

Indirect effects of tending ants on holm oak volatiles and acorn quality

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The indirect effect of ants on plants through their mutualism with honeydew-producing insects has been extensively investigated. Honeydew-producing insects that are tended by ants impose a cost on plant fitness and health by reducing seed production and/or plant growth. This cost is associated with sap intake and virus transmissions but may be overcompensated by tending ants if they deter or prey on herbivorous insects. The balance between cost and benefits depends on the tending ant species. In this study we report other indirect effects on plants of the mutualism between aphids and ants. We have found that two *Lasius* ant species, one native and the other invasive, may change the composition of volatile organic compounds (VOCs) of the holm oak (*Quercus ilex*) blend when they tend the aphid *Lachnus roboris*. The aphid regulation of its feeding and honeydew production according to the ant demands was proposed as a plausible mechanism that triggers changes in VOCs. Additionally, we now report here that aphid feeding, which is located most of the time on acorns cap or petiole, significantly increased the relative content of linolenic acid in acorns from holm oak colonized by the invasive ant. This acid is involved in the response of plants to insect herbivory as a precursor or jasmonic acid. No effect was found on acorn production, germination or seedlings quality. These results suggest that tending-ants may trigger the physiological response of holm oaks involved in plant resistance toward aphid herbivory and this response is ant species-dependent.

To achieve an indirect effect it is necessary to have a minimum of three species, two focal species that interact directly and an associate species whose presence promotes an indirect effect on one or both focal species. In general, indirect effects of a third species are defined by how and to what degree a pairwise species interaction is influenced by the presence and density of this third species.¹ There are several examples of interactions presenting indirect effects: apparent competition,¹ facilitation,² tri-trophic level interactions,³ cascading effects⁴ and exploitative competition.⁵ But, indirect effects have been studied most extensively in the context of trophic cascades when top predators are removed⁶ or added⁷ and in the context of mutualisms.⁸⁻¹⁰ Usually, indirect effects are investigated as changes in abundance of the focal species occur. However, indirect effects may result in biologically significant changes in a species that are not reflected only to its abundance.¹¹ There are many examples of changes in physiology, behavior, morphology and/or genotypic composition of the focal species.^{11,12} These changes on density and/or morphological, physiological and behavioral traits of the focal species are not mutually exclusive, and all can act at the same time.¹³ The magnitude and direction of both direct and indirect effects should influence the relative resilience of communities to perturbation, which in turn will affect species coexistence and community evolution.¹⁴ In this regard, indirect effects had been postulated as one of the main forces structuring communities² and shaping the evolution of communities.¹⁴

In terrestrial communities ants interact with plants both directly and indirectly.

Key words: tended aphid, invasive ants, linolenic acid, jasmonic acid, monoterpene emissions

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Table 1. Means and standard error of the emission rates of the main compounds emitted by *Quercus ilex* saplings (n = 4 for T1 and T2 and n = 8 for T3) infested with untended aphids (T1) or infested with aphids tended by the native ant *Lasius grandis* (T2) or by the invasive ant *Lasius neglectus* (T3)

Compound	Emission rates: $\mu\text{g g}^{-1}\text{h}^{-1}$ above and $\text{nmol m}^{-2}\text{s}^{-1}$ below		
	T1 Non tended	T2 Tended by native ant	T3 Tended by invasive ant
α -Thujene	0.007 \pm 0.004 ^a 0.006 \pm 0.004 ^a	0.015 \pm 0.005 ^a 0.006 \pm 0.003 ^a	0.005 \pm 0.001 ^a 0.009 \pm 0.008 ^a
α -Pinene	0.391 \pm 0.182 ^a 0.244 \pm 0.139 ^a	2.072 \pm 0.033 ^b 0.532 \pm 0.082 ^a	0.551 \pm 0.105 ^a 0.244 \pm 0.127 ^a
Camphene	0.007 \pm 0.003 ^a 0.005 \pm 0.003 ^a	0.047 \pm 0.014 ^b 0.014 \pm 0.004 ^a	0.012 \pm 0.004 ^{ab} 0.007 \pm 0.004 ^a
Sabinene	0.084 \pm 0.042 ^a 0.100 \pm 0.076 ^a	0.387 \pm 0.045 ^b 0.210 \pm 0.097 ^a	0.075 \pm 0.017 ^a 0.128 \pm 0.107 ^a
β -Pinene	0.227 \pm 0.105 ^a 0.159 \pm 0.097 ^a	1.454 \pm 0.269 ^b 0.322 \pm 0.134 ^a	0.306 \pm 0.075 ^a 0.179 \pm 0.097 ^a
Myrcene	0.443 \pm 0.057 ^a 0.101 \pm 0.034 ^a	0.482 \pm 0.044 ^a 0.119 \pm 0.026 ^a	0.093 \pm 0.020 ^b 0.060 \pm 0.034 ^a
Δ^3 -Carene	0.003 \pm 0.002 ^a 0.001 \pm 0.001 ^a	0.018 \pm 0.001 ^b 0.004 \pm 0.001 ^a	0.010 \pm 0.003 ^{ab} 0.002 \pm 0.001 ^a
α -Terpine	0.004 \pm 0.001 ^a 0.001 \pm 0.000 ^a	0.003 \pm 0.001 ^a 0.004 \pm 0.003 ^a	0.001 \pm 0.000 ^a 0.001 \pm 0.001 ^a
γ -Terpinene	0.012 \pm 0.002 ^a 0.003 \pm 0.001 ^a	0.011 \pm 0.004 ^a 0.013 \pm 0.010 ^a	0.013 \pm 0.005 ^a 0.006 \pm 0.003 ^a
Terpinolene	0.001 \pm 0.000 ^a 0.001 \pm 0.000 ^a	0.002 \pm 0.001 ^a 0.002 \pm 0.001 ^a	0.005 \pm 0.002 ^a 0.001 \pm 0.001 ^a
Leaf mass (g)	0.001 \pm 0.000 ^a	0.002 \pm 0.001 ^a	0.005 \pm 0.002 ^a
Leaf area (m ²)	0.104 \pm 0.005 ^a	0.146 \pm 0.026 ^a	0.113 \pm 0.006 ^a

The emission rate were compared first by Kruskal-Wallis test. Values given above were calculated as $\mu\text{g g}^{-1}\text{h}^{-1}$, while values below were calculated as $\text{nmols m}^{-2}\text{s}^{-1}$. At the last row, leaf morphology is shown for each treatment. Different letters indicate statistical differences of multiple non parametrical post hoc comparisons (Dunn's test, $p < 0.05$).

They can disperse or consume seeds, feed from specialized plant structures such as food bodies and extrafloral nectaries, act as or deter pollinators, prey on herbivorous insects and/or develop mutualisms with honeydew-producing insects indirectly modifying plant fitness.¹⁵⁻¹⁷ Additionally, through their nesting activities in soil, ants increase soil nutrient content available to plants, may change water infiltration and soil holding-capacity and modify biodiversity and abundance of soil organisms related to the decomposition process.^{18,19} As a consequence of their activities, ants may thus change behavior, density, physiology or fitness of other species.^{12,22,23} In the case of ants that tend honeydew-producing insects, evidence shows that their attention may change some traits of insect life history,²² their abundance or physiology.¹⁸ For the plant, the net outcome of the mutualism between ants and honeydew-producing

insects will depend on the balance between the costs for plant fitness via consumption of plant sap and transmission of plant pathogens and the benefit of ants deterring herbivorous insects.^{18,23} As a consequence, plant seed production, pod production or even plant growth may decrease when the cost of honeydew-producing insects exceed the benefit provided by tending ants.^{18,23}

Recently, we have described the changes that two tending ant species may exert indirectly on monoterpene emissions of holm oak (*Quercus ilex*) saplings through its mutualism with *Lachnus roboris* aphids.²⁴ One of these tending ant species was *Lasius neglectus*, an invasive ant species that displaces the local ant *Lasius grandis*. We found that aphids feeding on holm oak increased the emission of total volatile organic carbon (VOCs) by 31%. In particular, aphids feeding elicited the emission of a new monoterpene, Δ^3 -carene, and

increased the emission of myrcene (mean \pm SE; sapling alone: $0.105 \pm 0.011 \mu\text{g g}^{-1}\text{h}^{-1}$; sapling plus not tended aphid: $0.443 \pm 0.057 \mu\text{g g}^{-1}\text{h}^{-1}$) and γ -terpinene (sapling alone: 0.0013 ± 0.0001 ; sapling plus not tended aphid: $0.0122 \pm 0.0022 \mu\text{g g}^{-1}\text{h}^{-1}$) (Mann-Whitney, sapling alone vs. sapling plus not tended aphids, $U_{4,4} = 0$, $p < 0.05$ for both compounds). Changes of VOC emission in response to aphid infestation were noticed also in boreal trees.²⁴ When the aphids became tended by the invasive ant, *L. neglectus*, VOCs emissions increased only 19% because myrcene, the main compound of the blend, decreased significantly (Table 1). On the contrary, the native ant, *L. grandis* promoted a 400% increase of total VOCs compared to the situation of not tended aphids. The astonishing increment of VOCs was due to the increase of α - and β -pinene, sabinene, camphene and Δ^3 -carene (Table 1). We suggested that the aphids' regulation of their feeding and honeydew production according to ant attention could explain these results.²⁵ When our data was recalculated on leaf area basis ($\text{nmol m}^{-2}\text{s}^{-1}$), the general pattern was the same independently of the units, but the differences among treatments were not statistically significant (Table 1). The change of statistical differences depending on which unit basis data VOC emissions are calculated has been reported in other studies also in holm oaks.²⁶ These slight differences in the statistical significance of the differences of VOC emissions depending on the reference unit may be due to differences in leaf morphology, i.e., changes of leaf area and mass. However, in our study, all holm oaks showed a similar leaf morphology among treatments (Kruskal-Wallis, leaf mass: $H_{3,20} = 2.16$, $p = 0.53$; leaf area: $H_{3,20} = 2.64$, $p = 0.45$) (Table 1). Leaf area and mass may be also modified by aphid feeding. But the few studies that reported the effect of aphids feeding on leaf area and mass showed either decreases or no changes with aphid feeding.^{24,27} This lack of consistence of aphid effect on leaf area and mass limits the development of a clear pattern linking aphids feeding, leaf area or mass and VOC emissions. On the other hand, to achieve statistical significance of emitted VOCs among treatments, values should differ strongly given the high variability of VOC emission within

treatments.²⁶ Under this scenario, we recommend giving the values of leaf morphology and to give VOC emissions on both unit bases to facilitate comparisons among different studies.

The tended aphid, *Lachnus roboris*, feed most of the time on the petiole or on the cap of acorns of holm oaks.²⁸ Therefore, acorn quantity and quality (lipid content) and seedlings quality could be affected by tending ants through their mutualism with aphids. We analyzed lipid content as an estimator of acorn quality. Lipids and starches are synthesized in acorns from carbohydrates translocated from leaves.²⁹ However, before being used for metabolic functions, lipid content of acorns must be transformed into glucids and then can be used as respiratory substrate during germination.²⁹ As a consequence, when aphids suck sap from acorns they may act as a sink of translocated carbohydrates, thus decreasing the amount that reaches the seeds.³⁰

During two consecutive years, we counted all acorns from one branch (8–11 cm diameter) for each one of 6 holm oaks colonized by *L. neglectus* and 6 holm oaks colonized by *L. grandis* that we studied. We followed them at different stages of their development (July, September and December). Among holm oaks, the loss of acorn production varied between 87.9–96.8%. Acorn production (acorns that started to develop and reached maturity) did not differ between the tree colonized by one or another ant species (mean number of acorns per branch \pm SE, 2003: *L. neglectus* trees: 2.67 ± 1.38 , *L. grandis* trees: 2.67 ± 2.01 ; Mann Whitney, $U = 15$, $p = 0.69$; 2004: *L. neglectus* trees: 35.83 ± 19.23 , *L. grandis* trees: 49.80 ± 27.99 ; Mann Whitney, $U = 12$, $p = 0.66$). The only work in which researchers evaluated the effect of ants on acorn production was conducted by Ito and Higashi.³¹ These authors showed that the acorn production of *Quercus dentata* in the presence of the tending ant *Formica yessensis* did not differ either. However, there was a significantly lower proportion of infested acorns with weevil larvae when *Formica yessensis* were tending aphids.³¹ So, ants may indirectly increase the probability that acorns reach the maturity in healthy conditions, improving in this way one component of

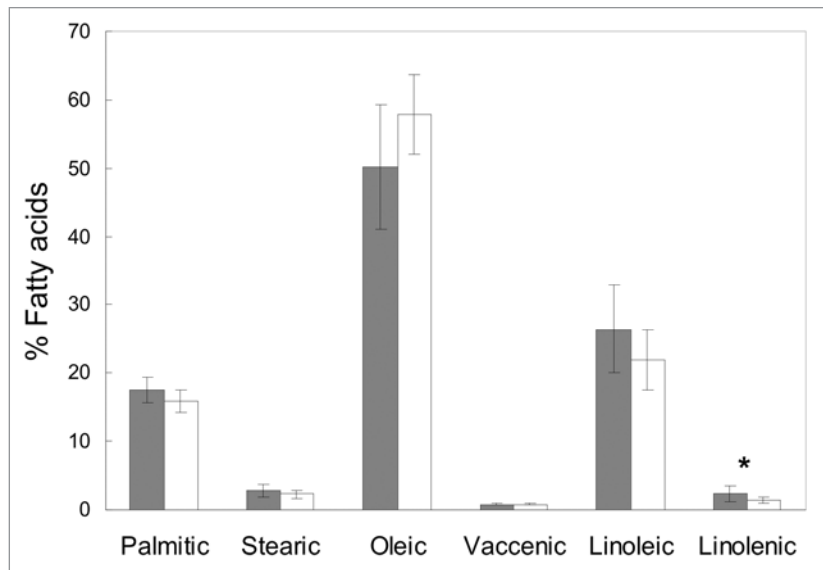


Figure 1. Mean (\pm SE) of the percentage of each fatty acid relative to the total amount of fatty acids of acorns from holm oaks colonized by invasive ants *L. neglectus* (in grey) or by native ants *L. grandis* (in white). Asterisk shows significant differences of linolenic content (Mann Whitney, $U = 7.5$, $p = 0.026$).

the fitness of the oak. In the case of the larvae of weevils, wasps and moth species that infest holm oak acorns³² during their development, they do not move to other acorn as in the case reported by Ito and Higashi.³¹ This behavior prevents ant predation during the move from one acorn to another.

Lipid content of acorn cotyledons was analyzed by gas chromatography-flame ionization detector (FID) after performing the derivatization of lipid acids to methyl esters with BF_3 in methanol.³³ Acorn quality only differed in the content of linolenic acid, which was significantly higher in acorns from oaks colonized by the invasive ant *Lasius neglectus* (Fig. 1). Linolenic acid acts as a precursor for the synthesis of jasmonic acid,³⁴ a signaling molecule involved in responses associated with insect herbivory.³⁵ The increase of linolenic acid suggests that a local response to aphid feeding was triggered during acorn development. In boreal trees, aphid feeding increased up to 50% the emission of methyl salicylate, a defence compound of plants, that acts as aphid repellent and an attractor of foraging predators and parasitoids.²⁴

We then performed a germination test at the second year when enough acorns reached maturity. We picked mature acorns from trees colonized by the invasive or by the native ant. Those acorns

with visual evidence of being infested by insect larvae were discarded as non-viable. From the group of healthy acorns, we chose randomly between 6 to 18 acorns per tree comprising in total 94 or 97 acorns for holm oaks colonized by *L. neglectus* or *L. grandis*, respectively. We performed a laboratory germination test at 20–25°C under natural light conditions. Acorns were planted in nursery flats of 300 cc filled with commercial compost (70% organic matter, $\text{pH} = 6.5$), watered twice a week and inspected daily from January to April until emergency. After 90 days, acorn viability (germination + seedling emergence) was 89% and 87% for acorns from holm oaks colonized by the invasive or by native ant, respectively. Puerta-Piñeiro et al. obtained a 90% acorn viability when acorns were sown in sterilized river sand. On the other hand, Leiva and Fernández-Alés³⁷ sowed 20 acorns per 71 pots filled with peat and obtained 59% of acorn viability. In our test, we sowed acorns in separate flats under a less competitive environment. The mean time of seedling emergence was 47.8 ± 13.1 days for acorns from holm oaks colonized by *L. neglectus* and 47.3 ± 14.1 days for acorns from holm oaks colonized by *L. grandis*. We randomly chose 10 one-month-old seedlings to calculate their quality using the Dickson index.³⁸ This

index indicates the potentiality of a seedling to survive and to grow by combining the ratio between root biomass and total biomass with the height and the diameter of the sapling. Seedlings with a higher quality have a higher index. Seedlings showed a very low and similar Dickson index (Mann-Whitney, *L. neglectus*: 0.072 ± 0.015 ; *L. grandis*: 0.075 ± 0.015 , $U = 44$, $p = 0.68$, $n = 10$ seedlings). The low values of Dickson index of the two treatments suggest that from the chosen acorns, emerged seedlings had, per se, a low quality. Only a long term experiment, i.e., at least 10 years to achieve at least two masting years with reproductive holm oaks that never had been infested with aphids, and another group that was infested, could reveal if the effect of aphid feeding on acorns really affect holm oak fitness.

We conclude that ants, through their mutualism with tended aphids, may promote considerable changes of holm oaks VOCs emission and acorn quality. However, there was no effect on seedling quality in spite of the decrease of linoleic acid content of acorns from holm oaks where aphids were tended by the invasive ant. These results indicate that the physiological response of acorns to aphid feeding tended by invasive or local ants does not necessarily imply a low quality of seedlings as we previously expected. Under natural conditions, the emission of mature holm oak doubled those of saplings from a plantation.³⁹ So considering that we performed our experiment using 4-year-old saplings, it is probable that the indirect effect of ants on VOCs emissions and acorn quality could be magnified when aphid outbreaks occur in mature holm oak forest. Taking into account the contribution of monoterpenes and isoprene emitted by mediterranean and boreal forests to atmospheric VOC pools⁴⁰ and the species richness of aphids in the north hemisphere,⁴¹ we suggest, in agreement with Blande et al., that aphid infestations should be considered in future models of biogenic VOC emissions from forests.

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