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Genetic analysis of an introduced biological control agent reveals temporal and geographic change, with little evidence of a host mediated shift

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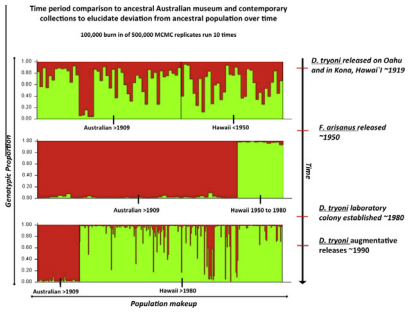
HIGHLIGHTS

- We evaluated the population structure Australian and Hawaiian *D. tryoni*.
- Both historical and contemporary specimens were used in the analysis.
- Australian and Hawaiian populations have diverged overtime.
- Hawaiian population structure is defined by historical influences.
- A host-shifted Hawaiian population was not genetically distinct.

GRAPHICAL ABSTRACT



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ABSTRACT

The evolution of introduced biological control agents is largely un-explored. Although much is theorized, there is little empirical evidence quantifying the evolutionary dynamics of a biocontrol agent after release into a new environment. In this study we use *Diachasmimorpha tryoni*, a purposefully introduced biocontrol agent of *Ceratitis capitata*, to model and quantify spatial, temporal, and host-related evolutionary patterns. This parasitoid has undergone a host shift in its introduced environment, Hawaii, to the gall forming weed biocontrol agent, *Eutreta xanthochaeta*, an interaction likely mediated by competition for *C. capitata* with the egg-larval parasitoid *Fopius arisanus*. To elucidate potential evolutionary patterns we analyzed microsatellites and sequence data extracted from Hawaii and Australian population clusters defined by Structure, in Genepop, Canoco, and IBDWS. Our analysis revealed structuring of Hawaiian *D. tryoni* populations as defined by significant historic influences related to temporal structure, geographic space, host guild, and augmentative releases. The host-shift parasitoids were not genetically distinct from other Hawaii populations. There were small changes in microsatellite DNA at the population level, but only between Australia and Hawaii populations, not at the host level. These results show that *D. tryoni* has not undergone host-mediated evolution since introduction to Hawaii, despite the fact that they have expanded their host range in Hawaii to include the gall-forming *E. xanthochaeta*. To our knowledge this is the first study to quantify genetic differentiation of a biological control agent over geographic space and time using contemporary and museum specimens.

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1. Introduction

The deliberate introduction of biological control agents to manage invasive pests has been practiced in the United States for over a century (Van Driesche et al., 2008). These controlled introductions have helped to prevent billions of dollars in damage to high value crops, impacts on other resources in the U.S. (such as indigenous species), and around the world. The average cost/benefit ratio for biological control programs has been estimated to exceed 1:250 (Neuenschwander, 2001; Jetter et al., 1997; Bale et al., 2008). Despite this overall net benefit, some authors have argued that biological control should be avoided, given that any classical biological control release is essentially an assisted invasion (Howarth, 1991). Both opponents and advocates of biocontrol use historic instances of attack on non-target hosts as catalysts for the development of more specific and predictable techniques to aid in the selection and introduction of new biological control agents (Howarth, 1991; Simberloff and Stiling, 1996; Louda et al., 1997; Messing and Wright, 2006).

To allay some of these concerns, risk assessment approaches that address host specificity and basic organismal biology in relation to the target pest have been developed and implemented (Messing and Wright, 2006; Bigler et al., 2006; Barratt et al., 2010). Except for initial host range testing, these approaches do not take into consideration the potential evolutionary dynamics that may occur due to direct or indirect ecological interactions.

Classical biocontrol introductions are characterized by the separation of a cohort of individuals from their ancestral population(s) (Van Driesche et al., 2008). This separation may lead to the divergence of distinct evolutionary lineages over time due to a reduction of genetic variation and a lack of gene flow (e.g. through a founder effect). Thus, when considering the evolutionary trajectory of introduced biocontrol agents, it is not a matter of *whether* agents differentiate from the ancestral populations, but rather *how*, *when*, *why*, and *how much* they diverge (Roderick and Navajas, 2003; Hufbauer and Roderick, 2005).

In this study we evaluate the processes that may have influenced the evolutionary trajectory of an arrhenotokous parasitoid, *Diachasmimorpha tryoni* (Cameron) (Hymenoptera; Braconidae), following its introduction into the Hawaiian archipelago ~100 years ago. Here, we attempt to address three main objectives using the natural history of *D. tryoni*:

(1) Whether *D. tryoni* has evolved in Hawaii ~100 years after purposeful release
(2) If so, can we resolve the historic influences that may have contributed to this evolutionary process?
(3) Whether *D. tryoni* has undergone a host range expansion or host shift onto the non-target host *Eutreta xanthochaeta* (Aldrich) (Diptera; Tephritidae).

This analysis strives to understand the dynamics that may influence the evolutionary trajectory of *D. tryoni* in Hawaii and, by inference, the potential evolutionary future of biocontrol agents elsewhere. By doing so we hope to stimulate further work into how evolutionary processes can be predicted, and how these predictions can be applied in a tangible form to biocontrol theory and practice.

2. Materials and methods

2.1. History of D. tryoni as a biological control agent in Hawaii

D. tryoni was first described in 1911 as a parasitoid of the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera; Tephritidae), in Australia (Carmichael et al., 2005; Ramadan, 1989). It was collected by H.A. Silvestri in ~1913 from New South Wales for importation to Hawaii to control a large outbreak of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera; Tephritidae). Only seven wasps (four females and three males) survived the voyage from Australia to Hawaii (Pemberton, 1964). After an unsuccessful captive mass-rearing effort and fearing colony loss, nine wasps were released in a *C. capitata* infested coffee plantation on the Kona coast of Hawaii. From this small founding population the statewide distribution of *D. tryoni* descended (Pemberton, 1964). This introduction proved to be partially effective, resulting in reduced infestation of *C. capitata* in coffee, and displacing a less effective parasitoid, *Psyttalia humilus* (Silvestri) (Hymenoptera; Braconidae), introduced from Africa around the same time as *D. tryoni* (Pemberton, 1964).

Fopius arisanus (Sonan) (Hymenoptera; Braconidae), an egg/larval parasitoid, was released (erroneously identified as *Opius persulcatus*) in ~1949 to control *Bactrocera dorsalis* (Hendel) (Diptera; Tephritidae). *F. arisanus* was later found to out-compete *D. tryoni* within *C. capitata* hosts, this competitive interaction seems to have reduced the geographic range of *D. tryoni* in the islands (Mainland et al., 1950; Van Den Bosch and Haramoto, 1951; Wang, 2004; Messing and Wang, 2009). Approximately a decade after the introduction of *F. arisanus*, it was noted anecdotally that the larvae of a tephritid gall-fly introduced from Mexico as a weed biocontrol agent, *E. xanthochaeta*, was parasitized by *D. tryoni* in the field (Bess and Haramoto, 1959). *E. xanthochaeta* and *D. tryoni* have no historic evolutionary association and both were brought to the archipelago as biocontrol agents (Mainland et al., 1950; Bess and Haramoto, 1959; Wong et al., 1991; Duane et al., 1998). In 1988 *D. tryoni* was also successfully used in an augmentative release campaign to suppress populations of *C. capitata* in Hawaii. Approximately 4.1 million captive mass-reared *D. tryoni* were released in the Kula area of Maui to supplement the established wild population (Wong et al., 1991).

2.2. Population sampling

2.2.1. Australian populations: collection

We collected and analyzed 48 contemporary (field collected), and museum specimens of Australian *D. tryoni* from eight locations (Appendices B, Table B1). Contemporary Australian specimens were collected from putative ancestral populations of *D. tryoni* by R.H. Messing and Jennifer Spinner in New South Wales (NSW) Australia (Gosford, Cootamundra, and Wagga Wagga). Museum specimens were obtained from the Australian National Insect Collection (ANIC) in Canberra, Australia and the Bishop Museum (BM) in Honolulu. All collections of Australian contemporary and museum *D. tryoni* were from ripe fruits of *Solanum* sp., *Prunus persica*, *Eriobotrya japonica*, or *Schizomeria ovata*, and were parasitoids of either *C. capitata* or *B. tryoni*. An overview of all Australian collections is given in Appendices B (Table B1).

2.2.2. Hawaiian populations: collection

A total of 271 contemporary field-collected and historic Hawaiian specimens were used in this analysis (Appendices B, Table B2). Field collected *D. tryoni* from each of the major Hawaiian Islands (Hawaii, Kauai, Oahu, Maui, and Molokai; see Fig. 1) were obtained from target- and non-target hosts. All necessary permits were obtained for the described field studies. Collection, colony maintenance, and rearing methods are described in detail in Appendices C. A map of collection locations (Fig. 1) was made in ArcMap vers. 9.3 (ESRI Inc., 2009).

Hawaii museum specimens were loaned from the Bishop Museum, the Australian National Insect Collection (ANIC), the