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Biological control reduces herbivore's host range

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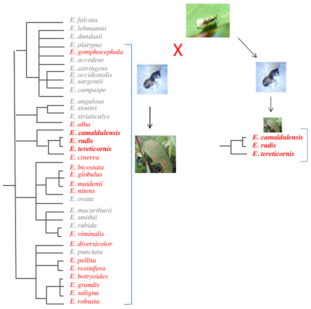
HIGHLIGHTS

- 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 recorded. Due to the low levels of galling observed on *E. globulus* on both sampling dates, observations were carried out directly in the field. For each *E. globulus* half-sibling family, 2–3 trees were monitored and five branches per tree were inspected. The presence of galls and the percentage of leaves with galls were determined for each branch by selecting foliage which had sprouted before samples were gathered. Only branches with young leaves were selected, recognizable by the leaves development, which offer ideal conditions for gall development (Protasov et al., 2007).

2.3. Data analysis

A generalized linear model (GLM) was used to compare observed host range in Tunisia, with two factors: before and after *C. chameleon* establishment as the time factor, and the four sites as the site factor. The dependent variable was presence/absence of galls at species level using Binomial probability distribution with logit link function.

Generalized linear models with Binomial distribution were also used to analyse the proportion of galled leaves per branch (dependent variable), in relation to the factor plant species/hybrid types. In Tunisia, the predictor variable site was further considered. Separate analyses were performed for the first period, 2008, and the second period, 2011–2012, using the affected species/hybrids in each period. Similar GLM models were used to compare differences in proportions of galled leaves between the two sampling periods (factor time) for the plants species/hybrids commonly affected during both periods.

3. Results

3.1. Host range

In Tunisia there was a significant decline in the ecological host range of *O. maskelli* between 2008 and 2012, expressed as the number of species with the presence of galls Chi-square $X^2 = 18.8$, df = 1, $P < 0.001$) (Fig. 1). The probability (±SE) of a species being galled decreased from 0.34 ± 0.050 in 2008 to 0.06 ± 0.026 in 2012. Galling was higher at Choucha and Zerniza than at Jbel Abderrahmane while lowest levels where recorded at Korbous where the number of galled species in 2008 was only three ($X^2 = 8.7$, df = 3, $P = 0.034$) (Fig. 1). Only two *Eucalyptus* species in Zerniza and Choucha, *E. camaldulensis* and *E. tereticornis*, two in Korbous, *E. camaldulensis* and *E. rudis*, and one in Jbel Abderrahmane, *E. tereticornis*, had galls in 2012. *Eucalyptus rudis* was absent from Jbel Abderrahmane and *E. tereticornis* was absent from Korbous. From a total of 50 *Eucalyptus* species surveyed, 18 species were attacked by the gall wasp in 2008, and only three species in 2012, *E. camaldulensis*, *E. tereticornis* and *E. rudis*, a decrease of 83% of the ecological host range ($X^2 = 8.27$; $P < 0.001$).

At Pegões in 2008, all 37 hybrid types had galls. In 2011 six of the hybrids had galls, a decrease of 84% (Fig. 1). A similar pattern was observed within *E. globulus* families, where the number of families with galls dropped from 16 to one, representing a 94% decrease (Fig. 1). The six hybrids with galls in 2011 originated from the following crosses: *E. camaldulensis* × *E. trabuti*; *E. tereticornis* × *E. globulus*; *E. camaldulensis* × *E. globulus* (two hybrids of this type); *E. rudis* × *E. saligna* and *E. saligna* × *E. trabuti*. The results show that, in 2011, all hybrids with galls had as parent species one of the three species used by the insects in Tunisia: *E. camaldulensis*, *E. tereticornis* and *E. rudis*.

3.2. Phylogenetic closeness of susceptible Eucalyptus species

In 2008, all of the species that were galled in Tunisia, and the parents of the hybrids that were galled in Portugal, belonged to the subgenus *Symphyomyrtus* and to the sections Exsertaria, Maidenaria and Transversaria, with the exception of *E. gomphocephala*, which is in section Bisectaria. Several other species surveyed in Tunisia, belonging to other sections or subgenera, did not have galls (Fig. 2). The three species found with galls in 2012, *E. camaldulensis*, *E. tereticornis* and *E. rudis*, group together in the section Exsertaria, series Exsertea and subseries: Camaldulensosae and Tereticornosae.

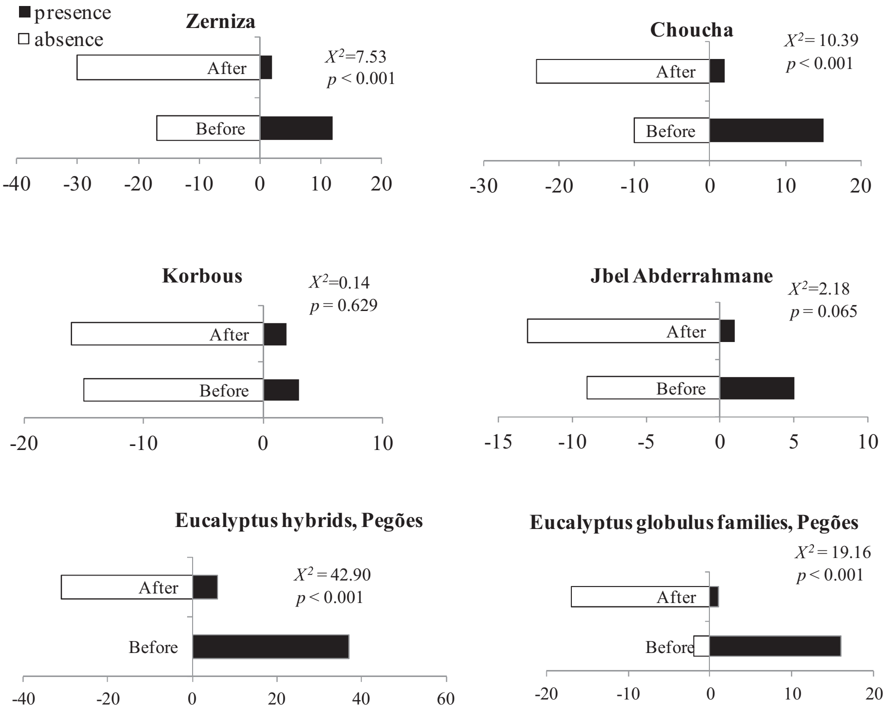

Fig. 1. Number of *Eucalyptus* species hybrids and families, with presence and absence of galls of *Ophelimus maskelli*, in four sites in Tunisia, and one site in Portugal (Pegões) during the two samplings periods, before (March–April 2008) and after (March–April 2011 and 2012) establishment of its parasitoid.

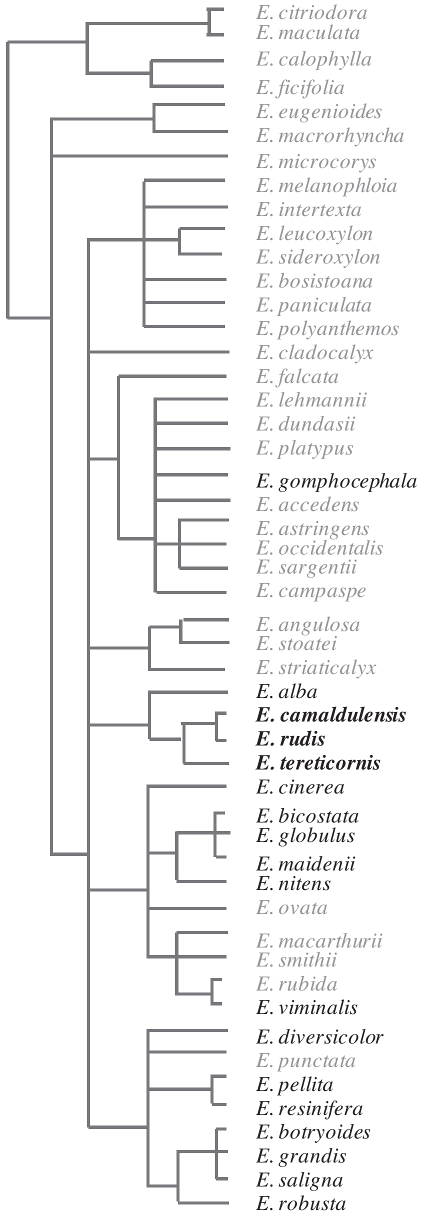

Fig. 2. Phylogenetic tree of the sampled *Euclayptus* species: in grey – without galls of *O. maskelli*; in black – with galls in 2008; in black and bold with galls in 2008 and 2012.

3.3. Infestation level

Considering the galled species at each site, there were differences in the intensity of galled leaves between the four sites in 2008 ($X^2 = 9822.8$, df = 3, $P < 0.001$), among species ($X^2 = 33206.3$, df = 17, $P < 0.001$) and there was a significant site by species interaction ($X^2 = 2136.5$, df = 14, $P < 0.001$). The percentage galled leaves was higher in Choucha, followed by Zerniza, next Korbous and finally by Jbel Abderrahmane (Fig. 3). The intensity of galled leaves still differed between sites ($X^2 = 26.9$, df = 3, $P < 0.001$) and species ($X^2 = 75.1$, df = 2, $P < 0.001$) for the three *Eucalyptus* species with galls sampled in 2012. *Eucalyptus camaldulensis* had a significantly higher proportion of attacked leaves than *E. rudis* or *E. tereticornis* ($X^2 = 37.06$, df = 1, $P < 0.001$); these two species had similar values ($X^2 = 0.725$, df = 1, $P = 0.394$). The levels of galling declined at all of the sites and for the three *Eucalyptus* species with galls between the two periods studied ($X^2 = 1939.4$, df = 1, $P < 0.001$) (Figs. 3 and 4).

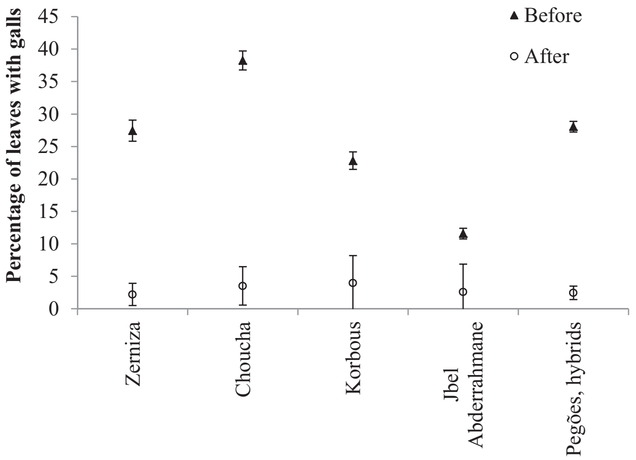

Fig. 3. Mean ± 95% CI percentage of leaves with galls of *Ophelimus maskelli* at four sites in Tunisia and one site in Portugal, Pegões: (surveyed March–April 2008, and March–April 2011 and 2012).

In Portugal in 2008, the 37 hybrid types differed in the proportion of galled leaves ($X^2 = 1597.6$, df = 36, $P < 0.001$) and these significant differences persisted among the six affected hybrids observed in 2011 (42.9, df = 5, $P < 0.001$). The six hybrids with galls in 2011 had lower infestation rates than those observed in 2008 ($X^2 = 444.5$, df = 1, $P < 0.001$), with the percentage of galled leaves declining from 44.4 ± 2.2% (mean ± SE) in 2008 to 3.5 ± 0.9% in 2011 (Fig. 5). In 2008, the intensity of galling within *E. globulus* half-sibling families was low, 6.5 ± 3.3%. In 2011 only one *E. globulus* family still had galls but in less than 1% of the leaves. In 2008 only *O. maskelli* emerged from the galled leaves. In 2011, both *C. chamaeleon* and *O. maskelli* emerged with following proportions 28:27, 53:5, 76:2, 11:0. Thus *C. chamaeleon* represented 51%, 91%, 97% and 100% of wasp emergences.

4. Discussion

The ERH suggests that populations of both plants and animals will grow rapidly in an invaded area when released from specialist natural enemies. Additionally, aggressive colonisation by invasive species can threaten native competitors, and reduce available resources, sometimes driving native species to local extinction (Kenis et al., 2009). The recent introduction of the gall wasp *O. maskelli* into the Mediterranean basin, followed 1–2 years later by its parasitoid *C. chamaeleon* (Protasov et al., 2007), provided an opportunity to study the indirect effect of the parasitoid on the host plants used by the herbivore. After the establishment of the parasitoid, the observed host range of the herbivore pest decreased across different taxonomic levels, i.e. galling declined by 83%, 84% and 96%, respectively on the number of eucalypt species, hybrids and families used. This significant decrease was observed at all of the study sites except Korbous. This was probably because, even in 2008, the intensity of galling, and the number of host plant species with galls, was already low, suggesting that the parasitoid was already well-established in this arboretum. Indeed, the parasitoid was first detected at an early stage of its introduction in the vicinity of Korbous (in Tunisia) in 2007 (Lo Verde et al., 2010).

The results support the hypothesis that in the absence of regulation by natural enemies, the high densities attained will result in an increase in the range of hosts used by an exotic herbivore, possibly due to movement onto marginal hosts because of intraspecific competition on preferred hosts. In these circumstances,

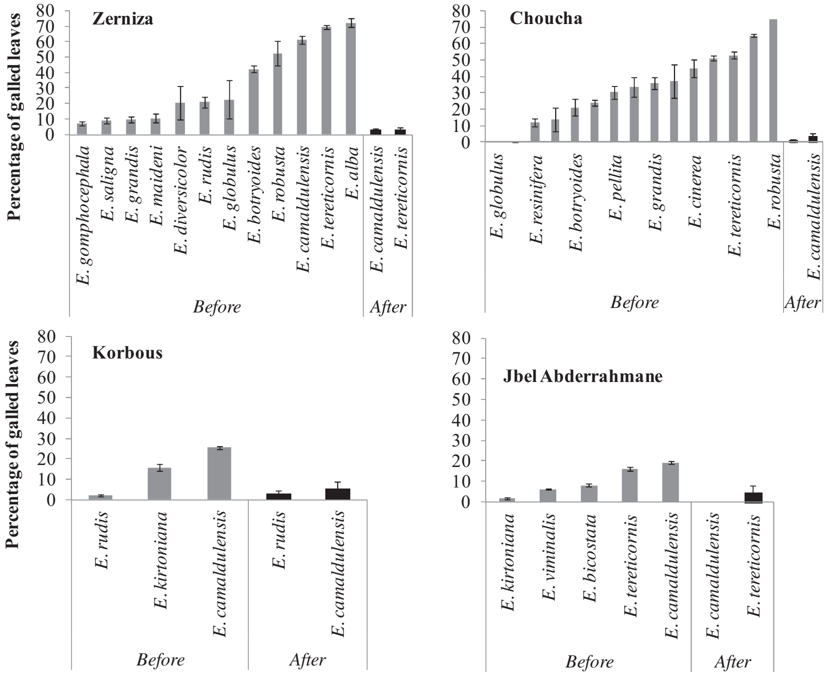

Fig. 4. Mean ± SE percentage of leaves galled by *Ophelimus maskelli* on *Eucalyptus* species exhibiting presence of the gall wasp at four sites in Tunisia before (March–April 2008) and after (March–April 2012) the arrival of the parasitoid.

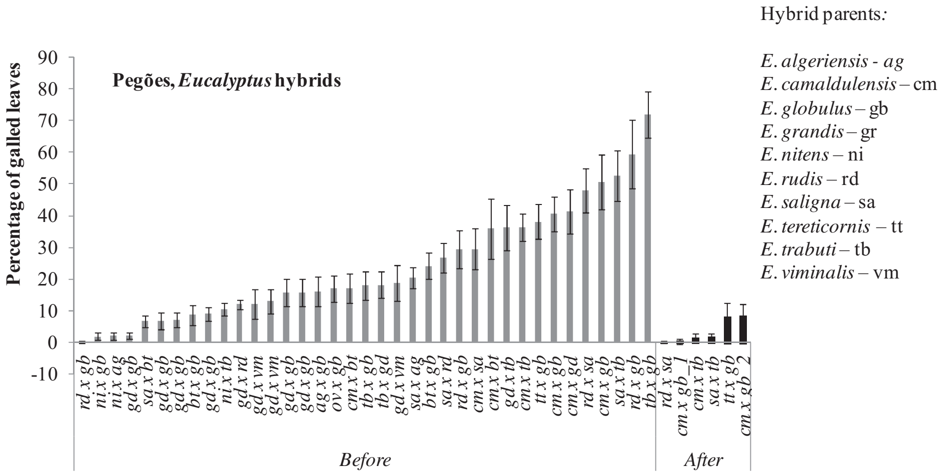

Fig. 5. Mean ± SE percentage of leaves galled by *Ophelimus maskelli* on *Eucalyptus* hybrids exhibiting presence of the gall wasp, in Pegões, Portugal: before (March 2008) and after (March–April 2011) parasitoid arrival.

exotic herbivores may use host plant species they do not normally use in their native range. As far as we are aware such modulation of host choice has not previously been reported on related gall wasps. Declines in the density of the host due to the natural enemy, may reduce intraspecific competition and allow the gall insect to develop solely on its usual host species. Our hypothesis is consistent with the foraging theory proposition that individuals tend to become generalists when intraspecific competition is high and preferred resources are scarce (Svanbäck and Bolnick, 2007). However, a population can only extend its diet range as far as it is able to cope with the morphological and physiological traits found in the new potential hosts. This likely limitation may explain why only 18 out of 50 species available were found with galls in 2008. With time, high competition in an enemy-free space may eventually lead to rapid evolution and adaptation to new host species as observed with novel contacts among alien species (Carroll et al., 2005).

An alternative explanation would be that galling on the least-preferred hosts could be undetectable with the sampling methods. In this case it is unlikely because sampling was intensive. About 40,000 leaves from each *Eucalyptus* species were inspected in the laboratory during the second period in Tunisia while for the *Eucalyptus* hybrids 25–50% of all the foliage was thoroughly scrutinised in the laboratory without any galls being observed on 31 of the hybrid types.

Before the establishment of the parasitoid, *Eucalyptus* species belonging to four sections, Bisectaria, Transversaria, Exsertaria and Maidenaria, had galls. However, under regulation by the parasitoid, *O. maskelli* narrowed the phylogenetic breadth of the host plants to only three closely related species: *E. camaldulensis*, *E.*

tereticornis and *E. rudis*, all of which belong to the series Exsertae, section Exsertaria. These species are most likely major natural hosts of the gall wasp in its native range showing specialization and an evolutionary history between *O. maskelli* and the series Exsertae. In fact, in an extensive survey of *O. maskelli* conducted in Australia to search for candidate biological control organisms, the gall wasp was observed only in *E. camaldulensis* and *E. tereticornis* (Mendel and Branco, pers. observations). Such high specialization agrees with the general understanding that gall-formers and gall-inducing insects, in particular, have extremely narrow host ranges (Abrahamson et al., 1998). Thus, our results further suggest that under regulation by natural enemies, there is a phylogenetic affinity in the host plants used by specialist herbivores.

Apart from the narrowing host range observed, in all studied regions the frequency of galled leaves by *O. maskelli* was significantly reduced on the preferred host species following the establishment of *C. chamaeleon*, showing it to be an effective agent of biological control. This was also observed by Protasov et al. (2007) and Caleca et al. (2011). Effectively, when successfully established, biological control agents may noticeably reduce damage caused by the target pest as observed for the biological control of: (i) alien insects affecting indigenous plant species, e.g. the scale insect *Iceria purchasi* (Mask) affecting native plant species in the Galapagos (Kenis et al., 2009); (ii) alien insects affecting their associated 'native' plant species when both are introduced into a new area, such as the control of the *Eucalyptus* defoliator *Gonipterus platensis* (Marelli) in Europe (Reis et al., 2012) and; (iii) of alien insects affecting alien plants from different origins, e.g., the control of the European wood wasp *Sirex noctilio* (F.) in *Pinus radiata* (D. Don) plantations in New Zealand (Morgan and Griffith, 1989).

In conclusion, the present study highlights that the ecological host range of herbivores is density dependent and therefore it can be modulated by the pressure imposed from third trophic level. This finding has practical consequences as the numbers of plant species used by herbivorous insects are expected to decrease under effective biological control. The present results provide further evidence that, in the absence of natural enemies, the restricted host range of specialist herbivores could expand to include new, phylogenetically distant, host species. Thus, the lack of natural enemies could play a role in plant-insect evolutionary history by promoting host diversification.

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