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Biological control reduces herbivore's host range

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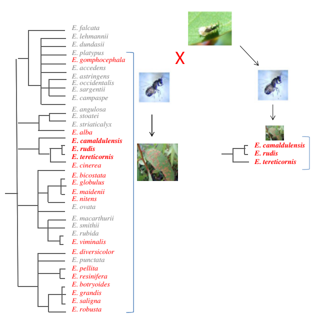
HIGHLIGHTS

- Host range of a gall wasp is compared before and after its parasitoid introduction.
- The number of plant species with galls decreased to less than 20%.
- Host plant range was narrowed to three phylogenetic closely species.
- The control by the parasitoid helps to clarify the insect–plant evolutionary history.

GRAPHICAL ABSTRACT



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ABSTRACT

The enemy release hypothesis predicts that alien populations are more vigorous and grow faster in introduced areas than within their natural range due to lack of natural enemies. An extension of this theory would be that the lack of natural enemies on an herbivore species will indirectly increase the number of host plant species that it can infest. The eucalyptus gall wasp *Ophelimus maskelli* is a recent introduction to the Mediterranean basin. Its arrival was followed after about two years by its parasitoid, *Closterocerus chamaeleon*. We evaluated the range of hosts used by the gall wasp by surveying 50 *Eucalyptus* species, 37 *Eucalyptus* hybrids and 18 *E. globulus* half-sibling families, before and after the establishment of the parasitoid. We found a consistent reduction in the observed host range of the gall wasp after the establishment of the parasitoid with a reduction of 83% on *Eucalyptus* species, 84% on hybrids, and 94% on *E. globulus* half-siblings. Host range narrowed down from 18 to three closely-related host species, all in the section Exsertaria, series Exsertae, *E. camaldulensis*, *E. tereticornis* and *E. rudis*, which are probably the standard hosts of *O. maskelli*. In the remaining affected species the intensity of attack decreased significantly in all studied regions. These findings show that, besides the direct gains from classical biological control, there may be indirect benefits through a natural-enemy-induced reduction in the range of host plants used by herbivorous insect pests.

1. Introduction

The enemy release hypothesis (ERH) predicts that in their native range most organisms are subject to multiple regulation mechanisms driven by specific natural enemies exerting a "top down" effect (Torchin et al., 2003). However, outside their native ranges, released from such regulation processes, exotic species of both plants and animals can attain population levels not normally observed in the native area (Keane and Crawley, 2002; Torchin et al., 2003). Evolutionary processes in "enemy free" locations may further promote the allocation of resources to growth rather than to defence strategies (Wolfe et al., 2004; Hahn et al., 2012). An extension of the ERH, for consumer organisms, would be that the lack of natural enemies would increase their ecological or realized host range, i.e. the number of host species fed on or used for reproduction in the field (Nechols et al., 1992; Araújo et al., 2011).

Understanding host range constraints is particularly relevant for alien species, whereby the introduction of herbivorous insects to new geographical areas provides opportunities for host range

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expansion. Furthermore, the impact of both native and alien herbivores in the plant communities is determined to a great extent by their host range. Shifts to novel hosts have been observed in herbivorous insects which were either deliberately (Pemberton, 2000), or inadvertently (Kenis et al., 2009), introduced into new areas. In these cases, the widened ecological host range included indigenous plant species that became hosts to the newly-introduced insects in the invaded areas. Similarly, native herbivores may broaden their host range by shifting to non-indigenous plants (Graves and Shapiro, 2003), which may eventually promote evolutionary processes of adaptation (Carroll et al., 2005). A question that remains is to what extent the natural enemies of an exotic herbivore can indirectly curb the range of plant species it can use.

Non-indigenous plants are used globally in agriculture, forestry and industry, often contributing significantly to local economies. Following their introduction, non-indigenous plant species benefit from a release from natural enemies, contributing to the plants high productivity. However, over time, introduced plant species may accumulate insect herbivore species which are inadvertently introduced from the native range of the plant and which may become pests if the plants are being used for commercial gain, as happened with exotic *Eucalyptus* plantations in America and Europe (Paine et al., 2011; Reis et al., 2012). The ERH may also account for the aggressiveness of the alien insects. Released from their natural enemies, these insects will in general cause higher damage to their host plant in the introduced range than in the native range. In some cases the alien pests are inconspicuous, or even unknown to science, in their native range, as in the case of the gall wasp *Leptocybe invasa* (Mendel et al., 2004).

Classical biological control using natural enemies introduced from the native ecosystems of the alien organism is a way to restore regulatory processes disrupted by the enemy release status (Hoddle, 2004). Alien herbivores under classical biological control provide an opportunity to study the "top-down" effects of a predator or parasite. Whereas reduced levels of plant damage through biological control have been well demonstrated, possible indirect effects on the ecological host range of herbivorous insects are not as clearly understood.

Our study focused on the gall wasp *Ophelimus maskelli* (Ashmead) (Hymenoptera: Eulophidae), which recently invaded several regions outside its native range in Australia. The gall wasp was first recorded in the Mediterranean basin in Israel in 2004 (Protasov et al., 2007). It was detected in Tunisia (Dhahri et al., 2010) and Portugal (Branco et al., 2009) in 2006. It induces circular, swollen galls which are very noticeable on eucalyptus leaves.

The Australian parasitoid *Closterocerus chamaeleon* (Girault) (Hymenoptera: Eulophidae) was deliberately introduced into the Middle East in 2006 for biological control of *O. maskelli* (Mendel et al., 2007). Later *C. chamaeleon* was deliberately introduced into Italy (Caleca et al., 2011), and it spread from there into other Mediterranean areas. In Portugal, the parasitoid was observed for the first time in 2007 near Lisbon (Branco et al., 2009) and in the same year in Tunisia, not far from the Sicilian coast. The parasitism rate was low (5%), indicating that the insect had recently reached this region (Lo Verde et al., 2010). Observations thus indicate that the establishment of the parasitoid closely followed the establishment of the gall wasp, with a lag of only a few years.

In this study, we compare the ecological host range of the herbivore gall maker, *O. maskelli*, before and after the establishment of its parasitoid in order to test the hypothesis that the host range (the plant) is constrained by the third trophic level (the parasitoid). We address three main questions. First, does ecological host range (i.e., number of plant species, or plant genetic materials used) differ before and after the parasitoid establishment as an indirect effect of the parasitoid? Second, is there a difference in levels of galling before and after *C. chamaeleon* establishment? Thirdly, can the host plants used under the pressure of the natural enemy help to clarify the insect-plant evolutionary history through their phylogenetic relationship?

2. Material and methods

2.1. Study sites and plant materials

Sampling was carried out in arboreta of *Eucalyptus* spp. in four sites in Tunisia: Choucha (37°03′ N 9°14′ E, 159 m a.s.l.), Zerniza (37°09″ N 9°07′ E, 60 m a.s.l.), Korbous (36°50′ N 10°35′ E, 180 m a.s.l.) and Jbel Abderrahmane (36°40′ N 10°40′ E, 255 m a.s.l.), and in one site in Portugal: Pegões (38°40′06″ N 8°38′07″ O, 90 m a.s.l.). In Tunisia the four arboreta consisted of 25, 30, 18 and 40 *Eucalyptus* species, respectively in Choucha, Zerniza, Korbous and Jbel Abderrahmane. In total 50 *Eucalyptus* species were surveyed. In Pegões (Portugal) 37 different *Eucalyptus* hybrids and 18 half-sibling families of *E. globulus*, all from one arboretum, were assessed. Half-siblings were obtained by open-pollinated trees and grown for seed production. The 37 hybrid types consisted of crosses of parents of the following species: *E. algeriensis*, *E. camaldulensis*, *E. globulus*, *E. grandis*, *E. nitens*, *E. rudis*, *E. saligna*, *E. tereticornis*, *E. trabuti* and *E. viminalis*. It should be noted that *E. algeriensis* and *E. trabuti* are themselves hybrids of *E. camaldulensis* (formerly known as *E. rostrata*); *E. algeriensis* = *E. camaldulensis* × *E. rudis* and *E. trabuti* = *E. camaldulensis* × *E. botryoides* (Maiden, 1924). The height of the *Eucalyptus* hybrids was about 1.0–1.5 m and the *E. globulus* trees were about 2–2.5 m high.

A phylogenetic 'tree' of the *Eucalyptus* species (subtribe Eucaliptinae) used in the present study was constructed based on nomenclatural information on the Eucalink PlantNet website (Hill, 2002-2004). Phylogenetic distance between species was estimated as the number of nodes in the phylogeny between the particular plant species.

2.2. Sampling methods and periods

In both Portugal and Tunisia observations were carried out over two periods. Portugal monitoring was in March 2008 and in March–April 2011. Tunisia sampling was in March–April 2008 and in March–April 2012. These periods correspond to the time before and after establishment of *C. chamaeleon* in each country. In Portugal, several leaves with fully developed galls were taken from the hybrid plants in the field and kept in vials (ca. 50 cm^3 volume), 3–4 leaves per vial, four replicates on each sampling period, and left for one month to check for the emergence of the parasitoid.

In Tunisia in 2008, the total number of trees surveyed in each arboretum was 2352 (Zerniza), 3417 (Choucha), 3442 (Korbous) and 2436 (Jbel Abderrahmane). In 2012, 10 trees of each species were surveyed on each site, in total 320, 250, 180 and 150 trees, respectively for Zerniza, Choucha, Korbous and Jbel Abderrahmane. For each tree, four branches, 80 cm in length, were removed from each of the cardinal aspect of the tree (N, S, E, W), at heights which varied between 1.3 and 2.5 m. The branches were brought to the laboratory where all leaves were examined and the numbers of leaves with and without galls were counted. The number of leaves on each branch ranged between 50 and 200.

In Pegões (Portugal), on both sampling dates, three plants were selected from each hybrid type and five branches were removed from each plant. Due to the small size of the plants, this represented about 25–50% of all foliage. Plants were selected along transect rows, separated at 3–5 m intervals, irrespective of gall wasps being detected. Branches were then placed individually in plastic boxes and brought to the laboratory where all leaves were inspected and the number of leaves with and without galls was re-