creating a broad array of both biotic and abiotic factors that may contribute to speciation (Haffer, 1969; Bush, 1994; Graham, 1997; Haffer and Prance, 2001; Struwe et al., 2011), both in the past and presently.

The Neotropics experienced climate oscillations in the Pleistocene and along with volcanism in Central America, the closing of the Isthmus of Panama, and the Andean orogeny, climates would have been varied and changing across northern South America and the Caribbean (Gentry, 1982; Graham, 1997). Over the past three to five million years such shifts created an array of selective environments that resulted in numerous species adapted to them. The combination of abiotic and biotic interactions have been suggested to accelerate speciation in the tropics (Gentry, 1989; Schemske, 2002), particularly as a result of plant-pollinator interactions (Johnson and Steiner, 2000). Plant-pollinator interactions and shifts in morphology as a response to pollinator-driven selection have also increased diversity in other regions such as South Africa, where one third of all lineage splits in *Gladiolus* are the result of pollinator shifts (Valente et al., 2012).

Gesneriaceae is a tropical plant family whose evolutionary history provides insights into the speciation process. Wide variation in flower shape and color have been hypothesized to be the result of selection by different pollinator syndromes (Harrison et al., 1999; Perret et al., 2007; Martén-Rodríguez et al., 2010), different vegetative growth forms have been shown to have high rates of lability (Möller and Cronk, 2001), and long distance dispersal events have contributed to allopatric speciation of sister species on islands arrayed across the Pacific Ocean (Woo et al., 2011). These previous studies have implied a number of biotic and abiotic factors that drive speciation in the family. Within Gesnerioideae, *Columnea* L. is the largest genus. The 200+ species of *Columnea* are distributed in the Caribbean islands and throughout the Andes, from Mexico to Bolivia and eastward into northern Brazil (Smith, 1994). Recent molecular phylogenetic analyses show that the 200+ species of *Columnea* are divided into seven clades. These clades are still the focus of ongoing investigations, are supported by molecular synapomorphies (Smith et al., 2013), and preliminary data indicate that some clades are further supported by morphological synapomorphies, geographic distribution, or a combination of the two. One of these clades is section *Angustiflorae* which has been defined by morphological characters (Schulte et al., 2014).

Species of *Angustiflorae* are characterized by small tubular corollas that are radially to subradially symmetric, narrow calyx lobes loosely clasping the corolla, and sparse pubescence on the corolla (Fig. 1; Schulte et al., 2014). The species also have opposite leaves that range from isophyllous to strongly anisophyllous, with a dorsiventral arrangement in *Columnea byrsina*, *C. orientandina*, *C. manabiana*, *C. tandapiana*, and *C. spathulata*. Leaf coloration is green, sometimes purple, suffused with pink, or with violet spots. Corollas range from cream to lemon-yellow, orange, red or violet, with darker colored lobe spots in some species (Fig. 1). The species of section *Angustiflorae* cover nearly the full geographic and climatic range of *Columnea*, from sea level to 4000 meters in elevation. Their distributions vary from narrow endemics, such as *C. ambigua* and *C. domingensis* on Caribbean islands, to species that are widespread, such as *C. angustata* that ranges from Costa Rica to Ecuador (Schulte et al., 2014). All species are either epiphytic, or both epiphytic and epipetric (*C. orientandina*). A wide range of morphological variation, distributions (allopatric, parapatric, and sympatric), and climate requirements makes section *Angustiflorae* a good model system for studying factors influencing speciation events.

This study aimed to estimate species trees for section *Angustiflorae* with five unlinked gene regions. Species that belong in section *Angustiflorae* have been identified based on molecular analyses and morphological characters, however, previous molecular data have not resolved phylogenetic relationships among the species of *Angustiflorae* (Schulte et al., 2014). We sampled 36 accessions representing 14 of the 15 species of section *Angustiflorae* (Appendix A). *Columnea antiocana* is a rare Colombian endemic known only from three collections. We were unable to procure sufficient DNA material to include this species in our phylogenetic analyses but based on morphological data this species would likely be related to *C. crassicaulis*, *C. katzensteiniae*, *C. ovatifolia*, and *C. rileyi* (Schulte et al., 2014). *Columnea antiocana* shares corolla lobe spots with this clade, but has entire calyx margins. It is the only species known from Colombia among this clade and would thus be allopatric from its most likely sister species. Phylogenetic analyses were conducted using five chloroplast DNA (cpDNA) gene regions along with nuclear ribosomal internal transcribed spacers (ITS1 and ITS2, hereafter referred to as ITS), and the external transcribed spacer (ETS). In addition, two low-copy nuclear genes, glyceraldehyde 3-phosphate dehydrogenase (*G3pdh*; Strand et al., 1997) and NADP-dependent isocitrate dehydrogenase (*idh*; Weese and Johnson, 2005), were used to increase phylogenetic support for major branching events within *Angustiflorae*. All gene regions were chosen because they have proven successfull in resolving species level phylogenetic relationships (Linder et al., 2000; Ingram and Doyle, 2003; Levin et al., 2005; Johnson and Johnson, 2006; Huertas et al., 2007; Smith et al., 2008a; Ruiz-Sanchez and Sosa, 2010; Steele et al., 2010).

Our objectives were to investigate the processes of speciation in section *Angustiflorae* by (1) reconstructing a species level phylogeny to estimate patterns of specation, (2) estimating the impact of geographic isolation on speciation in this group, (3) determining ancestral character states for morphological and phenological character states that have been used to differentiate these species, (4) determining the lability of these morphological and phenological character states, (5) estimating differences in climatic tolerance across the phylogeny, and (6) correlating shifts in morphology with shifts in climate tolerance to determine whether climate may have driven shifts in morphology.

2. Materials and methods

2.1. DNA extraction, amplification, and alignment

A complete list of samples, voucher specimens, and GenBank numbers for all sequences used in all analyses is in Appendix A. DNA was extracted from silica-dried leaf material using Qiagen DNeasy plant mini kits (Valencia, CA) according to manufacturer's instructions. Two separate datasets were used, the first dataset included sampling for all accessions (31 species, 54 individuals) for seven gene regions and is herein referred to as the full dataset. The second dataset sampled from monophyletic clades (24 species, 30 individuals) using analyses of the full dataset to minimize the total number of *Columnea* species that were not members of section *Angustiflorae* and reduce the number of accessions for each species of section *Angustiflorae*. This reduced dataset included more DNA sequence data through the addition of two low-copy nuclear genes.

The ingroup for phylogenetic analyses included 36 accessions for the full dataset and a subset of 20 accessions for the reduced

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