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Presence of *Quercus Suber* Soft-Leaf Defoliators on Trees with Distinct Foliar Monoterpene Emission Profiles

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Featured Application: This work could serve as a basis for exploring the potential value of applying remote sensing and geographic information system procedures to elaborate defoliator risk maps based on differences in soft-leaf defoliator activity associated with the relative position of *Quercus suber* trees within stands, as well as differences that can be found in the appearance (size/colour) of leaves from cork oak trees exhibiting distinct foliar monoterpene emission profiles.

Abstract: The cork tree, *Quercus suber* L., is a characteristic species of the Dehesa agrosilvopastoral system, typical of western Spain. Defoliating insects are an important component of these ecosystems. This study assessed the presence and impact of defoliators feeding on *Q. suber* soft leaf tissue and their relationship with foliar monoterpene emission profiles. Samplings consisted of weekly tree beating (15 times per tree per sample) during the flight period of key species. We studied 26 cork trees with known profiles of foliar monoterpene emission (13 pinene and 13 limonene chemotypes). We identified a total of 272 larvae from 9 species. The main species were *Catocala nymphagoga* Esper (40.8%) and *Periclista andrei* Know (27.6%). Notably, 70.6% of larvae were found on trees with a pinene chemotype. The combined abundance of the four key defoliator species (C. *nymphagoga* L., *P. andrei*, *Bena bicolorana* L., and *Cyclophora punctaria* L.) was 62.7% lower on limonene-chemotype trees than pinene-chemotype trees. Significant differences were found in defoliation damage between leaves with distinct terpene emission profiles. These results suggest that both the abundance and damage caused by defoliators differ with trees' emission profiles, and this may indicate differences in palatability and/or nutritional quality between *Q. suber* trees with distinct foliar monoterpene emission profiles.

Keywords: Lepidoptera; Hymenoptera; cork oak; *Catocala*; *Periclista*; *Bena*

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1. Introduction

Dehesas (*Quercus*-dominated open woodlands) are characterised by ecological and economic complexity, reflecting the biological and environmental diversity of Mediterranean agrobiosystems [1], and these systems have permitted the social development of certain historically impoverished areas. Cork oak, *Quercus suber* L., is the dominant tree species in dehesas in western Spain [2]. Defoliating insects are an important component of forest ecosystems: they influence tree growth and have an impact on the nutrient cycle, providing food for upper trophic levels, while some species contribute to pollination [3]. Among the defoliators of the genus *Quercus*, there are 60 species of Lepidoptera (in 14 families, the majority Noctuidae), one Hymenoptera (*Periclista andrei* Konow), and the genus *Coeliodes* Shonherr (Coleoptera) [4]. The effects of defoliators range from damage to tree flowering and foliation, diminishing fruit and wood production, to physiological changes [5]. Numerous defoliator species, such as *Catocala nymphagoga* Esper, tend to persist at relatively low population densities, only causing marked damage occasionally in the event of population "explosions" [6–8]. On the other hand, some species tend to frequently cause substantial damage, and these include *Lymantria dispar* L., *Tortrix viridana* L., and the Hymenoptera species *P. andrei* in the western Mediterranean region [4,8–10]. For example, sustained defoliation by *T. viridana* over 2 years can reduce tree growth by as much as 70% [11], with an estimated yearly acorn loss due to this tortricid species of more than 500 kg ha^{-1} [12]. Severe continuous defoliation is considered a trigger of tree decline, predisposing trees to attack by other organisms, such as pathogens or xylophagous insects [8,13].

Terpenes and other volatile organic compounds play a key role both in plant physiology and the interactions between plants and their environment; for example, protecting plants against stressors, acting as a mechanism for both intra- and inter-specific plant communication (e.g., releasing chemical signals after herbivore damage), and even attracting predators and herbivore parasitoids [14,15]. Trees of the *Quercus* genus are among the highest emitters of volatile organic compounds [16], with *Q. suber* being considered a strong emitter of monoterpenes [17,18]. Foliar compounds have various effects on defoliating insects. For example, they act as signals for intraspecific host selection or as repellents if emitted specifically by a plant affected by grazing [19]. It has been suggested that volatile compounds such as α-pinene, β-pinene, and 1-hexanol may attract *L. dispar* towards *Larix gmelinii* Rupr. [20] and that terpenoids influence patterns of *L. dispar* grazing on *Quercus ilex* L. [21].

This study aimed to help improve our understanding of factors that determine the species composition of defoliating insects (Lepidoptera and/or Hymenoptera) on *Q. suber*, especially regarding the relationship between leaf-eating larvae (their presence as well as the leaf damage they cause) and foliar monoterpene chemotypes. The objective of this study was to investigate how the profile of foliar monoterpene emission from trees affects (i) the species composition and (ii) the field grazing activity of soft-leaf defoliating insects.

2. Materials and Methods

2.1. Trees under Study

The study was carried out in 2019 in San Enrique dehesa (Almonte, Huelva, Spain, 37°15′43.73″ N, 6°28′34.65″ O; 80 m asl), where *Q. suber* is the main tree species. Previous research on the incidence of the xylophagous cerambycid *Cerambyx welensii* Küster in this dehesa allowed us to determine the foliar monoterpene emission profile of certain trees [22]. Specifically, we randomly selected 26 cork oaks: half with a limonene chemotype (limonene accounting for > 30% of all monoterpene emissions [23]) and the other half with a pinene chemotype (α-pinene-, β-pinene-, and sabinene-enriched emissions, while limonene accounted for < 30%) (Figure 1). Those emission profiles were confirmed by gas chromatography–mass spectrometry (GC-MS) analysis of headspace volatiles collected in situ from each studied sprig, following the procedure described in [22]. Briefly, monoterpenes were sampled using an "aeration system", as proposed in [24]. That system comprised a measurement chamber (polyester oven bag, Albal, Cofresco, Madrid, Spain), provided with a Teflon sampling line connected to a diaphragm pump (SP 200 EC–LC; Schwarzer Precision, Essen, Germany). Charcoal-filtered air entering the chamber was drawn through a glass sorbent tube (403 Orbo Tenax TA tube, 150 mg, 60/80 mesh; Sigma-Aldrich, Madrid, Spain) for 5 min at a flow rate of 120 mL min^{-1}. All sample tubes were sealed immediately after collection and stored at 4 °C and at −28 °C in the laboratory until analyses (in the following 24 h). Blank controls (empty measurement chambers, not enclosing sprigs) were collected simultaneously using the same sampling system.

Samples were analysed with a GC-MS system (GC type 6890N, MSD 5973; Agilent, Santa Clara, USA), employing an HP-5MS column (0.25 mm × 30 m × 0.25 μm), helium as the carrier gas (1 mL min^{-1}), and the following oven program: the starting temperature (46 °C) was increased to 70 °C (at a rate of 30 °C min^{-1}), held steady (4 min), and then increased to 80 °C (at 5 °C min^{-1}), to 90 °C (at 4.5 °C min^{-1}), and to 300 °C (at 50 °C min^{-1}). Peaks were identified by comparison with pure standards (Sigma-Aldrich; Madrid, Spain; purity ≥ 94%) and with mass spectra in the NIST 02 library (MSD Chemstation Build 75 software, G2070BA version). For quantitative analysis, calibration curves were determined for α-pinene, β-pinene, sabinene, limonene, and myrcene.

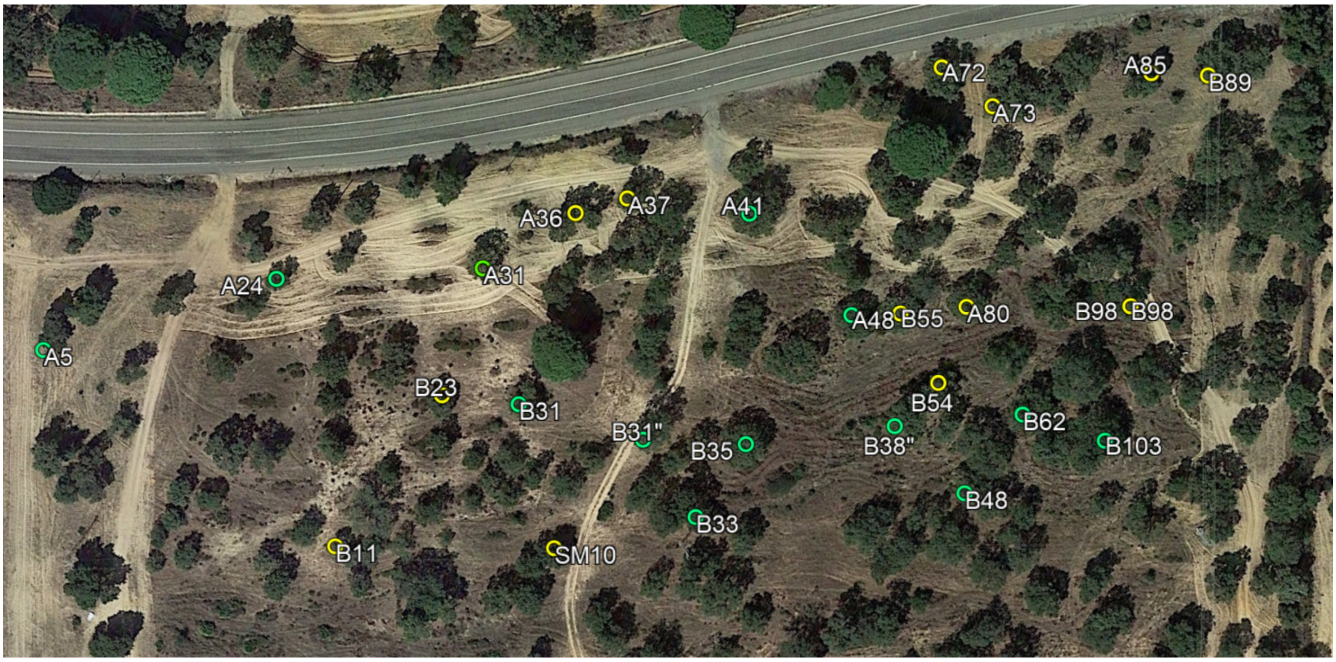

Figure 1. *Quercus suber* trees assessed for the presence of soft-leaf defoliators. Green and yellow dots indicate trees with pinene- and limonene-type emission profiles, respectively. Southwest Spain (Huelva, Andalusia).

2.2. Insect Sampling

Sampling was performed weekly between 28 March and 10 May, in 2019. This covered the period of larval development of the species under study. The mean temperature ranged from 15 °C (the first four sampling weeks) to 18 °C (the last 2 weeks). We recorded 14 days of precipitation during the sampling period, with a maximum of 13 mm and a mean of 4.6 mm (Bodegones weather station, Almonte).

Each sampling consisted of beating each of the trees 15 times [25] with a telescopic aluminium pole (maximum length of 3.6 m). At each sampling, the south sides of all 26 trees were beaten. Larvae were collected on a plastic sheet (4 m × 4 m) spread under the tree crown (on the south side and covering 1/3 of the crown's projection). Collected specimens were kept in the laboratory in plastic chambers (50 cm × 30 cm × 30 cm) under environmental conditions (20 °C; 70% relative humidity) and regularly provided with fresh sprigs of cork oak (with leaves).

2.3. Field Estimation of Defoliation

In the field, defoliation was estimated by collecting three 30 cm long sprigs per tree from the south side of the tree, 1 m apart and at a height of 1.70 m. For each sprig, we counted the total number of leaves and the number of leaves that had been bitten, and, based on photographs, the largest length, width, and area of the limbus were measured using ImageJ software (1.50e version, 19 November 2015). To estimate the impact of grazing on each leaf, we used two regression lines obtained from 60 intact leaves (measured range: 0.5 to 6.7 cm^2; mean of 3.7 cm^2): on the one hand, the regression between width and area (R^2 = 0.81), and on the other, the regression between length × width and area (R^2 = 0.97). Grazing damage on each leaf was recorded as area lost (%) on each leaf after comparing the measured area with the total estimated area from the regressions (using the length × width regression whenever possible).

2.4. Statistical Analysis

The specimens collected per tree and the percentage of foliar damage were analysed using the robust Yuen-Welch test for trimmed means ($\mathrm{Mean}_{0.2}$, arithmetic mean obtained after removing the highest and lowest 20% of values in each starting sample—WRS2 package [26]). The aim of using this approach was to reduce the potentially distorting effect of the extreme values of specimens collected or damage to a few trees. The Brown-Mood quantile test (snpar package [27]) was used to analyse the damage per leaf for different percentiles of damage.

To analyse the species composition of leaf-eating insects and its relationship with the *Q. suber* emission profile, we used non-metric multidimensional scaling (NMDS, Chord distances), followed by permutational multivariate analysis of variance (PERMANOVA; Chord distance, 999 permutations), and checked the multivariate dispersion (vegan package [28]). As PERMANOVA classifying variables, we used the "type" of the emission profile and the "position" of the trees in the forest stand. Tree position was included as a factor after observing in the field (Figure 1) that while most trees had a certain amount of free space around them (generally, at least twice the diameter of the vertical projection of the tree crown in at least two different directions), three trees were effectively surrounded by neighbouring trees (A73, A80, and B31; Figure 1). We considered that this clustering might affect the host location of flying insects. Finally, the 10% percentage-bend correlation coefficients were calculated between species abundances within each emission profile dataset (WRS2 package [26]). Statistical analysis was carried out using R software version 3.1.0, setting the level of statistical significance at $\alpha = 0.05$.

3. Results

3.1. Defoliating Species

We collected a total of 272 larvae of 9 different species (8 species of Lepidoptera and 1 species of Hymenoptera) from 7 families (Table 1). Notably, from 7 out of the 26 trees (3 pinene and 4 limonene chemotypes), no larvae were collected. We should also note that we found 15 *Cryphia algae* B moths, which eat lichen, and these have not been included for the purposes of this study. The most common species were C. *nymphagoga* (40.8%) and *P. andrei* (27.6%). Overall, 93.4% of the specimens were from the species *C. nymphagoga*, *P. andrei*, *Cyclophora punctaria* L., or *Bena bicolorana* L.

Table 1. Soft-leaf defoliators of *Quercus suber* in southwest Spain (Huelva, Andalusia).

Family	Species (Abbreviation)	N (%)
Noctuidae	*Catocala nymphagoga* Esper (Catnym)	40.8
	Bena bicolorana L. (Benbic)	11.0
Lycaenidae	*Syntaurucus pirithous* L. (Synpir)	0.7
	Satyrium esculi Hb. (Satesc)	1.1
Tenthredinidae	*Periclista andrei* Konow. (Perand)	27.6
Tortricidae	*Archips xylosteana* L. (Arcxyl)	2.2
Drepanidae	*Drepana uncinula* Bkh. (Dreunc)	2.2
Lasiocampidae	*Lasiocampa trifolii* D. and S. (Lastri)	0.4
Geometridae	*Cyclophora punctaria* L. (Cycpun)	14

The variation in specimens collected over time, during the spring of 2019, is shown in Figure 2a. The earliest peak in catches corresponded to *B. bicolorana* and *Archips xylosteana* L. (around 17 April 2019); then there was a similar peak in *C. nymphagoga* and *P. andrei* catches (around 25 April 2019); and the latest species was *C. punctaria* (with a peak around 3 May). The overall temporal pattern of larvae collection was similar on trees with the two types of emission (Figure 2b), with a marked increase around 3 April 2019, a first peak on 17 April 2019, and the largest number of specimens being collected on 25 April 2019.

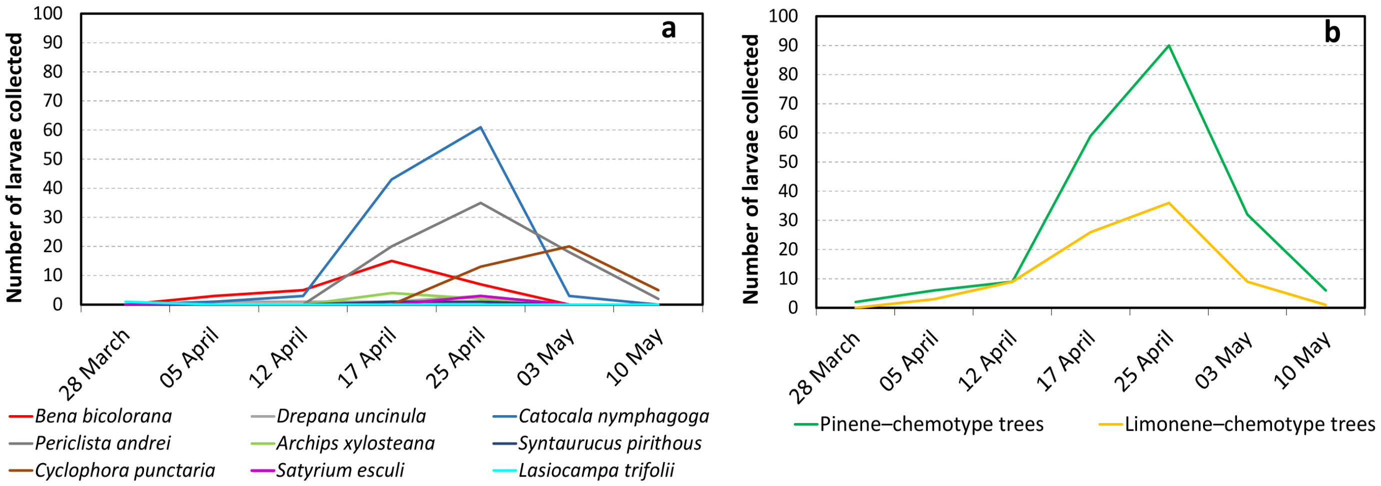

Figure 2. (**a**) Changes in catches of soft-leaf defoliators on *Quercus suber* in southwest Spain (Huelva, Andalusia); (**b**) changes in overall catches in *Q. suber* trees stratified by foliar monoterpene emission profile.

3.2. Relationship between the Presence of Defoliators and Tree Emission Profile

Overall, 70.6% of the larvae were found on pinene-chemotype trees ($\chi^2 = 46.12$, $p < 0.001$). Nonetheless, mean catches (12.14 ± 5.06 and 5.83 ± 0.97, pinene chemotype and limonene chemotype, respectively. Mean$_{0.2}$ ± Error$_{0.2}$) were not significantly different (Yuen-Welch: $p = 0.167$). Two rarely found species, namely, *Syntaurucus pirithous* L. and *Lasiocampa trifolii* D. and S., were found only on pinene-chemotype trees.

The exploratory NMDS analysis (Figure 3) showed the presence of two gradients, one in the distribution of species and another in the distribution of trees of each emission type. The two ellipsoids representative of each group of trees indicated that the distribution of limonene-chemotype trees was associated with the axis defined by the species *C. nymphagoga*, *A. xylosteana*, and *B. bicolorana*, and that of pinene-chemotype trees with the axis defined by *C. nymphagoga*, *P. andrei*, *S. pirithous*, and *L. trifolii*. The multivariate analysis of variance revealed marginally significant differences in species composition among trees with different emission profiles (PERMANOVA: $F = 2.20$, $p = 0.066$) that, in turn, were influenced by tree position (PERMANOVA: $F = 3.51$, $p = 0.016$, for the position*type interaction). Considering the subset of trees obtained after excluding the three trees effectively surrounded by neighbouring trees (N = 16), there was an even clearer difference in insect species composition as a function of emission type (PERMANOVA: $F = 2.76$, $p = 0.035$).

The correlation analysis within the limonene-chemotype group showed one significant association (negative), specifically that between *P. andrei* and *A. xylosteana* ($R = -0.76$, $p = 0.03$). In contrast, five significant positive associations were found within the pinene-chemotype group. Three of them involved *C. punctaria*, whose abundance was correlated with that of *P. andrei* ($R = 0.95$, $p < 0.001$), *S. pirithous* ($R = 0.84$, $p < 0.01$), and *C. nymphagoga* ($R = 0.74$, $p = 0.02$); the remaining two associations involved *P. andrei*: with *C. nymphagoga* ($R = 0.67$, $p = 0.046$) and with *S. pirithous* ($R = 0.89$, $p = 0.001$).

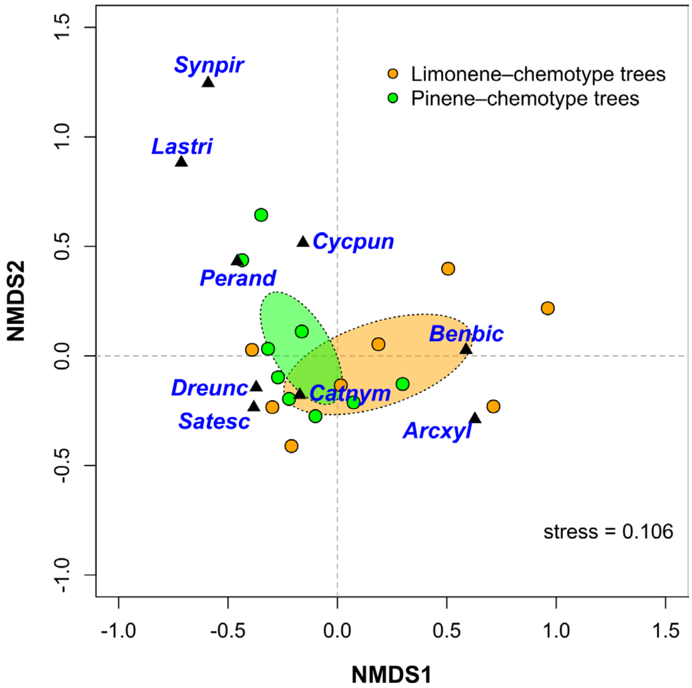

Figure 3. Non-metric multidimensional scaling (NMDS, chord distances) for the distribution of defoliating species (triangles) and trees (circles) with distinct foliar monoterpene emission patterns. The species names (see Table 1) are abbreviated. The ellipsoids show the confidence interval (95%, from the standard error) for the centroids of each tree group.

3.3. Relationship between Defoliation Damage and Tree Emission Profile

The leaves of pinene-chemotype trees were 13% shorter and 17.5% narrower than those collected from limonene-chemotype trees (Yuen-Welch: $t = 8.72$ and $t = 6.72$, respectively, $p < 0.001$). In the field, the percentage of leaves with grazing-related damage was similar for both emission profiles (31.2% on pinene-chemotype trees vs. 37.5% on limonene-chemotype trees). On the other hand, overall, the amount of damage per leaf was slightly greater in the case of pinene-chemotype trees (damage to 13.73% of the leaf vs. 11.98% in limonene-chemotype trees; Yuen-Welch: $t = 1.69$, $p = 0.091$); however, the leaf damage in pinene-chemotype trees was found to be significantly greater for both low (percentile 10%) and high (percentile 85%) levels of damage (Brown-Mood quantile test: Difference = -3.57 and -1.1; $p = 0.044$ and $p = 0.021$, respectively).

4. Discussion

Two species clearly dominated the samplings performed in this study: *C. nymphagoga* and *P. andrei*. While *C. nymphagoga* has previously been reported as a potential threat to *Quercus*, *P. andrei* has been considered a species with a very small distribution range and a markedly epidemic behaviour [8,10]. Other defoliators found in this study have previously been considered important in *Quercus* species, especially *Q. ilex* and *Q. suber*; these included *A. xylosteana* [6,25], *Drepana uncinula* Bkh., and *Satyrium esculi* Hb [6,7]. The first striking issue was that we did not find any larvae of *T. viridana*, though another study also noted a lack of this species of defoliator on *Q. suber* [29]. Synchronization between larval development and host phenology is a critical factor for this defoliator species [4,30], and it may be that the sprouting season of corn oak—later than that of holm oak (*Q. ilex*)—is not suitable for *T. viridana* under some circumstances. Interestingly, when there is a low population of *T. viridana*, the action of this species tends to be replaced by that of other tortricids, e.g., those of the genus *Archips* [31].

Appropriate host selection is essential for phytophagous insects to meet their nutritional requirements and find oviposition sites; plant volatile compounds play a key role in this process [32,33]. Induction of volatile compounds due to herbivory is a widely investigated topic, but few studies have explored intraspecific divergence in the production of volatile compounds induced by stress and its relationship with plant defence against herbivore attack [34]. Moreover, herbivory changes host plant phenotypes, and this affects the ability of other individuals of the same species or other herbivores to locate, select, and use the same host [35]. On the other hand, relative tree position within stands has been reported to influence infestation by defoliators, with isolated trees and forest edges being prone to suffering high infestation levels, which can be due to defoliating species preferences [36] or predator richness, as in insectivorous birds [10].

In this study, only a relatively small number of larvae were collected, possibly due to the generally low population level of the soft-leaf defoliator complex or the sampling method used. It is notable, however, that an analysis of both overall catches and species composition has shown differences between *Q. suber* trees with distinct emission profiles. In relation to this, there may be a link between types of foliar emission, widely described for this tree species [17,18,22,23], and preferential intraspecific host location by defoliating insects. Plant secondary metabolites, such as terpenes and phenols, have been reported to have a range of effects on defoliating insects. While in general, they are credited with repellent properties [37], some groups of volatile compounds, such as conifer monoterpenes, may both have this type of effect (the case of limonene) and also serve as a dietary source of pheromone precursors (the case of α-pinene) [38]. The emission of volatile compounds induced by herbivory may also be exploited by organisms at different trophic levels, with a dose–response relationship; for example, it may attract the natural enemies of phytophagous insects [19,39].

Our results indicate that trees with distinct emission profiles have been shown to have different leaf morphology (and we also observed different leaf colours), as well as experiencing a different intensity of herbivory. This is particularly striking if we recall that the foliar emission profile of *Q. suber* is genetically determined [23]. It has been suggested that visual stimulation may play a key role in food location by larvae [4]. Food quality may affect not only larval development but also pheromonal activity. Interestingly, three different ways in which this may happen have been proposed [40]: (1) a good diet allows high-quality pheromone production (and hence a stronger sexual signal), (2) a diet provides pheromonal resources that cannot be synthesized de novo by insects, and (3) a diet directly influences the nature of the pheromone signature. Among the species found in this study, to date, sexual pheromones have only been identified for *A. xylosteana* [38] ((Z)-11-Tetradecenyl acetate and (E)-11-Tetradecenyl acetate) [41,42]; however, pheromonal activity has been reported for other closely related species, such as for *Drepana bilineata* Packard and *Drepana lacertinaria* L., involving the generalist pheromone (Z,E)-9,11-Tetradecadienyl acetate in both cases [43,44]. More recently, it has also been suggested that *Catocala grynea* Cramer shows pheromonal activity [45].

The results described indicate that the presence of soft-leaf defoliating insects, as well as the leaf damage they cause, differ between trees with distinct foliar emission profiles. This finding allows us to put forward two hypotheses: on the one hand, there are potential differences in palatability and/or nutritional quality between leaves with distinct monoterpene emission profiles; and on the other, the nutritional quality of leaves with distinct emission profiles influences the success of pheromonal activity in some species. We should bear in mind, however, that monoterpene precursors are derived from photosynthetic activity, and environmental and biotic stress induces physiological and biochemical changes in plants that affect monoterpene emission [18,46]. Therefore, it would be interesting to study in more detail whether genetic constitution—which determines the different emission profiles—also determines differences in the quantity and/or quality of food for defoliators; further, we should investigate whether these relationships are influenced by environmental and biotic stress, given its impact on tree physiological status.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

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