Genetic analysis of natural hybrids between endemic and alien Rubus (Rosaceae) species in Hawai‘i

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Abstract

A population of putative hybrids between the endemic Rubus hawaiensis and naturalized R. rosifolius was discovered in Kipahulu Valley, on the island of Maui in the Hawaiian archipelago. The goal of this study was to molecularly characterize this natural hybridization event, investigate the mode of hybridization, and determine the male fertility of the hybrid individuals. Both morphological and RAPD marker data indicate that the putative hybrid individuals are the progeny of R. rosifolius and R. hawaiensis. All 39 hybrid individuals sampled had the chloroplast DNA haplotype of R. rosifolius. Thus hybridization appears to be asymmetric, with R. rosifolius acting as the maternal parent. All hybrid individuals assessed for pollen stainability were sterile, and there was no evidence of backcrossing to either parent. This result suggests that hybrids are of the first filial generation and that variation among hybrids reflects differences within the parental populations. Sympatric populations of R. hawaiensis and R. rosifolius occur on four islands and six additional alien species of Rubus are naturalized and sympatric with R. hawaiensis in Hawai‘i. Further investigation is merited to assess whether hybridization may pose a threat to the long term viability of R. hawaiensis. This study highlights the increasing frequency and negative consequences of native-alien hybridization and the importance of maintaining active alien species control programs in the Hawaiian Islands.

Introduction

Island chains have long been considered natural laboratories for studying evolutionary processes. Spectacular examples of adaptive radiation and speciation in insular communities have captured the interest of naturalists for centuries (e.g., Darwin 1859). Many of these examples from island biology have been integral to the formation of the modern synthesis (Mayr 1942; Stebbins 1950). Evolution in isolation with narrow geographic distributions and in close proximity to diverse habitats is the hallmark of island systems and has been implicated in the formation of evolutionary novelties (Carlquist 1974). These same qualities, however, also make island species extremely susceptible to extinction (Rieseberg and Swensen 1996; Frankham et al. 2002). Evolution with geographic isolation in the absence of large mammals has left insular species poorly prepared to cope with frequent habitat disturbance associated with human incursion. Competition with aggressive alien species that are well adapted to disturbance, and the introduction of new predators and pathogens all compound the impact of habitat degradation. The likelihood of small population extinction is exacerbated by the narrow geographic distributions of island species. Not only are small populations more likely to go extinct through stochastic processes such as landslides, hurricanes, or fires, there are often few or no refuges on islands from which extirpated populations may be regenerated, ulti-
mately resulting in species extinction (Ellstrand and Elam 1993; Frankham et al. 2002). Further, island species are often obligately outcrossing (Carlquist 1974), and reproductive isolation is by ecological, rather than intrinsic, isolating mechanisms making formerly discreet species more likely to hybridize following habitat disturbance and the introduction of alien species (Levin et al. 1996).

Hybridization has played an important role in the evolution of the Hawaiian flora. Examples of hybridization in Hawai‘i reportedly involve species in 37 genera of 23 native plant families (Ellstrand et al. 1996) and has been intensively studied in the genera Argyroxiphium (Carr and Kyhos 1981, 1986), Cibotium (Motley and Morden 2001), Cyrtandra (Smith et al. 1996), Dubautia (Carr and Kyhos 1981, 1986; Caraway et al. 2001), Hibiscadelphus (Carr and Baker 1977), Labordia (Motley and Carr 1998), Lipochaeta (Rabakonandrianina and Carr 1981), Portulaca (Kim and Carr 1990), Scaevola (Gillett 1972), Wikstroemia (Mayer 1991), and Wilkesia (Carr and Kyhos 1981, 1986; Carr et al. 1996). Intergeneric hybrids have been characterized in the silversword alliance (Carr 1995) where it has also been demonstrated that reticulate evolution has played a major role in the evolution of this group (Baldwin 1997). Although hybridization among endemic species appears to have been a creative influence in the evolution of the Hawaiian flora, hybridization between native and alien species may pose a hazard to this diversity.

The threat of hybridization to the native flora of Hawai‘i is, of course, tied to the very high rate of plant invasion in the Hawaiian Islands. Nearly half of the flora of Hawai‘i consists of naturalized species, brought to the islands either intentionally or unintentionally through human practices (cf. Wagner et al. 1999). This alarming rate of alien species introduction has frequently brought non-native congeners into sympatry with native species, posing an additional threat of native species loss through hybridization either through genetic assimilation, outbreeding depression, and/or demographic means (Rieseberg 1991; Abbott 1992; Levin et al. 1996; Rhymer and Simberloff 1996). Genetic assimilation, the process by which the genome of one species is subsumed into that of another, is the most direct mechanism by which hybridization can facilitate extinction. Although the threat of genetic assimilation is not limited to insular species (e.g., Daehler and Strong 1997; Anttila et al. 1998), some of the most striking examples occur on islands (e.g., Brochmann 1984; Rieseberg et al. 1989).

However, even if hybrids are sterile, demographic threats of extinction are still enhanced through hybridization. The loss of reproductive effort through hybrid production, and the decrease in available habitat due to competition with hybrids and alien species pose a formidable threat to native species (Rieseberg 1991; Ellstrand and Elam 1993; Levin et al. 1996; Rhymer and Simberloff 1996). In Hawai‘i, 176 native species in 59 genera are estimated to be at risk from hybridization with naturalized alien congeners (Daehler and Carino 2001).

Despite the astounding regularity with which hybridization occurs among Hawaiian endemics, no definitive instances of naturally occurring hybrids between endemic and alien flowering plant species have been rigorously documented in the literature to date. However, a presumed allopolyploid derivative of an indigenous and alien species hybridization has been identified based on morphology and chromosome number (Kim and Carr 1990). Other examples of putative native/alien hybrids have been identified based on morphology including species in the genera Gossypium (Stephens 1964), Argemone (Wagner et al. 1999), Bidens, Chenopodium, Gnaphalium, Hibiscus, Sida, Solanum (reviewed in Daehler and Carino 2001), and several fern species (Wagner 1993). Further, artificial hybrids between alien and Hawaiian native species are readily created (Rabakonandrianina and Carr 1981; Kim and Carr 1990; DeJoode and Wendel 1992; Carr et al. 1996; Ganders and Nagata 1999). The lack of study of the incidence, extent, and rate of hybridization as well as the subsequent effect of alien-native hybrids on native populations is distressing given the frequency with which congeneric alien and native species exist in sympatric ranges and the propensity for hybridization among native species.

Blackberries and raspberries in the genus Rubus represent an excellent system with which to study invasive and native-alien interactions in Hawai‘i. There are two endemic species (R. hawaiensis A. Gray and R. macraei A. Gray), both with North American ancestry (Howarth et al. 1997; Morden et al. 2002). Rubus hawaiensis is a major component of forest ecosystems above 2000 m elevation whereas R. macraei is less widely distributed. However, both are at least partially sympatric with seven alien Rubus species that are naturalized in the Hawaiian Islands (Table 1, Figure 1). This is particularly salient given that four of the alien species have been identified as noxious weeds by the Hawaiian Department of Agriculture and one other has the potential to become such