



Concordance in evolutionary history of threatened plant and insect populations warrant unified conservation management approaches

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ABSTRACT

Threatened organisms may act as host to a suite of dependent organisms, which are potentially cothreatened, yet management is rarely coordinated between host and dependent species. Here, we test the congruency of patterns of genetic structure between two critically endangered interacting taxa; the feather-leaf banksia (*Banksia brownii* R.Br.), and its host-specific herbivorous plant-louse *Trioza barrettae* Taylor & Moir, to establish whether conservation actions should be implemented jointly for both species. We also examine the role of host population size and fire history on the density of psyllids on host plants. We show that the patterns of mtDNA variation in *T. barrettae* and microsatellite variation in both species support the presence of at least two conservation units across each species, with the microsatellites also showing a high evolutionary congruency between plant and insect populations. The extinction of divergent *B. brownii* populations, therefore, is likely to have resulted in the extinction of divergent plant-louse populations. Larger populations of host plant (>150) and more recent fire history (<20 years since fire) are important factors in maintaining *T. barrettae* densities. High molecular congruency indicates the importance of considering patterns of genetic diversity of source material from both host and dependent organisms for ex situ conservation, in situ supplementations and reintroductions. As dependents such as *T. barrettae* are often lost to extinction before their host, considering the conservation of dependent biota in the early stages of species management is paramount.

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1. Introduction

The sixth mass extinction event is currently in progress (Barnosky et al., 2011), with cascading secondary extinctions potentially common although largely unrecorded (Dunn et al., 2009; Moir et al., 2010; Colwell et al., 2012). Conserving all biodiversity is therefore a substantial challenge. Current conservation options for threatened plant species include seed banks, genebanks, translocations and restoring degraded habitat (Coates and Atkins, 2001; Safont et al., 2012; Monks et al., 2012). Despite the attention with which plants are managed, rarely is thought given to the many invertebrate species that may rely on these threatened plant species for their own survival (Moir et al., 2011).

Species dependent on another, such as herbivorous insects, may codiverge with their host, particularly if populations are isolated either biotically (e.g., presence and suitable population sizes of host species) or abiotically (e.g., fragmentation of populations due to patchy climate suitability) (Loxdale et al., 2011; de Vienne et al., 2013). This codivergence through isolation may manifest itself in the ecology of the dependents, for example, some herbivorous insect species have a predisposition towards particular populations of their host plant species, and may not be able to complete life-cycles on alternative populations or subspecies (Dexter and Kitching, 1993; Turlure et al., 2013).

Despite the specificity of particular insect species on plants, conservation and restoration focus is often directed towards invertebrates that assist with the plant's survival and population sustainability, such as pollinators (i.e. Menz et al., 2011). Herbivorous insects (including seed predators) are often neglected, excluded (Watts et al., 2010), or actively eradicated (Bevill et al., 1999). Monophagous insects, those restricted in host-breadth to one plant species, are, however, rarely detrimental to individual plants. In a review of herbivores on rare plants, Ancheta and Heard (2011) found only one example of a monophagous insect killing its threatened plant host.

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Narrowly host-specific insect herbivores on threatened plants have high potential for extinction with their host (Hopkins et al., 2002; Moir et al., 2011, 2012), particularly as they may have a narrower geographic range than that of the plant (Strong, 1979; Taylor and Moir, 2009, 2014). The insect's extinction risk increases if their host is removed from the wild or the host population dwindles to a size unable to sustain an insect population (Moir et al., 2010). Its subsequent extinction is known as coextinction (c.f. Stork and Lyal, 1993, and reviewed by Colwell et al., 2012). Coextinction cascades may follow (Valiente-Banuet and Verdú, 2013).

Consolidating conservation actions for host plants with that of their dependent insect species may incur little additional cost (Moir et al., 2012). If an integrated approach to the conservation of host and dependent taxa is to be considered, then determining whether there is congruence in patterns of genetic differentiation or population genetic structure (hereafter termed molecular congruency) between different populations of host and dependent species is a fundamental step. Assessing the degree of molecular congruency between insect herbivore and host plant populations has been applied to biocontrol (Goolsby et al., 2006), fragmentation studies (Liu et al., 2013), coevolution and phylogeographic research (Ahern et al., 2009; Borer et al., 2012). For conservation management, the implications of congruency at a molecular level suggest that populations of both species be considered jointly and managed accordingly. Furthermore, if these matching populations are genetically and ecologically different from other populations, then they may be considered as separate units for conservation (see Allendorf et al., 2013) and possibly Evolutionarily Significant Units (ESU) (Crandall et al., 2000). Alternatively, if there is no significant genetic structure between different host populations or dependent populations, then the origins of specimens for augmentation or reintroduction may not be of paramount concern (e.g., McHugh et al., 2013). Here, we assess the molecular congruency between populations of highly threatened host and dependent, using a case study of a rare plant and its equally rare host-specific herbivorous plant-louse insect, representing the first population genetic assessment for conservation purposes for the Psylloidea. We examine factors that may influence the abundance of these insect herbivores on threatened plants and discuss management options.

2. Materials and methods

2.1. Study organisms

Banksia brownii R.Br. is a rare and geographically restricted long-lived woody shrub. It extends in small isolated populations over a range of approximately 90 km in the far south of Western Australia. It occurs in three geologically and climatically distinct regions; the Stirling Range National Park (SRNP) in the north, the middle populations, and the southernmost population south of Albany on the coast (for more detailed information see Appendix B). *Banksia brownii* is known from 30 populations, of which 10 are now extinct and six consist of five or less surviving plants (Coates et al., 2015). It is a non-sprouting species that is killed by fire and relies entirely on seed for regeneration. Due to the extinction of 10 populations, and the ongoing decline of all other extant populations, *B. brownii* is now ranked as critically endangered under World Conservation Union Red List criterion (IUCN, 2015) with a projected decline in total number of plants of $\geq 80\%$ within the next three generations due to the plant disease, *Phytophthora cinnamomi* die-back (Barrett et al., 2008; Coates et al., 2015).

Recently a species of plant-louse, *Trioza barrettae* Taylor & Moir (Triozidae: Hemiptera), was discovered on two of the highly fragmented populations of *B. brownii* and listed as critically endangered by the Western Australian State Government and IUCN Red List due to its putative high host-specificity and restricted distribution of its plant host (Taylor and Moir, 2014; IUCN, 2015). Psyllids are considered not to be strong or active dispersers. At most, free-living immatures may

disperse to a preferred feeding site on an individual host plant (Hollis, 2004). Adults may undertake limited flighted dispersal from their originating host, although long distance aerial dispersal in the direction of wind currents has been recorded for spring generations of *Cardiaspina densitexta* Taylor at high population densities (White, 1970). At low densities, being most often the case even for 'outbreeding' species such as *C. densitexta*, psyllids tend to concentrate progeny on a proven food resource rather than searching for new hosts (White, 1970).

2.2. Collection of insect herbivores

Sampling of insect herbivores was undertaken on populations of *B. brownii* across the plant's range. Sampling occurred in the Southern Hemisphere spring (September–November) from 2007 to 2015. In total, eight natural, and three translocated, *B. brownii* populations were sampled, some multiple times, and one population was determined as too small (Appendices A & B). Information on fire history and plant population size at each site was compiled from Western Australian Department of Parks and Wildlife records or survey (Appendix A).

The protocol of Moir et al. (2011) suggests that only a limited number of herbivorous insect individuals should be taken from a population to minimize impact on that population. We decided to sample a maximum of 30 plants within any one population to standardize the sampling (allowing for estimation of population size through detection rates), and also to sample at a maximum rate of once every two years to allow the insect population to recover. Phylogeographic patterns and population genetic structure have, however, been satisfactorily detected using a limited number of individuals per population from previous work on insect-plant molecular congruency (e.g. Thiel-Egenter et al., 2011; Borer et al., 2012).

Trioza barrettae specimens were collected from *B. brownii* individuals using the complementary methods of vacuuming and beating (Moir et al., 2005), which involved vacuuming insects from all branches of plants using a petrol-driven weed-blower, or tapping every branch of plants using a large stick and collecting the insects from a net placed under the bush. Fifteen plants were sampled per method where possible to obtain comparable measures of population size, with the exception being translocated plants at Kamballup, Warriup, and Snake Hill, which were only vacuum sampled at the request of the management agency, Department of Parks and Wildlife. Specimens of *T. barrettae* were put in 100% ethanol and kept in the freezer for genetic analysis.

2.3. Sampling and DNA extraction

To assess the molecular congruency between populations of *B. brownii* and *T. barrettae* genetic analysis was required on both species. These analyses are detailed in the next three sections.

DNA was extracted from *T. barrettae* using the QIAGEN DNeasy Blood and Tissue Kit (see Moir et al., 2015). Individual psyllids from known populations on *B. brownii* were sampled as follows: Mt Hassell (10), Yungemere (19) mountain (both in SRNP), Mill Brook Nature Reserve (13), Vancouver Peninsular (9) and Waychinicup National Park (13) (see Appendix A).

DNA was extracted from leaf samples of 11 extant *B. brownii* populations and seedlings of five extinct populations based on seed collected between 1987 and 2000 (detailed in McArthur and Coates, 2010). However, here we only examined the five *B. brownii* populations where *T. barrettae* was found (Mt Hassell, Yungemere, Mill Brook, Vancouver and Waychinicup), and these were a subset of 16 populations and 359 individuals investigated in a broader study (Coates et al., 2015).

2.4. Mitochondrial DNA amplification, sequencing and data analysis

Sequence variation was investigated in the mitochondrial COI gene (mtDNA). Twenty-five *Trioza* specimens were sequenced for variation

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