



Untangling reticulate evolutionary relationships among New World and Hawaiian mints (Stachydeae, Lamiaceae)[☆]



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ABSTRACT

The phenomenon of polyploidy and hybridization usually results in novel genetic combinations, leading to complex, reticulate evolution and incongruence among gene trees, which in turn may show different phylogenetic histories than the inherent species tree. The largest tribe within the subfamily Lamiaceae (Lamiaceae), Stachydeae, which includes the globally distributed *Stachys*, and one of the largest Hawaiian angiosperm radiations, the endemic mints, is a widespread and taxonomically challenging lineage displaying a wide spectrum of morphological and chromosomal diversity. Previous molecular phylogenetic studies have showed that while the Hawaiian mints group with Mexican–South American *Stachys* based on chloroplast DNA sequence data, nuclear ribosomal DNA (nrDNA) sequences suggest that they are most closely related to temperate North American *Stachys*. Here, we have utilized five independently inherited, low-copy nuclear loci, and a variety of phylogenetic methods, including multi-locus coalescence-based tree reconstructions, to provide insight into the complex origins and evolutionary relationships between the New World *Stachys* and the Hawaiian mints. Our results demonstrate incongruence between individual gene trees, grouping the Hawaiian mints with both temperate North American and Meso-South American *Stachys* clades. However, our multi-locus coalescence tree is concurrent with previous nrDNA results placing them within the temperate North American *Stachys* clade. Our results point toward a possible allopolyploid hybrid origin of the Hawaiian mints arising from temperate North American and Meso-South American ancestors, as well as a reticulate origin for South American *Stachys*. As such, our study is another significant step toward further understanding the putative parentage and the potential influence of hybridization and incomplete lineage sorting in giving rise to this insular plant lineage, which following colonization underwent rapid morphological and ecological diversification.

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1. Introduction

1.1. Natural hybridization, polyploidy and factors affecting species relationships

Natural hybridizations have had far-reaching effects in angiosperm evolution, and it has been estimated that approximately 25% of vascular plants hybridize with other plant species and about 11% of plant species are products of hybridization events (Ellstrand et al., 1996; Mallet, 2007). Changes in ploidy levels are the most common effect of hybridization, mostly resulting from the union of unreduced gametes from two parental species (Soltis and

Soltis, 2000; Husband, 2004). The novel genetic combinations in polyploid genomes lead to innovative genetic changes, which often give rise to new species and other forms of organismal diversity (Mallet, 2007; Van de Peer et al., 2009) and may affect their colonization and dispersal abilities allowing them to occupy environmental niches unavailable to their parents (Soltis and Soltis, 2000; Bento et al., 2008).

Hybrid progeny with genetic material displaying a mosaic of phylogenetic signals may lead to incongruence between different gene trees thereby confounding phylogenetic reconstructions. However, incongruence can also arise as a result of stochastic or population-level events, including incomplete lineage sorting, non-homologous sampling of duplicated genes leading to misinterpretations between orthologs and paralogs, and horizontal gene transfer (Álvarez and Wendel, 2003; Maddison, 1997), causing individual gene trees to differ from the underlying species tree (McBreen and Lockhart, 2006; Holland et al., 2008). Reticulate

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evolution is well documented among plants throughout their genealogical histories (Rieseberg, 1997; Mallet, 2007), and phylogenetic incongruence within plant genomes has been observed in numerous molecular studies (Pirie et al., 2008; Vargas et al., 2009). Thus, reconstruction of species relationships in polyploid groups with a high degree of reticulation may be a challenging task. In such instances, adding larger numbers of markers does not necessarily lead to a better resolution of the species trees, but instead the study of different kinds of markers can shed further light into the evolutionary histories of such species complexes (Small et al., 2004; Hughes et al., 2006; Rousseau-Gueutin et al., 2009).

1.2. Low-copy nuclear loci in the study of hybridization history

Historically, plant molecular phylogenetics has depended to a great extent on data generated from plastid (cpDNA) and nuclear ribosomal (nrDNA) DNA sequences, since their high copy number facilitates their utility (Álvarez and Wendel, 2003; Shaw et al., 2005). However, the uniparental inheritance of cpDNA masks evidence of reticulation in hybridizing species, and nrDNA undergoes concerted evolution due to gene conversion and unequal crossing over, leading to reduction in variation, lack of sufficient resolution for phylogenetic inferences, and masking of hybridized histories. In such cases, single or low-copy nuclear genes are able to compensate for some of the problems encountered with cpDNA and nrDNA markers (Sang, 2002; Small et al., 2004; Curto et al., 2012). Single- or low-copy nuclear genes are biparental, independently inherited, and exhibit less concerted evolution leading to a greater conservation of gene homeologs from ancestral genomes, providing evolutionary signatures of unique gene copies tracing hybrid reticulate history within lineages (Mort and Crawford, 2004; Duarte et al., 2010). Introns from low-copy markers may provide higher variability than coding regions, due to a higher rate of nucleotide substitutions in the former, and synonymous positions not being conserved in the latter group (Sang, 2002), thereby presenting the possibility of being phylogenetically more informative in closely related species where unambiguous alignments can be performed. Low-copy nuclear markers have been successfully used in previous studies to reconstruct allopolyploid origins in plants (Brysting et al., 2007; Rousseau-Gueutin et al., 2009; Liu et al., 2011). Despite numerous positive attributes, low-copy genes are not completely devoid of drawbacks, including paralogy, and population genetic processes, such as incomplete lineage sorting, in which cases the individual gene trees may not resemble the actual species tree, obfuscating actual phylogenetic relationships. However, these drawbacks can be overcome when combined with cloning, wherein the utility of low-copy nuclear genes can aid in the difficulties involved in direct reconstruction of reticulate evolution. By cloning the homoeologous loci derived from both parents, an allotetraploid genome can be separated into two independent units, with each homoeolog tracing its own parental lineage. Phylogenetic reconstructions from the cloned homoeologs together with the genes of the putative parents may aid the reconstruction of the diverged histories of the parental lineages from reticulate evolutionary history (Sang and Zhong, 2000).

1.3. New World *Stachys*, Hawaiian endemic mints and our current study

Stachydeae, the largest tribe of the subfamily Lamiioideae (Lamiaceae), consists of about 470 species, has a globally widespread distribution, and exhibits considerable chromosomal diversity (Scheen et al., 2010; Bendiksby et al., 2011; Salmaki et al., 2013). Stachydeae is comprised of three endemic Hawaiian genera and at least seven Old World (OW) genera (e.g., *Sideritis*,

Prasium, *Chamaesphacos*, *Suzukia*, and *Thuspeinanta*) that are nested within the largest genus *Stachys*, making this genus paraphyletic (Lindqvist and Albert, 2002). *Stachys* itself has a worldwide distribution, with the New World (NW) *Stachys* (Fig. 1) presenting a particularly challenging yet interesting system for phylogenetic reconstructions due to its wide range of morphological and cytological features and the inclusion of one of the largest plant lineages in the Hawaiian Islands, the Hawaiian endemic mints. The chromosome numbers for this Stachydeae lineage vary between $2n = 34$ or 68 in species with a predominant eastern or widespread North American (NA) distribution and $2n = 64$ and 66 in western NA species, as well as the Hawaiian mints. Only few chromosome numbers have been reported from Meso-South American (Meso-SA) *Stachys* species and they vary from $2n = 32$ to $2n = 80$ – 82 or 84 (Mulligan and Munro, 1989; Lindqvist and Albert, 2002).

The Hawaiian endemic mints consist of 59 species in three genera, *Haplostachys*, *Phyllostegia* and *Stenogyne*, characterized by a high degree of morphological variation contrasted with a low level of genetic diversity (Lindqvist and Albert, 2002; Lindqvist et al., 2003, 2006, 2007). Our previous studies have shown that the Hawaiian mints are monophyletic, having colonized the Hawaiian Islands once during the early to late Pliocene, and possibly having originated from one or more hybridization events involving temperate NA and Meso-SA *Stachys* members (Lindqvist and Albert, 2002; Lindqvist et al., 2003, 2006, 2007; Roy et al., 2013). Based on cpDNA and nrDNA sequences, we showed that there were at least two independent migration events of *Stachys* into the NW, once during middle to late Miocene and another toward the beginning of Pliocene (Lindqvist and Albert, 2002; Roy et al., 2013). Descendants of the first migration survived only in Meso- and South America (SA), whereas the latter event colonized different parts of temperate North America.

In this study, we have further disentangled the phylogenetic relationships among the NW *Stachys* and the Hawaiian endemic mints through low-copy nuclear genes. Our main goals were: (1) To reassess the origin and ancestry of the Hawaiian mints, tracing their evolutionary relationships within their closest NW *Stachys* relatives; (2) Investigate whether hybridization or incomplete lineage sorting (ILS) leads to the phylogenetic incongruence of these groups of lamioid mints when markers from different genomic regions are used; and (3) Delineate further the reticulate evolutionary relationships observed between the Mesoamerican and SA *Stachys*. We utilized five low-copy nuclear loci: (1) *AFO* (putative homolog of the axial regulator ABNORMAL FLORAL ORGANS; also known as FILAMENTOUS FLOWER or YABBY1), spanning the last intron and exon, (2) a region of *WAXY* (also known as Granule Bound Starch Synthase or GBSSI), spanning exons 11–13, (3) the third intron of *NIA* (Nitrate reductase), (4) intron regions of *COR* (Cold acclimation protein), and (5) intron regions of *ADK* (Adenosine kinase). *NIA* in most land plants have been previously shown to act as a homodimer utilizing NADH as a cofactor, to catalyze the first reaction in the uptake of nitrogen from the soil, the reduction of nitrate to nitrite (Hoff et al., 1992). A previous study by Howarth and Baum (2005) concluded that the third intron of *NIA* (*NIA*-i3) was the most divergent marker for phylogenetic analyses among the three *NIA* introns tested in *Scaevola* (Goodeniaceae). Although *NIA* appears to be single-copy in the majority of genera studied, there may be duplicate copies present in plants with polyploid origins (Levin et al., 2009). The *WAXY* locus (GBSSI) has also been used widely in phylogenetic reconstructions in a variety of plant groups, and has been shown to exist either as single or duplicate copies (Mason-Gamer et al., 1998; Mason-Gamer, 2013; Yuan and Olmstead, 2008; Levin et al., 2009). The other two low-copy loci *ADK* and *COR* were used by Curto and Colleagues (2012) in a phylogenetic study of subfamily

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