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Hybridization as a source of evolutionary novelty: leaf shape in a Hawaiian composite

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Abstract

Hybridization is increasingly recognized as a significant creative force in evolution. Interbreeding among species can lead to the creation of novel genotypes and morphologies that lead to adaptation. On the Hawaiian island of O'ahu, populations of two species of plants in the endemic genus *Lipochaeta* grow at similar elevations in the northern Wai'anae Mountains. These two species represent extremes of the phenotypic distribution of leaf shape: the leaves of *Lipochaeta tenuifolia* individuals are compound and highly dissected while leaves of *L. tenuis* are simple. Based primarily on leaf shape morphology, a putative hybrid population of *Lipochaeta* located at Pu'u Kawiwi was identified. Individuals in this population exhibit a range of leaf shapes intermediate in varying degrees between the leaf shapes of the putative parental species. We analyzed individuals from pure populations of *L. tenuifolia*, *L. tenuis* and the putative hybrids using 133 AFLP markers. Genetic analysis of these neutral markers provided support for the hybrid origin of this population. The correlation between genetic background and leaf morphology in the hybrids suggested that the genome of the parental species with simple leaves might have significantly contributed to the evolution of a novel, compound leaf morphology.

Introduction

The diverse flora and fauna of remote island chains have been studied by evolutionary biologists for many decades (e.g., Darwin, 1859; Mayr, 1942; Carson, 1996; Grant & Grant, 1996). Geographic isolation and founder-mediated speciation have historically been emphasized as the driving forces behind adaptive radiation on these islands (e.g., Weller, Sakai & Straub, 1996). However, there has long been interest in the role of interbreeding among species, or hybridization, as a creative force in evolution (Anderson & Stebbins, 1954; Lewontin & Birch, 1966). Hybridization is increasingly recognized as an evolutionary force that can lead to adaptation through the creation of novel genotypes and morphologies (Rieseberg, 1995; Arnold, 1997).

Despite its recognition as a recurrent process in the diversification of flowering plants, the importance of hybridization as a general mechanism of evolution driving speciation and adaptation has been and remains unclear (Heiser, 1973; Levin, 1979; Rieseberg, 1991). Many workers have pointed to the fact that early-generation hybrids often exhibit significant reductions in viability and fertility (Barton & Hewitt, 1980; Templeton, 1981), thought to be caused by the disruption of coadapted gene complexes (Dobzhansky, 1951; Mayr, 1963) or by the introduction of maladapted genes (Waser & Price, 1991). Additionally, hybridization may result in the creation of morphologically

intermediate offspring, adapted to neither parental habitat and outcompeted by non-hybrid individuals (Arnold & Hodges, 1995).

Given these findings, it is perhaps not unexpected that the role of hybridization in speciation on islands has historically been considered minor (Humphries, 1979; Ganders & Nagata, 1984; Francisco-Ortega, Jansen & Santos-Guerra, 1996). In fact, contemporary examples of hybridization in the Hawaiian flora, for example, appear to be rare, presumably because the allopatric distribution of species prevents pollen flow (Mayer, 1991). However, there are reasons to suspect that hybridization may, indeed, play a role in plant speciation on oceanic islands. For example, within the Hawaiian flora, a high rate of fertility is often observed in artificially induced interspecific and intergeneric hybrids (Carr, 1995). Examples include a number of groups within the Asteraceae: *Bidens* (Gillet & Lim, 1970), *Tetramolopium* (Lowrey, 1986), and the silversword alliance (Carr & Kyhos, 1981), which are known to hybridize freely in the few locations where different species co-occur (Caraway, Carr & Morden, 2001). Furthermore, non-concordance between nuclear- and organelle-derived phylogenies of groups such as the silversword alliance (Baldwin, Kyhos & Dvorák, 1990) and the Drosophilidae (DeSalle & Giddings, 1986) are generally interpreted as indicative of a role for hybridization in the diversification of these groups. These findings, along with the general lack of post-zygotic genetic barriers to hybridization among congeners, makes the fact that hybridization has been generally discounted as a factor in adaptive radiation in island settings surprising (Crawford, Whitkus & Stuessy, 1987).

In this study, we examined a putative example of natural hybridization in plants from the Hawaiian Islands. On the island of O'ahu, two species of plants in the Hawaiian endemic genus *Lipochaeta* (family Asteraceae) grow in the northern Wai'anae Mountains: *Lipochaeta tenuifolia* and *L. tenuis*. Both species are found at similar elevations in mesic forest, with *L. tenuifolia* found in the extreme northern portion of the mountain range and *L. tenuis* known from locations to the south. Individual species of *Lipochaeta* have diverged in a number of vegetative and floral traits, including leaf shape. *Lipochaeta tenuifolia* and *L. tenuis* represent the extremes in the genus with regard to leaf shape: the leaves of *L. tenuifolia* are compound and highly dissected, while the leaves of *L. tenuis* are simple. A population of *Lipochaeta* in the northern Wai'anae Mountains has been hypothesized to be of hybrid origin because individuals within the population possess a variety of leaf morphologies intermediate between those characteristic of *L. tenuifolia* and *L. tenuis* (J. Lau, Hawai'i Natural Heritage Program, pers. comm.). Our primary objective in this study was to use genetic markers to test the hypothesis that the population of *Lipochaeta* in the northern Wai'anae Mountains is of hybrid origin. Furthermore, within this putative hybrid population, we were interested in identifying correlations between leaf shape and the parental origin of our genetic markers.

Materials and methods

Study species

Lipochaeta DC (Asteraceae) is an endemic Hawaiian genus of about 20 species of primarily suffruticose perennials (Wagner, Herbst & Sohmer, 1990); two sections, based on morphology and cytology (*Lipochaeta*, $n = 26$, four-petaled disk florets; *Aphanopappus*, $n = 15$, five-petaled disk florets), are recognized within the genus. Artificial hybrids can be induced in crosses within and between sections (Rabakonandrianina, 1980), and between *Lipochaeta* and *Wollastonia biflora* ($n = 15$), the presumed progenitor of *Lipochaeta* (Rabakonandrianina & Carr, 1981). Although the exact relationship between the two sections is unclear, section *Lipochaeta* likely arose from a hybridization event involving a member of section *Aphanopappus* and another member of the genus *Wollastonia* (Gardner, 1977; Chumley et al., 2002).

Members of section *Aphanopappus* ($n = 14$, of which 11 are extant) are distributed in a classic adaptive radiation pattern; all but two species are single-island endemics (Wagner & Robinson, 2001). Individual species have diverged in vegetative and floral morphology including leaf shape, growth habit, and the color, number, and size of ray florets. Natural hybridization within the group appears to be uncommon (Gardner, 1979) but not unknown (Wagner Herbst & Sohmer, 1990). Heretofore, reports of natural hybridization within *Lipochaeta* were based solely on morphological