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Original Article

Introducing 3D-printed oak galls as artificial nests for arboreal ants, with first results on leaf damage reduction on olive trees

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Abstract

Gall formation in plants often imposes physiological costs from which secondary colonizers may benefit. Oak galls induced by *Andricus* wasps are later colonized by arboreal-nesting ants that may provide a service to the plant in anthropogenic environments. Trees in these environments frequently lack appropriate structures or deadwood to host arboreal-nesting ants. We constructed artificial galls of *Andricus quercustozae* using 3D printing and biomaterials to determine whether ants would colonize these structures and then tested whether colonization rates differed between natural and urban environments. We recorded a high colonization rate (> 90%) by five different ant species and found that leaf damage caused by *Otiorhynchus* weevil beetles and the leaf miner *Dasineura oleae* in agricultural olive trees equipped with artificial galls and colonized by the acrobat ant, *Crematogaster scutellaris,* was significantly less than in olive trees without ants. Hence, the use of artificial oak galls to promote ant colonization may represent a significant tool for agricultural pest management.

Key words: Hymenoptera, Formicidae, biostructures, artificial gall, new technology, *Andricus quercustozae*.

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Introduction

Galls are structures that develop on plants in response to a parasitic attack, often by insects. The attack on different points of the plant can inactivate reproductive areas, such as in the buds. However, secondary colonization of the galls can provide new ecological niches for some species, especially ants; for this reason, galls are regarded as a product of ecosystem engineering (Redfern & al. 2002, Stone & al. 2002, Wetzel & al. 2016). Oak galls, particularly those induced by *Andricus* cynipid wasps (Hymenoptera: Cynipidae) are often colonized by wood-nesting ants in temperate regions. Although galls may initially represent a physiological and energetic cost for the plant, secondary colonizers, such as ants, may ultimately offset this cost. Many ant species can provide different ecosystem services in both agroecosystems and urban environments, such as protection for the plants in which they live (Rico-Gray & Oliveira 2008, Del Toro & al. 2012, Anjos & al. 2022). Once active on the plants, they can prey upon many phytophagous insect species, discourage others with their presence and the pheromones they release, or even suppress some types of plant pathogens by releasing antibiotic substances (Offenberg & Damgaard 2019, Anjos & al. 2022, Offenberg & al. 2022). This also applies to oak trees with galls colonized by the acrobat ant *Crematogaster scutellaris* (Olivier, 1792) that suffer less damage from phytophagous insects and leaf pathogens (Giannetti & al. 2019). Ants themselves can also exert costs on the plants, for instance if their mutualistic partnership with honeydew-producing phytophagous insects (sometimes even sheltered inside galls, see Giannetti & al. 2021) causes their population to increase dramatically, and these costs may or may not be counterbalanced by the aforementioned benefits (Schifani & al. 2023a, 2024).

Ant species of several genera colonize galls, distinctively modify the gall's external and internal architecture, and utilize the galls as either their main nest or a satellite nest in polydomous species (Giannetti & al. 2019, 2022a). This appears similar to the domatia produced by myrmecophyte plants, with special structures that allow ant colonies to settle on the plant and provide them subsequent benefits (Giannetti & al. 2019). In managed environments such as agricultural or urban settings, there can be a scarcity

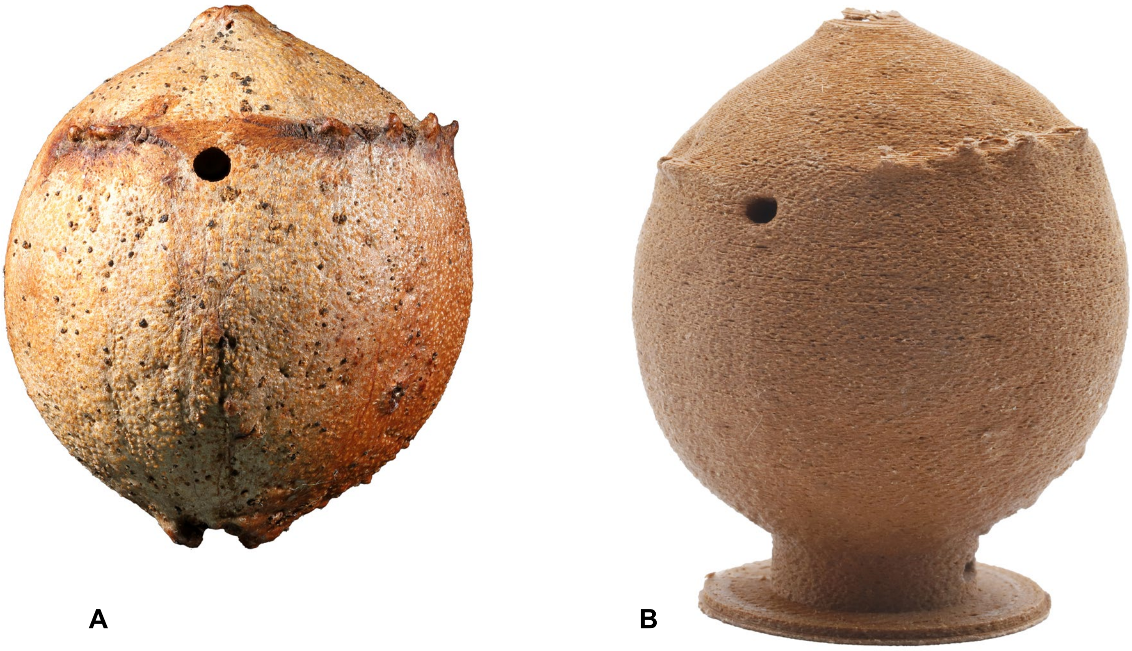

Fig. 1: (A) Natural gall of *Andricus quercustozae*; (B) artificial gall created with 3D printing. Scale bar: 0.5 mm.

of deadwood (on the ground or trees) that offers crucial nesting sites for ecologically impactful wood-nesting ants (Philpott & Foster 2005). One solution is to provide artificial nesting sites that allow wood-nesting ant colonies to develop (Philpott & Foster 2005).

Here, we aimed to produce an artificial reproduction of *Andricus quercustozae* oak galls using 3D printing technology and biomaterials and to test its effectiveness as an artificial ant nest in a natural environment with the co-presence of natural oak galls, and in an urban environment in which oak galls do not occur. Finally, we tested their use by introducing already colonized galls in an agricultural context and recording the effects of ant activity on olive trees (*Olea europaea*).

Material and methods

Designing of artificial galls: photogrammetry, 3D printing, and stress test

A total of 50 galls of *Andricus quercustozae* were collected in the field as a basis to develop artificial galls. A 3D image of the model gall was created by taking 100 images of a natural *A. quercustozae* gall using an EOS 6 DMARK II + 100 mm Canon Macro 2.8 (Tokyo, Japan). Galls were placed on a rotating platform located inside a cube box (Fig. 1A). A 3D printer (Fused Deposition Modeling) FLSun Super Racer with a direct extruder and a 0.6 mm volcano-type stainless steel nozzle was used to construct the artificial gall (Fig. 1B; Appendix 1 >> Video S1, as digital supplementary material to this article, at the journal's web pages). The artificial gall was made from fir wood using a 1.75 mm BIO Extrudr (Lauterach, Austria) wood filament. The product is biodegradable according to DIN EN ISO 14855. The printing parameters were the following: layer height 0.12 mm, printing temperature 200 °C (210 °C for the initial layer), print bed temperature 67 °C (72 °C for the initial layer), flow rate 108%, printing speed 55 mm / s (for empty galls) and 50 mm / s (for galls with chambers), fan speed 70%, and fill density 20%. The maximum size of natural galls of *A. quercustozae* was 41 × 43 mm; however, to optimize the printing process due to the extruder and improved printing efficiency, a size of 44 mm × 46 mm was used instead (i.e., a 10% increase in width and 7% in height), as well as an average value for the entrance hole of 2.5 mm (Fig. 2D). Because of the increase in size, the internal chamber was 3 cm^3 instead of 1 cm^3 of natural galls (Giannetti & al. 2019). Two types of galls were created following Giannetti & al. (2019), which were aimed at imitating two different conditions observed in the natural dynamics of gall secondary colonization. The gall with chamber had a smaller internal chamber similar to galls with no secondary colonization by ants (Fig. 2A). The gall without chamber simulated galls where the internal material of the gall was removed by an ant colony of *Crematogaster scutellaris* (Fig. 2B). To maintain a 40-minute printing time per piece, thicknesses of 1 mm and 2 mm for each wall were tested. To facilitate positioning in the field under different conditions, a cylinder (18 mm × 5 mm) with a passage hole (2 mm) (Fig. 2C) and a support base (diameter = 27 mm) was created in the lower portion of the galls, useful for securing the galls with bands.

The optimal thickness necessary to ensure resistance and minimize printing time was assessed by subjecting artificial galls to two stress tests and determined to be between 1 and 2 mm. Galls were dropped from a height of 2 meters (n = 20) or compressed with a 2 kg weight for one minute (n = 20). The structural integrity of the nest and the presence of any fractures or cracks were evaluated.

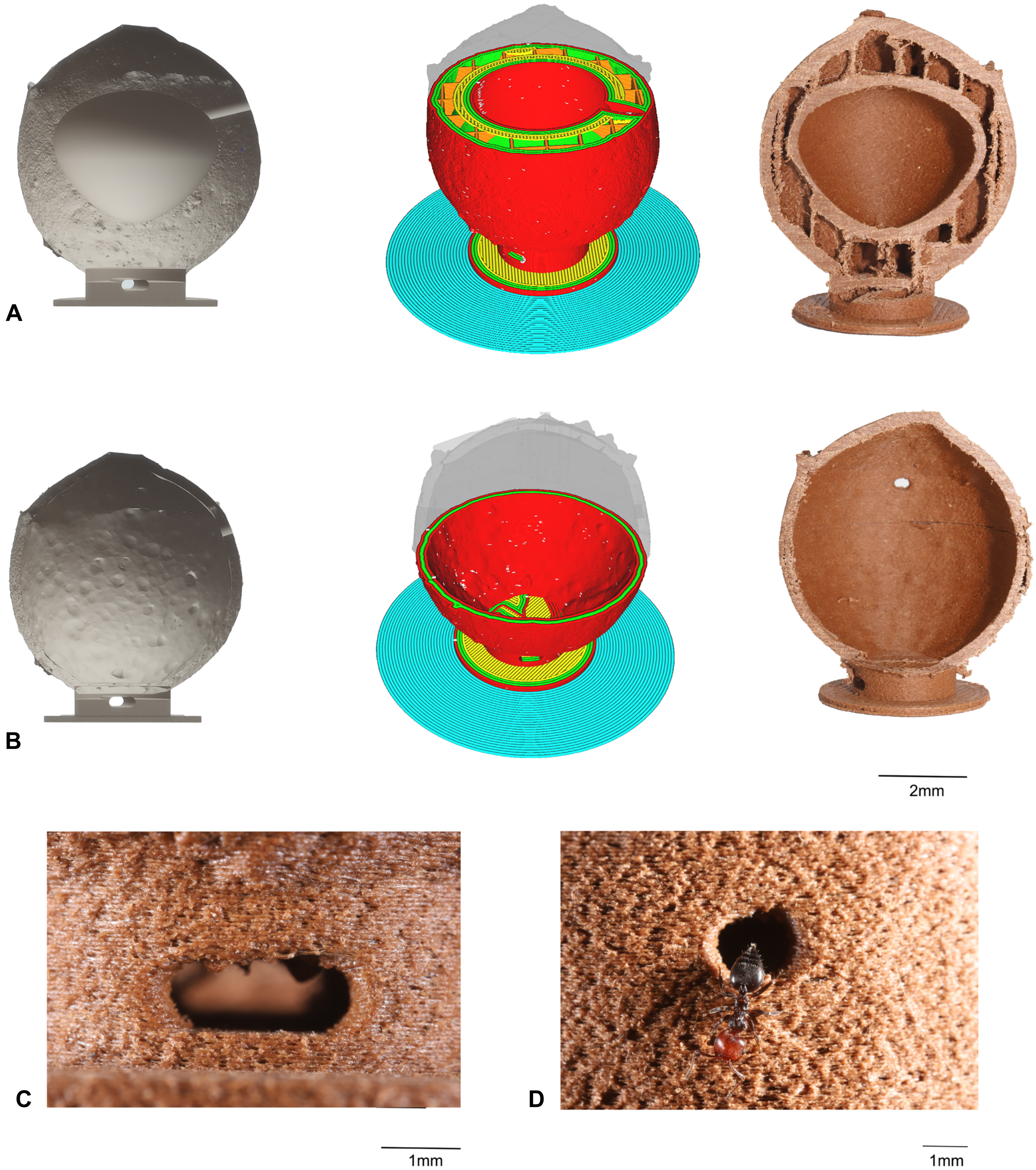

Fig. 2: Structure of artificial galls. (A) gall with chamber (3 cm³); (B) gall without chamber; (C) base fixing hole for fixing the galls on the plants with cable ties or on the ground using pickets; (D) entry hole, with a worker of *Crematogaster scutellaris*.

No cracks or structural failures from the stress tests were found in galls that were 2 mm thick, while 100% of the 1 mm thick galls were damaged. Hence, only galls that were 2 mm thick were used for the experiments.

The project of artificial galls has led to the filing of a patent (Giannetti & Grasso 2023).

Study areas

The study was conducted in two areas, representing natural and urban sites. The natural sites were near the village of Fornoli (Tuscany, Italy) (44° 15' 16.9164" N, 9° 58' 7.7844" E; 44° 15' 17.9352" N, 9° 58' 12.0504" E) where oak trees naturally host *Andricus quercustozae*. In a preliminary survey, we identified ten oak trees with galls already colonized by *Crematogaster scutellaris*, ten additional trees whose galls were empty and were sealed with sticky barriers to prevent ant colonization, following the same method of Giannetti & al. (2019), and ten plants without galls.

The urban sites were in the city of Parma (Emilia-Romagna, Italy), in five selected green areas at least one km apart. In each area, we selected oak trees without galls. The five green areas were the following: Parco Ducale Parma (44° 48' 22.0248" N, 10° 19' 4.7928" E),

Fig. 3: Artificial galls on plants (A) and on the ground (B). Colonization of artificial galls by a queen of *Colobopsis truncata* (C) and a queen of *Crematogaster scutellaris* (D). Complete colony of *Dolichoderus quadripunctatus* (E).

Parco Cittadella (44° 47' 31.3368" N, 10° 19' 56.154" E), Parco Bizzozzero (44° 47' 16.9332" N, 10° 19' 50.4768" E), Parco Torre Pelpira (44° 46' 40.1844" N, 10° 19' 15.9996" E), and Parco Giacomo Ferrari (44° 47' 27.5784" N, 10° 20' 19.0716" E).

Gall colonization experiments

On 1 March 2022, a set of 80 artificial galls was placed on 20 different oak trees without galls, equally divided between the natural and the urban site. On each of the previously identified trees without natural galls, four artificial galls were placed (two per model; Fig. 3A) at an approximate height of two meters and a distance of at least 50 cm from one another. In addition, 40 artificial galls were placed on the ground (Fig. 3B) at the base of each tree to evaluate the colonization rate by ground-dwelling ants, 20 cm from one another and fixed with a metal peg. At the beginning of the experiment, these empty natural galls that were previously sealed were opened to allow ant colonization. After six months on 1 September 2022, all galls were collected. Each gall was then cut into two and the content of all galls (artificial and natural) was analyzed to check whether galls had been colonized by ants and which ant species colonized them. All specimens collected in the study area were examined under a Zeiss (Oberkochen, Germany) Stemi 508 stereoscopic microscope (5 - 200 magnification range) with the support of an Axiocam Erc 5 s and ZEISS ZEN core software used to take morphometric measurements. Ants were identified according to the keys provided by SEIFERT (2018).

Use of artificial galls for plant defense

A total of 22 plants of *Olea europaea* were selected close to the collection field station. The plants were approximately four years old, had 34 to 44 leaves each and were planted 10 m from each other. These were divided into two treatments (with ants and without ants), each consisting of 11 experimental plants.

Artificial galls (n = 22) which had been previously colonized by *Crematogaster scutellaris* ants were placed on half of the olive trees on 1 March 2023 and removed on 1 August 2023. On the remaining half of the trees (control group), 22 empty galls were placed instead; sticky barriers were used at the base of the stems to prevent ants from accessing these trees.

From June to August 2023, 10 scan samplings (one per week on all 22 plants) were used to check for the presence of phytophagous insects on plants. In addition, the number of damaged leaves (chewing damage), was counted at the end of the experiment, and all galls were removed to verify ant presence and number inside.

Statistical analyses

Statistical analyses were performed using IBM SPSS software (v.29). Colonization rate and gall selections (with a chamber and without a chamber) were assessed using Chi-square tests. One-way ANOVA tests were used to evaluate the differences between plants with and without ants concerning all the characteristics quantified. All data are given as mean ± standard error, degrees of freedom of Chi-squared tests are given as subscript numbers in parentheses. The significance threshold was set at $\alpha = 0.05$.

Results

Gall colonization experiments

In the natural area, there were no significant differences in the type of artificial gall that ants colonized ($\chi^2_{(1)} = 1.84$, $p = 0.187$). Ants colonized 95.0% of galls with a chamber and 97.5% of galls without a chamber (Tab. 1). We observed five ant species that colonized both types of galls: *Camponotus fallax* (NYLANDER, 1856), *Colobopsis truncata* (SPINOLA, 1808) (Fig. 3C), *Crematogaster scutellaris* (OLIVIER, 1792) (Fig. 3D; Appendix 2 >> Video S2), *Dolichoderus quadripunctatus* (LINNAEUS, 1771) (Fig. 3E), and *Temnothorax italicus* (CONSANI, 1952); a preference was observed only for *D. quadripunctatus*, colonizing galls with a chamber significantly more often (Tab. 1; Tab. S1).

Natural galls were colonized less often than artificial galls (52.5% instead of 95%, $\chi^2_{(1)} = 37.32$, $p < 0.001$). The ant species encountered were the same as in the previous experiments, except for *Colobopsis truncata* and with the addition of *Camponotus lateralis* (OLIVIER, 1792) (Tab. S2).

Tab. 1: Data on ant colonization of artificial galls in a natural area. Chi-squared tests were used to assess the preference for galls with or without chamber by the five ant species collected.

	Field area		
	Colonization rates of gall types		
Species	With chamber	Without chamber	**Statistical output**
Crematogaster scutellaris	47.5%	62.5%	$\chi^2_{(1)} = 0.57$, $p = 0.326$
Colobopsis truncata	17.5%	22.5%	$\chi^2_{(1)} = 0.208$, $p = 0.428$
Dolichoderus quadripunctatus	22.5%	2.5%	$\chi^2_{(1)} = 3.92$, $p = 0.01$
Temnothorax italicus	5.0%	7.5%	$\chi^2_{(1)} = 0.188$, $p = 0.511$
Camponotus fallax	2.5%	2.5%	$\chi^2_{(1)} = 0$, $p = 1$

Tab. 2: Data on ant colonization of artificial galls in an urban area. Chi-squared tests were used to assess the preference for galls with or without chamber by the five ant species collected.

	Urban area		
	Colonization rate of gall types		
Species	With chamber	Without chamber	**Statistical output**
Crematogaster scutellaris	47.5%	25.0%	$\chi^2_{(1)} = 4.38$, $p = 0.031$
Camponotus lateralis	5.0%	12.5%	$\chi^2_{(1)} = 1.40$, $p = 0.235$
Colobopsis truncata	20.0%	2.5%	$\chi^2_{(1)} = 6.13$, $p = 0.029$
Dolichoderus quadripunctatus	42.5%	12.5%	$\chi^2_{(1)} = 9.02$, $p = 0.03$

For ground-level galls (Fig. 3B), we recorded a 52.5% colonization rate for empty galls and 40% for galls with a chamber, with the presence of seven species (Tab. S3). As above, *Crematogaster scutellaris* was the species most present with a 35% colonization rate for galls without a chamber, and 40% for galls with a chamber; no difference was recorded in gall preference $\chi^2_{(1)} = 0.952$, $p = 0.232$. We detected the presence of four incipient colonies of *Lasius fuliginosus* and two colonies of the rolling ant *Myrmecina graminicola* (see Grasso & al. 2020).

In the urban area, we recorded a high colonization rate of 77.5% for empty galls and 88.5% for galls with a chamber, featuring the presence of four species (Tab. 2). As above, the most present species was *Crematogaster scutellaris* which preferred galls with a chamber significantly over empty galls (47.5% vs. 25%, $\chi^2_{(1)} = 4.38$, $p = 0.031$). Moreover, compared with galls in natural settings, we recorded a significant difference in the choice of galls by *Dolichoderus quadripunctatus* ($\chi^2_{(1)} = 9.02$, $p = 0.03$), with a preference for galls with a chamber (42.5%), as opposed to empty galls (12.5%) (Tab. 2; Tab. S4).

For ground-level galls, we recorded the lowest colonization rate of 30% for empty galls and 20% for galls with a chamber (Tab S5). A total of 52.5% of the galls were destroyed, likely due to human vandalism or the actions of pets.

Use of artificial galls for plant defense

We found phytophagous weevil beetles *Otiorhynchus* spp. (Coleoptera, Curculionidae) on the experimental plants, and their abundance was significantly affected by treatment ($F_{1,21} = 24.82$, $p < 0.001$), with a higher number of weevil beetles occurring on plants without ants (4.36 ± 0.57 individuals) as compared with plants with ant-colonized galls (1.09 ± 0.31 individuals). There was also a significant difference in the number of leaves showing chewing damage ($F_{1,21} = 33.08$, $p < 0.001$), with a higher number of leaves affected in the absence of ants (11.27 ± 0.97 individuals) as compared with plants with ant-colonized galls (4.36 ± 0.70 individuals) (Fig. 4A). Finally, there was also a significant difference between treatments regarding the damage inflicted by *Dasineura oleae* (Diptera, Cecidomyiidae) ($F_{1,21} = 80.43$, $p < 0.001$), with a higher number of leaves exhibiting damage in the absence of ants (26.18 ± 1.10 individuals) compared with plants with ant-colonized galls (13.0 ± 0.97). The average number of ants per gall was 156.86 (± 5.3) (Fig. 4B).

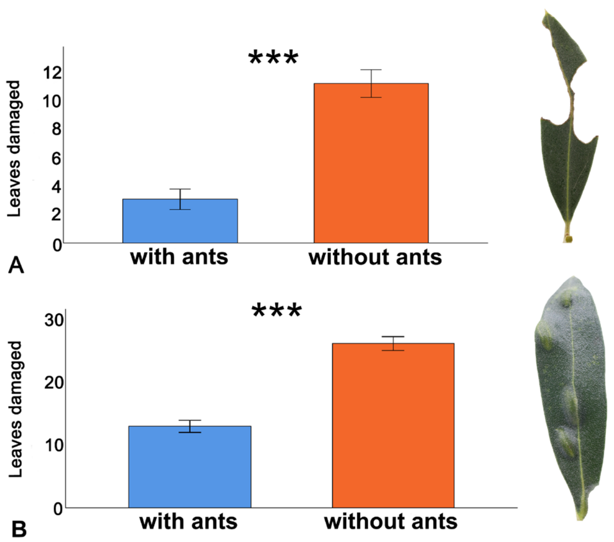

Fig. 4: Effects of ant-colonized galls on olive leaves damaged by weevil beetles (A) and on olive leaves damaged by *Dasineura oleae* (B). Asterisks indicate statistical significance of the differences (*** for p < 0.001). Whiskers indicate standard error.

Discussion

Biomimetics is an emerging field with multiple potential applications that has been mostly explored in the biomedical field so far, where 3D printing constitutes an important tool to process biomaterials and promote their adaptation to the human body (Raheem & al. 2021). In entomology, 3D printing has allowed the creation of wing models mimicking different insect species to study insect flight (Richter & al. 2011, Salami & al. 2016, Saito & al. 2021) and the creation of artificial coffee berries to study the predation of cryptic phytophagous insects that spend most of their life cycle inside host plants (Liang & al. 2023). Ecological examples of biomimetics and 3D printing include the creation of artificial reefs to support marine biodiversity (Berman & al. 2023), but we are not aware of similar attempts concerning insect colonization.

Here, we present the first application of biomimetics to produce artificial galls mimicking a special structure that various species of ants naturally use to establish their colony on plants and in some cases even on the ground (Giannetti & al. 2019, Grasso & al. 2020).

Habitat loss or degradation are key factors driving declines in animal populations worldwide. One potential approach for mitigating these threats is to create artificial habitat structures as substitutes for lost or degraded natural structures (Watchorn & al. 2022). Currently, systems used to promote ant presence by offering artificial nesting sites have been utilized particularly in tropical agroforestry systems, using wooden and bamboo sticks (Philpott & Foster 2005, Jiménez-Soto & Philpott 2015). In this context, the use of artificial galls can be a useful strategy to address this issue for several species of ants in both natural and anthropogenic environments. We demonstrated a high rate of ant colonization of artificial galls even in urban environments with the presence of different species. Previous studies have described the positive effect of promoting the presence of ants in natural and agricultural settings, increasing the benefits of the ecosystem services they offer, such as seed dispersal, soil enrichment, scavenging of urban food waste, and pest control (e.g., Sandford & al. 2009, Offenberg 2015, Hosaka & al. 2019, Schifani & al. 2020, Giannetti & al. 2022b, c, Perfecto & Philpott 2023, Anjos & al. 2022).

In our testing on agricultural plants, deploying artificial galls already inhabited by ants led to a protective effect on olive plants against weevil beetles and the midge *Dasineura oleae*, a rapidly expanding olive pest (TONDINI & al. 2023). Ants may interfere with both phytophagous insects by direct and indirect interactions, and artificial galls could be implemented in biological control strategies in the future. In the case of *D. oleae*, ants could have either disrupted the egg-laying process (GONZÁLEZ-TEUBER & al. 2014, GRASSO & al. 2015) or attacked the emerging adults (BATTA 2019). Moreover, the results show the positive effect of ants in reducing the number of *Otiorhynchus* spp. presence on the leaves and the number of damaged leaves. This genus is characterized by polyphagous insects that could lay eggs on both the leaves and the soil surface. Root-feeding larvae are also polyphagous and cause considerable damage including the death of the plant (MOORHOUSE & al. 1992, 1993, CLARK & al. 2012). Hence, the present study further supports the effectiveness of ants as plant defenders against phytophagous enemies and so even their role, at least in certain circumstances, in sustainable agro-forestry (GIANNETTI & al. 2021). The defensive outcome may follow from the deterrent effect of ant presence and patrolling on other insects or from direct attacks on phytophagous arthropods or their eggs (BRONSTEIN 1998, HEIL & MCKEY 2003, GRASSO & al. 2015, SCHIFANI & al. 2020, 2023b, c). Increased ant presence may also imply an enhanced predatory role of ants on the ground in addition to their effect on the plants (CAMPOLO & al. 2015).

Further implementations of artificial nests are in progress for applications in different contexts. In fact, artificial galls may serve as a tool to increase ant activity on plants for agricultural purposes, to easily transfer ant colonies from plant to plant, and to promote ant colonization in anthropogenic environments as well as a new experimental tool for research on several still "hidden" aspects of ant biology, ecology and behaviour.

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Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence tools in any part of the composition of this manuscript.

Conflicts of interest

The authors have no conflict of interest to declare.

Data availability

The data that support the findings of this study can be found inside the text or are available from the corresponding author upon reasonable request.

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