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Invasiveness, seasonal dynamics, and impacts of *Xylosandrus compactus* on natural and cultivated vegetation in Israel, with notes on the implications of its management

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Abstract

The black twig borer (BTB) *Xylosandrus compactus* is a highly invasive ambrosia beetle that infests a wide range of living woody hosts. It was first detected in Israel in 2020, and since has caused substantial damage, particularly to ornamental trees in the Western Galilee. This study examined its distribution, host range, seasonal activity, reproductive success, and potential control measures. Field surveys conducted during 2022–2025 across Western and Upper Galilee documented infestation symptoms and confirmed reproduction through the presence of developmental stages within galleries. An observation plot including seven susceptible tree species was monitored from September 2023 to November 2025. Control strategies included canopy applications of *Beauveria bassiana* – based formulation and trunk injections of emamectin benzoate. Additionally, 21 commercial fungicides were evaluated in vitro against the beetle's symbiotic fungi (*Ambrosiella xylebori*, *Thyridium lauri*, and *Fusarium solani* suspected as such). Results indicate that BTB likely entered Israel from southern Lebanon around 2019 and spread ~30 km southward by 2023, followed by a marked population decline in 2024–2025. Infestation peaked during late summer and autumn, with minimal activity in winter. Among 22 recorded host species, approximately two-thirds were native Mediterranean shrubs and small trees. About 37% of the overall sampled twigs contained viable brood, whereas *Cercis siliquastrum* exhibited the highest infestation levels. Neither of the tested formulations demonstrated clear efficacy in managing BTB symptoms under field conditions at two locations. Only a few fungicides showed strong inhibitory effects on symbiotic fungi at low concentrations. The observed population decline could not be explained by host resistance, natural enemies, or abiotic factors. We propose that disruption of fungal symbionts by competing microorganisms may impair larval development, while dispersal of uncontaminated females may enable renewed outbreaks. These findings highlight the complexity of BTB population dynamics and the limited effectiveness of current control measures.

Key words

Ambrosia beetle, spread, tree susceptibility, seasonal activity, management, ornamental and forest tree species

Introduction

General biological background

The black twig borer (BTB), *Xylosandrus compactus* (Eichhoff) (Coleoptera: Curculionidae: Scolytinae: Xyleborini), is an ambrosia beetle native to East Asia (Wood 1982, Chong et al. 2009, Urvois et al. 2021b). The fungi carried by BTB are housed in mycangia located primarily in the mesothorax, but they are also found on other parts of the beetle's body (Hulcr and Stelinski 2017; Li et al. 2019). Until recently, the principal fungi identified from BTB populations were *Ambrosiella xylebori* Brader ex Arx and Hennebert (e.g., Kaneko and Takagi 1966; Bhat and Sreedharan 1988; Bateman et al. 2016) and *Ambrosiella macrospora* (Francke-Grosm.) Batra (Ceratocystidaceae) (Muthappa and Venkatasubbaiah 1981), with the records of the latter being rarely mentioned in the literature. *Fusarium solani* (Nectriaceae) was suggested to constitute the ambrosial feed for BTB and the cause of pathogenicity in the attacked woody host plants (Beardsley 1964). Members of the *Fusarium solani* species complex (FSSC) have been isolated from BTB and its galleries from many geographical areas (e.g., Ngoan et al. 1976; Bosso et al. 2012; Bateman et al. 2016); these isolates are considered stable associates of BTB. More recently, the fungus *Thyridium lauri* Voglmayr, D. Aiello & G.R. Leonardi (Thyridiaceae) has been identified as a second symbiont of BTB (Sun et al. 2025; Maymon et al., in preparation). Among these three representative genera only *Ambrosiella* Brader ex Arx & Hennebert contains species that are obligate, mutualistic symbionts of ambrosia beetles (Mayers et al. 2015).

Many other microbial species have been isolated from BTB (Gugliuzzo et al. 2021 and references therein). Some of these microorganisms are undoubtedly involved in the damage syndrome associated with BTB infestation. It appears that invasive ambrosia beetles acquire native fungi that may reshape their performance (Rassati et al. 2019). For example, severe wilting of cacao seedlings under BTB infestations has recently been reported to be associated with *Fusarium*, *Lasiodiplodia*, and *Colletotrichum* species (Asman et al. 2025).

BTB as an invasive species in the Mediterranean Basin

BTB is a highly successful invader and is now widely distributed across Africa, Asia, the Americas, and many Pacific islands (EPPO 2020a). In the Mediterranean Basin, BTB was first detected in central Italy approximately 16 years ago (Garonna et al. 2012). From Italy, the BTB population probably spread to the western Mediterranean and was first detected in France at the Alpes Maritimes region in 2016 (Roques et al. 2019) and in the Balearic Islands, Spain, in 2019 (Leza et al. 2020). In the eastern Mediterranean, BTB was first recorded in 2017 in the Beirut area of Lebanon (Moussa et al. 2021). Its occurrence there suggests introduction via wood imports rather than natural spread, as the beetle was reported in Greece only in 2018 (Spanou et al. 2018) and in Turkey in 2021 (Hızal et al. 2023). Over the past two decades, BTB has continued to expand throughout the region, causing local outbreaks and severe damage to maquis vegetation as well as to ornamental trees and shrubs (Pennacchio et al. 2012; Francardi et al. 2012, 2017; Vannini et al. 2017; Gugliuzzo et al. 2019; Spanou et al. 2019. Leza et al. 2020; Mendel et al. 2023, Fiala et al 2025, Pernek et al. 2025). In Israel, the concentration of damage is located in the Western Galilee, adjacent to the Lebanese border, indicating the likely direction of introduction. Molecular evidence further suggests that the population established in Israel belongs to a lineage previously established in Europe and the USA, originating from Shanghai, China (Urvois et al. 2021b).

Host trees

The black twig borer (BTB) attacks hundreds of woody plant species worldwide (EPPO 2025). In each newly invaded regions, however, a somewhat different assemblage of host trees is affected (e.g. Hara and Beardsley1979, Greco et al. 2015, Di Sora et al. 2023, Hızal et al. 2023; and references therein). This variation may be partly explained by significant genetic differences among invasive BTB populations across geographical areas (Urvois et al. 2021b). Overall, the known host range of BTB includes hundreds of perennial plant species (Ngoan et al. 1976; Beaver et al. 2014; CABI 2020), comprising primarily woodland and forest trees, numerous ornamental species, and several agricultural crops, such as coffee and avocado (Oliveira et al. 2008; Egonyu et al. 2015). In the Mediterranean Basin and southern Europe, BTB attacks a wide diversity of plant species; however, host lists vary locally according to differences in plant susceptibility. The BTB population established in the Mediterranean region primarily infests native broad-leaved woodland species (Francardi et al. 2012; Vannini et al. 2017; Gugliuzzo et al. 2020; Moussa et al. 2021).

Mechanism of tree damage

BTB typically infests living trees, with damage manifested mainly as twig wilting and dieback, accompanied by gum exudation on affected branches and trunks (Gugliuzzo et al. 2021 and references therein). Beetle tunneling appears to be critical for disrupting transpiration (Sun et al. 2025). However, the role of symbiotic fungi in inducing twig dieback remains unclear. The extent to which associated fungi—whether obligate symbionts or environmentally acquired, and their contribution to host damage or mortality, has yet to be determined. A prominent feature of BTB population dynamics in invaded regions such as Florida, where beetle was discovered already in 1941 (Ngoan et al. 1976) or the Mediterranean is rapid population growth leading to outbreak phases that may persist for several years and cause severe damage to susceptible host trees. These outbreaks are typically followed by population decline to an endemic phase. To date, no comprehensive explanation has been proposed to account for both the population collapse and the subsequent re-emergence of outbreaks when BTB invades neighboring or distant areas. However, a different picture emerges in coffee plantations. In India, where the BTB population is endemic; in Uganda, where the pest was first reported in 1993; and in Hawaii, where it was first detected in 1961 (Beardsley 1964), significant damage is still evident in these three regions (Greco and Wright 2015, Kagezi et al. 2020, Edwin et al. 2025, Parija et al. 2025).

Management Possibilities

Gugliuzzo et al. (2021) reviewed information on the natural enemies associated with BTB (and two other *Xylosandrus* spp.), as well as traditional and innovative control methods tested against them. As expected, synthetic insecticides such as pyrethroids and organophosphates were found to be lethal and to provide some protection against BTB (e.g., Mangold et al. 1977). However, these compounds were not considered in our study, because BTB damage occurs mainly on ornamental trees in countryside communities. The comprehensive review by Gugliuzzo et al. (2021) indicates that natural enemies or competitors are unlikely to provide a viable solution to the BTB problem. Natural enemies generally play a minor role in the population dynamics of ambrosia beetles. For example, in India, *Eupelmus* sp. (Hymenoptera: Eupelmidae) was found in fewer than 1% of coffee twigs colonized by BTB (Balakrishnan et al. 1989). *Eupelmus* spp. are primarily known as polyphagous (generalists, ectoparasitoids) (Noyes 2025), as well as other known arthropod natural enemies that accompany ambrosia beetles.

To date, no studies have demonstrated a clear effect of synthetic fungicides under field conditions on the BTB population or the symbiotic fungi associated with ambrosia beetles. Although Kagezi et al (2015) examined three fungicides in vitro for their effectiveness in inhibiting mycelial growth of ambrosia fungus isolated from BTB. Unfortunately, this study did not identify the target fungal species. Parija et al. (2025)

recommended the application by spray of the systemic fungicide Propiconazole (Tilt 25 EC). Therefore, a comprehensive selection of mainly systemic fungicides were examined in our study for the inhibition of *Ambrosiella xylebori*, *Thyridium lauri*, and *Fusarium solani*, the latter previously suspected to be a symbiont of BTB.

The effects of entomopathogenic or antagonistic fungi have been studied against several ambrosia beetles (Reverchon et al. 2021); however, information specifically on BTB is limited. Balakrishnan et al. (1994) reported that two weeks after treatment with a *Beauveria bassiana* (Hypocreales: Cordycipitaceae) formulation in a coffee plantation, 21% of examined BTB individuals were infected. Mukasa et al. (2019) reported more than 70% BTB mortality in laboratory assays and coffee plantations treated with *Aspergillus flavus* (Eurotiales: Trichocomaceae) in Uganda. Despite these promising results, *A. flavus* was not considered here because its aflatoxins pose serious health risks. Trunk injection of emamectin benzoate has been shown to be effective against other ambrosia beetles (*Euwallacea* spp.) (Eatough Jones et al. 2017; Grosman et al. 2019; Byrne et al. 2020; Mendel et al. 2025). In contrast, trunk injection of abamectin in carob trees was not effective against BTB colonies (Leza et al. 2020).

Research Objectives

This research aimed to establish two complementary knowledge bases: (i) an in-depth understanding of BTB population activity in invaded areas in Israel, and (ii) evaluation of management measures to prevent or mitigate damage caused by the beetle. To achieve these aims, four specific objectives were defined: (a) To examine the spatial distribution of BTB and the seasonal pattern of adult flight activity; (b) To assess the range of locally affected host tree species and their susceptibility in relation to population dynamics and reproductive success; (c) To evaluate the effectiveness of environmentally safe pest control approaches suitable for rural settlements experiencing severe damage to ornamental trees, specifically a *Beauveria bassiana*–based preparation and trunk injection of emamectin benzoate; and (d) To establish a knowledge framework for the application of systemic fungicides targeting the principal fungal species associated with BTB, as a potential complementary management strategy.

Materials and Methods

The spread of the black twig borer in Israel

The BTB survey, via two complementary paths, began following the discovery of damaged *Arbutus andrachne* trees in Kibbutz Hanita, located on the Northern Israeli border with Lebanon. The first involved surveys of ornamental trees in localities where BTB was found to be established. These sites were identified through research activities of the study team in the Western and Upper Galilee, as well as in response to reports from gardeners or residents who observed unusual damage to ornamental trees. These surveys were carried out by the research team in collaboration with the Department of Horticulture, Environmental Resources Division, and Extension Service of the Ministry of Agriculture. The second path consisted of targeted surveys of natural forest areas and nature reserves along the Lebanese border, extending up to approximately 40 km south of the border. These surveys were conducted by the research team together with personnel from the Forestry Department, Forest Health Unit (KKL-JNF), or the Science Division of the Israel Nature and Parks Authority.

Within each community, surveys were conducted by inspecting all ornamental trees along both sides of roads over distances of 500–800 m. Trees infested with BTB were identified by the characteristic wilting and dieback of affected twigs and branches. In forest areas and nature reserves, inspections were conducted while driving along habitat edges using an off-road vehicle, stopping to examine twigs suspected of BTB infestation. Typical BTB damage was characterized by wilting of the upper portion of the twig, while the section below the gallery entrance remained green. The beetle's entrance hole was located, and each affected twig was sectioned to expose the gallery and confirm the presence of active developmental stages or remnants of the beetle.

Sampling during 2022 and 2023 was conducted mainly between December and April, whereas in 2024 and 2025 sampling took place primarily in late summer and autumn (August–November). One sample was collected per site per year. The surveyed locations are listed in Fig. 1. Changes in the health status of 126 trees were monitored in four localities: Hanita, Adamit, Ga'aton, and Yechiam. Monitoring focused on trees that were severely damaged by BTB in 2023, and their condition was assessed over the subsequent two years. The monitored trees included 40 *Ceratonia siliqua*, 26 *Arbutus andrachne*, 17 *Quercus calliprinos*, 15 *Cercis siliquastrum*, 9 *Acer obtusifolium*, 8 *Laurus nobilis*, 6 *Quercus infectoria*, and 5 *Pistacia palaestina*.

BTB hosts recorded in Israel

The list of BTB host trees in Israel was compiled during the surveys described in the previous section, based primarily on information collected in 2022 and 2023 during the outbreak period. Host records were derived mainly from surveys of ornamental trees in locations where BTB outbreaks were documented in 2023. Only tree species in which twigs containing viable, early developmental stages of BTB were confirmed as suitable hosts. Special attention was given to eucalyptus species and to common fruit treesprimarily citrus and avocado growing adjacent to forest tree species planted as ornamentals within the surveyed locations. Three levels of damage were defined: (i) trees with single twigs infested by BTB, (ii) trees with numerous characteristically damaged twigs prominently visible in the crown; (iii) severely damaged trees, with extensive injury to twigs, branches, and trunk, in some cases resulting in complete tree mortality.

Seasonal flight activity and attack density

To monitor seasonal BTB attack activity and to compare host susceptibility among tree species in Israel, an observation system was established at the KKL–Cabri forestry station. (33^{0}01’44’’N: 35^{0}15'39"E) The system enabled quantitative monitoring of BTB activity and the collection of twigs with well-defined infested age data, including the timing of attack and the interval between attack and sampling. An observation plot was established comprising seven forest tree species selected for their known or suspected susceptibility to BTB. Three-year-old trees were used that had reached sizes suitable for standardized observation and sampling. All trees were supplied by KKL nurseries and originated from areas free of BTB.

Trees were planted in woven polypropylene grow bags. The species included *Ceratonia siliqua*, *Quercus calliprinos*, *Cercis siliquastrum*, *Acer obtusifolium*, *Laurus nobilis*, *Quercus ithaburensis*, and *Pistacia palaestina*. Each species was represented by 15 repetitive individuals. Six species were arranged in rows of five trees per row, while *L. nobilis* trees were interspersed among the other species (Fig. 2). Tree height at initial setup ranged from 2.0 to 2.5 m. An irrigation system consisting of a 20-mm diameter hard plastic pipe was laid along each row. Each tree was supplied by a tube branching into four drippers, delivering a total of 8 L h^{-1} per tree. Irrigation operated for one hour per day, seven days a week, throughout the warm season (March–November). The observation trees were partially shaded by nearby taller trees, mainly *C. siliqua* and *C. siliquastrum*. BTB activity in the area was high, and infestation of the observation trees occurred under natural population pressure.

Monitoring BTB activity in the observation plot began in early September 2023 and continued until late November 2025. The sampling procedure was performed accordingly. The observation plot was visited weekly, and each tree was inspected at least once a month. During each visit, trees were inspected from the root collar to the canopy, including twigs, branches, and trunks. Each newly detected penetration hole was marked with an indelible colored marker, and plastic tape was used to indicate the sampling period. When multiple adjacent penetration holes were present, they were numbered sequentially. All penetration data were recorded in a database, including sampling date, tree species, attacked plant part (twig, branch, or trunk), and position within the tree (lower, middle, or upper crown). The sampling process was inherently slow due to several factors. Entrance holes were often difficult to detect because of unfavorable viewing angles, variable light conditions, sun angle, wet bark following rainfall, or concealment by frass or gummy secretions. In addition, BTB entrance holes had to be distinguished from those of other borers, such as early instars larvae of the leopard moth (*Zeuzera pyrina*; Cossidae). Examination and marking of thin twigs required particular care due to their fragility. During the monitoring period, selected infested twigs were sampled by sectioning with pruning shears. These samples were used to (i) assess colonization success and (ii) examine the fungal flora developing within galleries or associated with the beetles. The fungi associated with BTB are presented and discussed in a separate manuscript in preparation (Maymon et al., in preparation).

Gallery reproduction success

Reproductive success within BTB galleries was assessed using twigs only. Attack sites on thick branches or the trunk were not sampled in order to avoid significant damage to the growth of the experimental trees. A total of 817 twigs were examined on five sampling dates in the KKL–Cabri observation plot (number of twigs sampled per date in parentheses): March–July 2023 (86), October–December 2023 (102), March 2024 (124), December 2024 (195), and November 2025 (161). A sixth sampling was conducted in February 2024 in Ga’aton and Yechiam and included adult trees, incorporating *Arbutus andrachne*, a species not represented in the KKL–Cabri observation plot. This sampling included 149 twigs. For all samplings, a twig was considered to exhibit successful reproduction if viable early developmental stages or clear evidence of completed adult development were detected, regardless of the number of individuals present. Reproductive success of BTB in branches and trunks was tested on mature trees in those locations where permission was granted to remove the branches. Testing was conducted on *C. siliquastrum*, and *A. andrachne* in Ga'aton and Mitzpe Hila, and on *C. siliqua* in Nahal Kziv.

Effect of *Beauveria bassiana* based product on BTB activity

The commercial preparation Bioveria, containing the entomopathogenic fungus Beauveria bassiana-GHA (Laverlam International, MT, USA. Distributed by RIMI Plant Protection, Petah Tikva, Israel), was evaluated for its effect on BTB activity in two independent experiments.

The first experiment was conducted in Kibbutz Adamit in 2023. Two preliminary surveys were carried out to select suitable trees and to assess their initial health status prior to treatment. Trees were selected based on three criteria: (i) mature individuals of tree species considered susceptible to BTB; (ii) trees with crowns that could be fully or largely observed; and (iii) easy access for a spray cart. On 24th April 2023, trees meeting these criteria were marked for inclusion in the experiment. The four tree species included were *Arbutus andrachne, Acer obtusifolium*, *Cercis siliquastrum*, and *Quercus infectoria*. A total of 27 mature trees were selected, of which 15 were assigned to the treatment group and 12 served as untreated controls. Bioveria was applied using a high-pressure sprayer mounted on a commercial spray cart at a concentration of 0.2% (v/v). The preparation was sprayed onto the tree canopy until runoff, with application volumes ranging from 4 to 10 L per tree, depending on crown size. Four applications were conducted on 24th May, 26th June, 7th August, and 12th September 2023.

To evaluate treatment effects, each experimental tree was photographed from two to four fixed angles. Baseline photographs were taken on 24th April 2023, prior to the first application, and follow-up photographs were taken on 12th September 2023. A third planned photographic assessment in the second half of November could not be conducted due to technical restrictions. Treatment effects were assessed by comparing paired photographs from the two dates, matched by tree and viewing angle. Image pairs were displayed simultaneously on adjacent computer screens, and a tree health index was assigned by consensus among two to three members of the research team. The health index ranged from 1 (poor condition, most twigs wilted) to 5 (healthy tree with no visible damage). Changes in tree health were quantified as the difference between the mean index values obtained on 12th September and those recorded on 24th April.

A second experiment was conducted at Kibbutz Yechiam in 2024. Ten trees aged 6–7 years were selected: eight *Cercis siliquastrum* and two *Arbutus andrachne*. Within each species, half of the trees were treated with Bioveria and the remainder served as untreated controls. Trees were selected in paired arrangements, such that each treated tree was adjacent to a corresponding control tree. All selected trees were initially in fair condition, some showing evidence of previous infestation, but none exhibited severe or acute BTB damage at the outset of the experiment. Tree health was assessed using the same 1–5 health index as described above, based on direct visual evaluation of the canopy and BTB-related damage. Initial assessments were conducted on 10th April 2024, with follow-up assessments on 10th December 2024. Bioveria was applied as described for Experiment 1, with three applications conducted on 17th April, 21st May, and 8th July 2024. Treatment efficacy was evaluated based on the change in health index for each tree between the two assessment dates.

Effect of emamectin benzoate on BTB activity

The first experiment was conducted at Kibbutz Ga'aton in 2023. Two preliminary visits were carried out by the research team in collaboration with kibbutz personnel to select suitable trees and to collect branch samples for assessing BTB damage. On 10 February 2023, 33 mature trees were marked for inclusion in the experiment. Trees were selected according to the first two criteria described in Section 2.5.1, and approximately half were assigned to the treatment group. The tree species included *Arbutus andrachne*, *Acer obtusifolium*, *Ceratonia siliqua*, and *Cercis siliquastrum*. The injected product was Dorclaim (Lidor Elements), containing 12 g L^{-1} emamectin benzoate. The dosage was 1 cm^3 of technical product per centimeter of trunk diameter at breast height (DBH).

Injection holes were drilled using a 6-mm double-helix drill bit to ensure efficient sawdust removal. The formulation was injected under high pressure using a QUICK JET AIR injection system (ArborJet Inc., Woburn, MA, USA). Injections were made into the active xylem of the trunk at a height of approximately 60 cm above ground level, with the injected volume adjusted to trunk diameter (one cc of the pesticide technical formulation per one cm of trunk diameter). Each borehole was sealed with a plug fitted with a one-way silicone valve to prevent backflow and minimize environmental contamination.Treatment effects were assessed using photographic evaluation as described in Section 2.5.1. Each tree was photographed from two to four fixed angles. Baseline photographs were taken on 28 February 2023, concurrently with the injection, and follow-up photographs on 12 September 2023. A third planned assessment in the second half of November was not conducted due to technical restrictions. Treatment efficacy was evaluated by comparing paired photographs from the two dates by two to three independent evaluators.

The second experiment was conducted at Kibbutz Yechiam in 2024. A preliminary survey was carried out by the research team together with the kibbutz gardener to select suitable trees, following the same criteria applied in the previous experiment. On 6th March 2024, 23 mature trees were selected, approximately half of which were assigned to the treatment group, with the remainder serving as untreated controls. The tree species included *Arbutus andrachne*, *Ceratonia siliqua*, *Cercis siliquastrum*, *Quercus* *ithaburensis*, and *Quercus infectoria*. The formulation and dose were identical to those used in the Ga'aton experiment. Injections were performed using an ArborJet AvoJect device. Treatment effects were assessed using the same photographic method described in Section 2.5.1. Baseline photographs were taken on 14th March 2024, and follow-up photographs on 4th November 2024. Changes in tree condition between the two dates were used to evaluate treatment efficacy.

Effect of fungicides on the development of three fungal species associated with BTB

Laboratory experiments tested 21 commercial fungicides licensed for use in Israel, most of which are systemic (Table 1). Fungicide efficacy was evaluated based on the degree of inhibition of in vitro fungal growth on Petri dishes compared to that on unamended PDA medium. The three fungal species tested were *Ambrosiella xylebori*, *Thyridium lauri*, and *Fusarium solani*, as previously mentioned in section 1.5. The fungi were grown on Potato Dextrose Agar (Difco, Leeuwarden, The Netherlands). The substrate was inoculated with the tested fungal species by placing a 5 mm diameter disc in the center of a standard Petri dish (80 mm in diameter, 14 mm in height), taken from the actively growing margin of the fungal culture. The plates were incubated at 25 °C in the dark. The degree of inhibition was assessed based on the growth rate of each fungus, measured as the time required for the mycelium to cover the entire surface of the Petri dish in the absence of the fungicide. Information regarding the source of the isolates tested and their respective growth rates is presented in Table 2. Each fungal species was tested separately at four concentrations: 0.1, 1, 10, and 50 ppm. Concentrations were calculated based on the active ingredient content of the commercial products. Each treatment, including the untreated control, was tested in triplicate. The results are presented as mean ± SD of three replicates of each preparation at each concentration against each fungus. The reported values represent pooled data from two experiments.

Results

Spread of BTB in the Galilee

The black twig borer apparently entered Israel from southern Lebanon in 2019. By 2020, the first significant signs of damage were already visible, mainly on Greek strawberry tree (*Arbutus andrachne*). In 2021, severe damage was observed in several villages in the western Upper Galilee, located a few kilometers along the international border with Lebanon. In 2022, severe damage was evident in trees at three localities in the Western Galilee within this area: Mitzpe Hila, Hanita, and Adamit. Initially, damage was most noticeable in mature trees of carob (*Ceratonia siliqua*), *A. andrachne*, and the common smilax vine (*Smilax aspera*). By 2023, significant damage was already conspicuous in additional locations, such as Ga'aton and Yechiam. In some cases, dozens of twigs were found dried, necrotic and damaged by BTB, depending on the tree size. The typical drying pattern of affected twigs was evident from the point of beetle penetration upward along the twig. In two other locations, Abirim and Cabri, however, damaged twigs occurred at low frequency. At the southernmost point of detection, in the village of Rakefet (Misgav Regional Council), located about 30 km south of the Lebanese border, isolated branch damage was observed in 2023. However, this typical damage in the Misgav Regional Council did not recur until the summer of 2025.

In natural forest areas, twig dieback attributed to BTB was recorded in 2022 and 2023 but was generally limited. Damage was observed mainly in carob trees in planted forests and less frequently in Kermes oak (*Quercus calliprinos*). In 2023, heavy infestations of BTB were observed in the Nahal Kziv and Nahal Betset nature reserves, mainly affecting *S. aspera*, *A. andrachne*, and *C. siliqua*. In the same year, BTB was also detected in the northern Golan Heights (Odem Forest, 795 m above sea level, approximately 12 km from the Lebanese border) at low density, manifested by boring activity and drying of only a few twigs in *Q. calliprinos*. BTB was not detected on the eastern side of the Upper Galilee.

Between 2024 and 2025, a sharp decrease in BTB prevalence was observed, as reflected by reduced twig dieback. Figure 3 illustrates changes in the health status of mature trees examined in the communities of Hanita, Adamit, Ga'aton, and Yechiam. Of the 126 affected trees monitored in 2023, only 18 were recorded as affected by BTB in 2024, and 26 were recorded as affected in the winter of 2025. The vast majority of affected trees during the latter two years were *A. andrachne*. Surveys conducted in the winter of 2025 revealed no BTB damage in Rakefet.

In October 2025, a slight increase in the incidence of characteristic dying or dead twigs was observed; however, this increase was not comparable to the high incidence of dried vines that peaked in 2022 and 2023. In the autumn of 2025, an outbreak was first recorded in the settlement of Yodfat (Misgav Regional Council) [35°16′19″E, 33°50′13″N]. This outbreak was characterized by mass drying of *S. aspera* and damage of many *A. andrachne* trees, and to a lesser extent, *Q. calliprinos*. Notably, the outbreak was not observed in the nearby village of Rakefet, located approximately 3 km away (straight-line distance). BTB was not detected from Nahal Betset, Sha'al, Shekhanya and Yiftach sampled between 2023-2025 (Fig. 1).

Seasonal flight activity and attack density

Seasonal BTB activity was examined in an observation plot at the KKL-Cabri forestry station comprising seven forest tree species. Between September 2023 and November 2025, a total of 3,876 BTB penetration points were recorded among all 105 trees. The majority of attacks occurred in the autumn of 2025 (60.7%), with relatively high numbers also recorded in the summer of 2025 (11.5%) and autumn of 2023 (9.1%). The lowest attack levels were recorded during the winters of 2023–2024 and 2024–2025, accounting for 2.1% and 1.6% of the total number of penetration holes, respectively (Fig. 4). The temporal pattern of attack was similar among five of the seven tree species examined. The exceptions were the terebinth tree (*Pistacia palaestina*), which showed relatively high activity only in autumn 2023, and *C. siliquastrum*, which exhibited high activity in autumn 2025—similar to most species except *P. palaestina*—but also displayed markedly denser attacks compared with other seasons for this species (Fig. 5).

BTB hosts recorded in Israel

Based on vegetation surveys conducted in locations of the Western Galilee and in natural forest areas, a list of BTB host species that were successfully colonized and supported beetle development was compiled and is summarized in Table 3. The damage intensity indicated in Table 3 refers to severity during the outbreak stage. Of the 22 woody plant species recorded, about two-thirds of them are native small trees and shrub-dominated (chaparral) ecosystem species. These include the most severely affected tree species: *C. siliqua*, *A. andrachne*, Judas tree (*Cercis siliquastrum*), and bay laurel (*Laurus nobilis*). In these four species, characteristic damage was manifested not only by twig boring but also by conspicuous, dense attacks on main branches and the trunk, although the native status of *C. siliqua* remains unclear (see Discussion for further details). This pattern was not observed in other tree species, even those that experienced severe damage, such as oak species. The most severe damage was observed in *Smilax aspera*, and mortality was expressed as complete drying of the entire plant mass. A few BTB galleries in the lower section of the typical elongated stem of this climber are sufficient to cause desiccation of 3–4 meters of growth, and even upward, from the point of BTB penetration. This was particularly noticeable in vines covering pine trunks along forest edges near ornamental trees in villages close to the Lebanese border, where the initial invasion front of the BTB population entering Israel was evident. Colonization and damage by BTB during the outbreak stage were limited in exotic tree and shrub species.

Comparison of attack intensity by BTB between tested tree species

A comparison of the average number of penetration holes per tree per month among the examined species showed that *C. siliquastrum* was the most heavily attacked (4.90 holes per tree per month), whereas Mount Tabor oak (*Quercus ithaburensis*) was the least attacked (0.17 holes per tree per month) (Fig. 5). High variability in attack intensity was also evident among individual trees within each species. Nevertheless, each species showed a characteristic density range; for example, *C. siliquastrum* trees exhibited between 32 and 237 penetration holes per tree, whereas *Q. ithaburensis* ranged from 0 to 10 holes per tree (Fig. 6). Analysis of attack distribution among tree parts—comparing twigs versus branches and trunk—suggested the division of species into two groups. In one group, which included *L. nobilis*, *C. siliquastrum*, and *C. siliqua*, attacks on branches and trunk accounted on average for 26–31% of all penetration holes. In contrast, in the remaining species this proportion was low, averaging 4–7% (Fig. 7).

Gallery reproduction success

Reproductive success in galleries was examined mainly with twigs. Most twigs from the seven tree species examined in the Cabri observation plot, were sampled from this plot. The highest proportion of twigs with reproductive success was found in *A. andrachne* - 64.4%, a tree species not represented in the observation plot, were all taken from mature trees in Yechiam and Ga'aton. The proportion of twigs with BTB galleries containing vital immature stages, from the egg stage to adult pre-emergence offspring, in the total branches sampled was 37.0% of the 817 branches examined. In the case of *P. palaestina* and *C. siliquastrum*, approximately half of the examined twigs were sampled with reproductive success while the lowest percentage was recorded in *Q. ithaburensis* - 14.3% (Table 4). In the case of *Q. calliprinos*, approximately half of the examined twigs that were sampled from mature trees in Yechiam displayed the reproductive stage, while only 16.7% of twigs of this tree species that were sampled in the experimental plot in Cabri were in the same situation. Due to technical reasons, the reproductive success of many of the examined twigs could not be determined. Successful reproduction in twigs was considered where more than five larvae or older offspring were present. Less than one-third of the twigs exhibited such reproduction rates. Reproductive success in the branches and the trunks was evident on *C. siliquastrum*, *A. andrachne* and on *C. silique*.

Effect of 'Bioveria' product treatments on BTB damage

The results obtained in both experimental locations were not significant. Different trends were seen between the tree species, regardless of the treatment with the product. The results of the 'Bioveriia' treatment are summarized in Fig. 8. Trees in both treated and untreated groups exhibited high variability in damage levels. Some trees in both groups appeared weak, likely due to infestation by the leopard moth (*Zeuzera pyrina*). In several trees from both groups, dozens of BTB penetration holes per tree were recorded, and active galleries containing adults and/or viable larvae were observed. In some cases, 30–40% of the twigs had dried. However, in none of the galleries examined did larvae or adults show signs of infection by this entomopathogenic fungus. Nevertheless, examination of galleries revealed no larval or adult stages affected by the fungus.

Effect of emamectin benzoate on BTB damage

The results of this experiment are summarized in Fig. 8. Overall changes in the health index during the period between the application of emamectin benzoate and subsequent assessments were minor and cannot be unequivocally attributed to the treatment. In both control and treated trees of *Q. calliprinos* and *Q. infectoria*, no change in health status was observed between sampling dates. In *C. siliqua* trees, BTB-related damage was evident, and although differences between treated and control trees were small, the results suggest a slight improvement in tree condition following treatment. However, this limited improvement does not allow a definitive conclusion that the observed effect was caused by the emamectin benzoate treatment. The *C. siliquastrum* trees included in the experiment were in poor health at the outset, in part due to infestation by other pests such as the leopard moth, which precluded meaningful comparison between treatments. Similarly, no significant seasonal or treatment-related changes were observed in *A. andrachne* trees. Importantly, no external signs of phytotoxicity were detected in any of the treated injected trees.

Effect of fungicides on the development of three fungal species associated with BTB

The inhibitory effects of 21 fungicidal preparations on the development of three major fungal species associated with the BTB complex were evaluated. The complete results for all fungicides at the tested concentrations are presented in Table S1. For comparative purposes, only fungicides that inhibited fungal growth by 85% or more were considered. Table 5 summarizes the effects of the 21 preparations of the three fungal species at a concentration of 0.1 ppm active ingredient (a.i.), highlighting those treatments that achieved ≥85% inhibition. At this concentration, the preparations Luna Experience, Luna Sensation, and Serenade inhibited the growth of *Ambrosiella xylebori*. Comparable inhibition of this fungus at a concentration of 1 ppm a.i. was achieved with Acanto Plus, Hosen, Mirage and Premium. For *T. lauri*, ≥85% inhibition at 0.1 ppm a.i. was observed with Serenade, while similar inhibition at 1 ppm a.i concentration was also achieved with Mirage and Tecto. For *F. solani*, ≥85% inhibition at 0.1 ppm a.i. was obtained with Mirage and Serenade, whereas comparable inhibition at 1 ppm a.i concentration was achieved using Switch, Tecto, and Twist.

Discussion

The black twig borer in the Mediterranean Basin and its establishment in Israel

Detection of BTB in central Italy in 2011, was the first evidence of the beetle's presence in the Mediterranean Basin (Garonna et al. 2012), was probably linked to timber trade. The drivers of its spread remain unclear, similar to its detection in Lebanon approximately seven years later. The distribution of BTB appears patchy, and the first reports from different countries do not follow a clear migration route between Italy and East Mediterranean. For example, BTB was discovered in Greece and Turkey in 2019 (Spanou et al. 2019; Hızal et al. 2023), similar to the timing of its detection in Israel, whereas it was reported in Croatia and Montenegro only in 2023 (Pernek et al. 2025; Fiala et al. 2025). Thus, it is difficult to determine whether the current pattern reflects natural spread or human-assisted dispersal, which may better explain the observed timelines.

Natural spread to Israel may have occurred from Lebanon, where BTB was detected two years earlier (Moussa et al. 2021). Beetles as a group of invasive species are considered to have relatively slow spread rates among insect orders, although substantial variation exists within orders (Roques et al. 2016). Among ambrosia beetles in the Mediterranean Basin, large differences in spread rates have been observed. For example, *Xylosandrus crassiusculus* (Motschulsky) was first reported in Italy in 2003 (Pennacchio et al. 2003) and has since been recorded in Italy, France, Spain, Slovenia, Malta, Switzerland, and parts of European Russia. Its spread may reach several kms per year when assisted by wind or human activities (Hoppe et al. 2020), suggesting that natural dispersal alone cannot explain its expansion. Another ambrosia beetle, *Megaplatypus mutatus* (Chapuis), established in Italy as early as 2000, has remained largely restricted to a few areas in that country (Anonymous 2020). In contrast, *Euwallacea fornicatus* Eichhoff, first recorded in Israel in 2009 (Mendel et al. 2012), was recently detected in the western Mediterranean Basin in Andalusia, southern Spain, in April 2022 (Goldarazena et al. 2025).

The continuous geographical belt extending across the northern, northeastern, and northwestern Mediterranean Basin where BTB populations have been established is characterized by hot-summer Mediterranean (Csa) and hot semi-arid (BSh) climates according to the Köppen–Geiger classification (Köppen 1936). These climatic conditions are suitable for BTB development and may facilitate its continued spread. Nevertheless, human-mediated dispersal likely plays a major role in the colonization of new areas where suitable host plants occur in the Mediterranean region. In Israel, the relatively rapid spread of BTB occurred between 2019 and 2023 and was largely confined to the western Galilee. Between 2024 and 2026, however, the population declined markedly in most previously occupied habitats. This decline may have caused a slower spread southwards and eastwards into habitats with suitable hosts, including the woody vegetation of Mount Carmel and ornamental trees. Notably, in habitats irrigated during summer, such as gardens and home yards in villages and kibbutzim, BTB population densities were much higher than in open areas, both during the outbreak years and during the subsequent population decline.

Host trees and their susceptibility to the black twig borer

BTB has been reported from more than 220 host species belonging to over 60 families (Ngoan et al. 1976; Beaver et al. 2014), including economically important crops such as cacao (Oliveira et al. 2008), coffee (Egonyu et al. 2015), and pecan (Monterrosa et al. 2022). Its establishment in the Mediterranean Basin has therefore created new interactions with the typical woody vegetation of the region. In the present study, most of the attacked species are native to Israel (15 of 22 species). A similar pattern was reported in Italy (~30 of ~42 species; Di Sora et al. 2023), and even more pronounced patterns were observed in Croatia (8 of 9 species; Pernek et al. 2025) and Turkey (5 of 6 species; Hızal et al. 2023). These findings suggest that BTB readily exploits native Mediterranean woody flora once established in the region. In this respect, BTB is very different from *E. fornicatus*, also of the Xyleborini, that established itself in Israel and the vast majority of its hosts, especially the severely damaged ones, are alien tree species (Mendel et al. 2021).

Smilax aspera, an evergreen climber indigenously found in Mediterranean groves and riparian forests, is widespread in Israel, where it grows as a climbing vine in Mediterranean habitats (Alon 2017). The severe damage observed in *S. aspera* vines was therefore not unexpected. The pronounced internodal elongation of the stems, together with indeterminate primary growth and a sympodial branching pattern, may increase the plant's susceptibility to BTB colonization. Owing to its high susceptibility and the conspicuous damage it exhibits, this vine species may serve as a useful indicator of BTB presence in forested areas and may even provide evidence that its spread in the Western Galilee has halted toward the south and east.

During the three years of severe BTB outbreaks in forest and ornamental trees in Israel, the most severe damage was recorded in four tree species: *C. siliqua*, *A. andrachne*, *C. siliquastrum,* and *L. nobilis*, with the most extensive damage occurring in the first two species. *Ceratonia siliqua* is the most frequently tree species associated with BTB damage in the Mediterranean, and extensive information on this interaction has been obtained from studies conducted in Sicily (e.g., Gugliuzzo et al. 2020). The origin of the carob tree, however, remains debated. While traditional views place its origin in the eastern Mediterranean Basin, alternative hypotheses suggest a pre-Mediterranean tropical origin, with early diversification linked to southern Arabia and the Horn of Africa (e.g., Mahdad and Gaouar 2023). The high susceptibility of these trees may be related to the ability of BTB to colonize not only twigs but also thicker skeletal branches. This behavior was first documented in *C. siliqua* in Sicily (Gugliuzzo et al. 2019a) and may be associated with the proliferation of the beetle's symbiotic fungi within attacked tissues (Mendel et al. 2021).

Although attacks on thick branches of additional tree species were recorded in the experimental plot, these involved young trees with relatively few attacks, and it remains unclear whether they resulted in successful reproduction. The attack patterns observed in the Cabri experimental plot, therefore, do not likely reflect the dynamics occurring in adult trees. For example, oak trees in the Cabri plot were seldom affected, whereas nearby mature oaks, mainly *Quercus calliprinos*, were heavily attacked. The timing of the main attack waves also differed among species in the experimental plot. Activity in *P. palaestina* was concentrated in autumn 2023, whereas in *A. obtusifolia* and *C. siliquastrum* most attacks were recorded during the summer and autumn of 2025.

Seasonal flight

Information on the seasonal flight of BTB adult females was obtained from Sicily using ethanol-baited traps. The flight occurs throughout the warm season and is characterized by two waves: a moderate spring flight and a larger wave during the second half of summer and autumn (Gugliuzzo et al. 2019b). Observations in the present study, based on monitoring BTB penetration holes dynamics in the Cabri plot, showed essentially the same pattern. Peak trap captures of the congener *X. germanus* have been reported in mid-May and early August (Gandhi et al. 2010). Such seasonal activity is typical of ambrosia beetles and is influenced, among other factors, by ambient temperature (Reding et al. 2013). Similarly, the flight activity of 64 species of Xyleborine ambrosia beetles in agricultural areas in Thailand did not differ significantly among cropping systems or study zones but fluctuated seasonally, with lower temperatures and higher relative humidity providing the most favorable conditions (Sittichaya et al. 2012). In Israel, attacks of *E. fornicatus* in avocado orchards begin in April (late spring), increase gradually until September, and decline from October to early December (Mendel et al. 2017).

In the present study, examination of twigs with active galleries of BTB according to colonization date and host tree species indicated that the twigs colonized in October contained young adults that emerged only with the rise in temperatures in spring (March–April). Thus, autumn colonization may lead to infestations that persist for 5–6 months. Although development of immature stages is rapid—requiring about 20 days from oviposition to young adult emergence at 25 °C (Ngoan et al. 1976)—adult maturation and emergence from the twigs take considerably longer periods.

Gallery reproduction success

Twig sampling indicated that most observed attack points represented developmental failures of BTB. This likely reflects the limited suitability of the young trees in the experimental plot for successful reproduction. Therefore, these findings do not necessarily indicate that a similar pattern would occur in mature trees of the same species, as suggested by the observations on *Q. calliprinos* in the present study. Several additional factors may influence the reproductive success of BTB in twigs. Data obtained from the Cabri study plot showed significant differences in reproductive success among the tested tree species. However, the underlying causes of these differences remain unclear. One possible explanation is variation among host species in the growth and establishment of the symbiotic fungi associated with BTB. Another possibility is that the relatively young age of the experimental trees affected their suitability for colonization and brood development. For example, *P. palaestina* trees examined in natural habitats and as ornamental plantings, as well as those in the experimental plot, exhibited minimal visible damage despite the relatively high reproductive success observed in branches of this species in the experimental plot. This discrepancy suggests that additional ecological or physiological factors may influence the expression of damage in the field. Reproductive success may also be affected by the presence of other fungal species introduced during gallery excavation. These fungi may establish within the galleries and could act antagonistically toward the symbiotic fungi and/or the developing BTB larvae (Maymon et al., in preparation).

Management

A wide range of tools and actions have been tested to mitigate the damage caused by Xyleborini species (e.g., Gugliuzzo 2021, Ranger et al. 2016). However, the most widely recommended and routinely applied management strategies remain sanitation, including removal of infested branches or entire trees, preventive insecticide sprays applied to stems and branches, and, to a lesser extent, trunk injection of systemic insecticides. Ambrosia beetles are generally difficult targets for biological control. Although many species respond strongly to host volatiles, unlike sex or aggregation pheromones, these attractants have not proven effective for population suppression. Integrated management approaches are considered the most effective, but their implementation is often too costly for large-scale application in most habitats.

In Israel, the outbreak and damage caused by BTB were concentrated mainly in ornamental trees. Damage in forest and maquis habitats was moderate, and no management measures were considered necessary in these environments. Although severe damage was observed in *S. aspera*, which was not perceived as a major concern, possibly since this climber is often regarded as a nuisance due to its thorns, and less attention is given to its ecological role and contribution to ecosystem services.

The extensive damage to ornamental trees during the outbreak years required a management response. In both Hawaii and Africa, continued damage caused by BTB is addressed primarily through pruning and destruction of infested twigs, which remains the most reliable control strategy (Greco and Wright 2015; Nanjego et al. 2024). Chemical control is generally considered of limited value because the beetles spend most of their life cycle protected within plant tissues. Nevertheless, preventive trunk sprays of pyrethroid insecticides have provided effective protection against attacks by related species such as *X. germanus* and *X. crassiusculus* in ornamental plant nurseries (Ranger et al. 2016). In the present study, we focused on products that could be applied to protect ornamental trees located in close proximity to human habitation. Dorclaim, a formulation based on emamectin benzoate administered through trunk injection, was intended to protect trees by targeting BTB stages developing deep within the twig tissue. A *Beauveria bassiana*-based preparation was evaluated as a preventive treatment, given the susceptibility of different BTB life stages to fungal infection (Balakrishnan et al. 1994; Greco and Wright 2015). Our results did not demonstrate clear effectiveness of either preparation. The concentration of emamectin benzoate in the twigs during autumn, when infestations were observed, may have been insufficient to cause substantial mortality of BTB, particularly since injections were performed in spring. However, in another study (Byrne et al., 2020), it was found that emamectin benzoate is well and quickly established if the substance is injected after dilution, it is maintained at a relatively high concentrations in avocado tree tissues for nine months. Preventive sprays using the *B. bassiana* preparation were likewise ineffective; following the series of applications, the fungus was isolated from only a single beetle (Maymon et al. in preparation). This experimental system also had several limitations. Assessment based on tree crown photographs provided only a coarse estimate of changes in tree condition. In addition, the general decline of the BTB population during the study period likely influenced the observed outcomes.

Inhibitory effect of tested fungicides

Integrated treatments combining systemic insecticides and fungicides have been proposed as an effective approach to target ambrosia beetles within their galleries and their associated symbiotic fungi (e.g. Mayorquin et al., 2018; Grosman et al., 2019). Following reports that propiconazole effectively controlled symbiotic *Fusarium* of *Euwallacea fornicatus* under laboratory conditions (Eskalen et al., 2016), subsequent studies demonstrated that trunk injection of emamectin benzoate combined with propiconazole significantly reduced infestations in sycamore trees and largely prevented colonization of healthy trees by the latter beetle (Grosman et al., 2019). However, another study (Roberts et al. 2024) found that the individual systemic treatments, emamectin benzoate and propiconazole, in American sweetgum did not reduce colonization attempts by *E. fornicatus*. These findings indicate that preventive systemic treatments can be highly effective. Accordingly, we hypothesized that accumulation of an effective systemic fungicide in twigs may inhibit BTB development.

Three fungal species were selected to evaluate the inhibitory effects of 21 fungicidal formulations. *Ambrosiella xylebori* was included due to its confirmed symbiotic role with BTB. *Fusarium solani* was selected despite its limited presence in the isolation dataset (Maymon et al., in preparation), based on prior evidence suggesting its involvement as a symbiont. *Thyridium lauri* was included as a positive control due to its high abundance. Its role as a symbiont was subsequently supported by Sun et al. (2025)-and independently proposed by our group (Maymon et al., in preparation) .

Several systemic fungicides exhibited significant inhibitory activity. Luna Experience (fluopyram + tebuconazole) inhibited growth of *A. xylebori* at 0.1 ppm (a.i.). At the same concentration, Mirage (prochloraz) and Tecto (thiabendazole) inhibited *F. solani*. Tecto (thiabendazole) showed comparable activity against *T. lauri* at 1 ppm (a.i.). The tested fungicides represent distinct modes of action. Fluopyram inhibits mitochondrial respiration via succinate dehydrogenase. Tebuconazole and prochloraz inhibit sterol biosynthesis by targeting C14-demethylase (CYP51), impairing membrane integrity. Thiabendazole disrupts microtubule assembly, thereby inhibiting cell division. All four fungicides are generally effective against Ascomycetes. Thus, the classification of *A. xylebori* within the Sordariomycetes may partly explain its sensitivity, particularly to a formulation combining two active ingredients with different modes of action (Mendoza-Duarte et al. 2024; Rashid et al. 2014; Zucollo et al. 2019). Serenade (*Bacillus subtilis* strain QST713) inhibited the growth of all three tested fungi at 0.1 ppm (a.i.). However, this fungicide is not systemic and has not yet been evaluated as a means of controlling ambrosia beetle populations.

Decline of BTB populations in the Galilee

Following the detection of BTB in the Western Galilee, management considerations were considered based on reports of population declines in previously invaded regions. BTB has been established in Florida for decades, but in recent years it has not been considered a significant pest (Jiri Hulcr, pers. comm.). Similarly, outbreaks in central Italy and Sicily have declined, although infestations in bay laurel nursery stock persist (Antonio Gugliuzzo, pers. comm.). In the Circeo area, declining BTB populations have been observed alongside an increase in *Xylosandrus germanus* (Andrea Vannini, Stefano Speranza and Mario Contarini, personal communication). In contrast, no comparable decline has been reported in coffee-growing regions such as Hawaii, Africa, and India, where BTB remains a persistent pest (Greco and Wright 2015; Shankarkumar 2021; Nanjego et al. 2024). In Uganda, it has become a major coffee constraint under shaded conditions favorable to infestation (Kagezi et al. 2020; Edwin et al. 2025).

Herbivorous insect dynamics are generally driven by bottom-up forces (host plant quality), top-down forces (natural enemies), and abiotic factors such as temperature and precipitation (Ylioja et al. 1999; Cudmore et al. 2010; Myers and Sarfraz 2017; Ekholm et al. 2019; Prasad 2022). However, this framework does not fully explain BTB dynamics in the Galilee. Host availability is not a limiting factor, and classical top-down regulation is also expected to be weak, as invasive ambrosia beetles are typically only marginally affected by predators, parasitoids, or entomopathogens, particularly within their protected gallery systems. While climate may influence tree stress or fungal symbionts, it does not adequately account for the observed patterns of both outbreak and decline of BTB in recent years.

We therefore propose an alternative mechanism based on microbial interactions. During colonization of new habitats, BTB females may acquire a diverse assemblage of non-symbiotic fungi and yeasts (see also Rassati et al. 2019). Approximately 40 such species have been isolated from galleries and developmental stages (Maymon et al., in preparation). These microorganisms may act as antagonists to the beetle's nutritional symbionts or directly disrupt larval development by altering the fungal food source. The gradual accumulation of these "contaminant" species within galleries could suppress population growth over time. Conversely, dispersal of adult females free from these "contaminant" species to new sites may enable renewed population outbreaks until the re-accumulation of foreign fungal and yeast species in the new habitat. This hypothesis is currently under investigation. The apparent absence of a similar decline in tropical coffee systems may reflect the origin of BTB in tropical environments, where such antagonistic microbial interactions may be weaker or more balanced, whereas in Mediterranean habitats the impact of foreign fungi may be more pronounced.

Conclusions

The invasion of the black twig borer (BTB) into Northern Israel resulted in substantial damage to several iconic tree species of the Mediterranean lowland forest. Despite efforts to elucidate the drivers of the outbreak and evaluate potential mitigation strategies, the findings highlight significant gaps in understanding the mechanisms underlying this invasion. The population dynamics observed during the initial three years following establishment—marked by a rapid increase followed by a pronounced decline— rendered BTB control interventions unnecessary and insignificant. Damage was largely confined to ornamental plantings of native trees, further limiting the immediate management implications. Accordingly, the efficacy and practical relevance of the tested treatments, including *Beauveria bassiana*–based formulation and emamectin benzoate, could not be conclusively determined under the observed conditions. The invasion trajectory of BTB in Israel is consistent with patterns reported for other invasive ambrosia beetles in the Mediterranean basin. However, the abrupt population decline, together with the potential involvement of environmentally acquired fungal associates, warrants further investigation. Elucidating these interactions may contribute to the development of more effective, predictive, and proactive management approaches for this ambrosia beetle.

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Author contributions

Conceptualization: DM, SF and ZM; methodology: HB, MM, DBS, SS and ZM, formal analysis: HB, MM and ZM, investigation: HB, MM, SF, DM and ZM. Resources: OG and NB; data curation: HB, DM and ZM; writing original draft and editing: ZM, DM, HB and SF, project administration: NB, OG, HB and DM, funding acquisition: DM, SF and ZM.

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Figure Legends

Figure 1. Map of surveyed locations in Israel where infestation by *Xylosandrus compactus* was recorded on ornamental trees (in villages and kibbutzim ●) and in natural vegetation (in forests or nature reserves ♣).

Figure 2. Layout of the trees in the experimental plot at Cabri – KKL-JNF.

Figure 3. Summary of the monitoring of 126 trees in four localities in the Western Galilee that were observed to be damaged by BTB in 2023, and their condition in 2024 and 2025, according to the tree species examined.

Figure 4. Comparison of attack intensity (total number of BTB penetration holes) in the experimental trees in the Cabri KKL-JNF observation plot, according to season and year.

Figure 5. Seasonal changes in the density of BTB penetration holes (average number per month per tree species per individual tree) in seven forest tree species in the Cabri KKL-JNF experimental plot. The values in parentheses next to each tree species indicate the average ± SD number of holes per tree species per individual tree for the entire monitoring period.

Figure 6. Comparison of attack intensity (total number of BTB penetration holes) in the experimental trees in the Cabri KKL-JNF observation plot, arranged according to

the total number of penetration holes recorded for each individual tree among the seven tree species examined.

Figure 7. Comparison of the proportion of BTB penetration holes in branches and stems out of the total number (including twigs) of penetration holes in each of the seven tree species examined at the Cabri KKL-JNF monitoring site. The values in parentheses indicate the total number of penetration holes observed for each tree species, used for percentage calculations.

Figure 8. Comparison of changes in health following pesticide application in four field trials. Values indicate the mean difference (SE±) in health index as affected by *Xylosandrus compactus* between spring pre-treatment and fall sampling as follows: Adamit April - September 2023; Yechiam (Bioveria) - April - October 2024; Ga'aton February - September 2023; Yechiam (Dorclaim) March - November, 2024. The negative and positive values indicate deterioration or improvement in the health index, respectively.

Table 1. Tested fungicides against symbiotic fungi carried by the *Xylosandrus compactus.*

Product	Active Ingredient(s)	Israeli marketer
Acanto Plus	Picoxystrobin + Cyproconazole	Gadot Agro
Amistar	Azoxystrobin	Adama Makhteshim
Beltanol*	Hydroxyquinoline sulfate	Gadot Agro
CeraMax	Netamycin	Luxembourg Industries
Dodine*	Dodine	Luxembourg Industries
Elatus Plus	Benzovindiflupyr	Adama Agan
Hosen	Flutriafol	Adama Makhteshim
Kenja	Isofetamid	Luxembourg Industries
Luna experience	Fluopyram + Tebuconazole	Lidorr Elements
Luna sensation	Fluopyram + Trifloxystrobin*	Lidorr Elements
Luna tranquility	Fluopyram + Pyrimethanil	Lidorr Elements
Mirage	Prochloraz	Adama Makhteshim
Miravis Solo	Triflufenac-hydroxylamine	Adama Makhteshim
Parade TOP	Pyraziflumid	Gadot Agro
Primium	Boscalid + Azoxystrobin	Tapazol Chemical Works
Serenade*	*Bacillus subtilis* strain QST713	Luxembourg Industries
Shido **	Penthiopyrad	RIMI

Switch **	Cyprodinil + Fludioxonil	Adama Agan
Tachigaren	Hymexazol	Adama Agan
Tecto	Thiabendazole	Adama Makhteshim
Twist	Fludioxonil + Pyrimethanil	Tapazol Chemical Works

* - Non-systemic fungicides

** - Local systemic fungicides

Table 2. Source of symbiotic fungal isolates and their growth rate (number of days required for mycelium to cover the entire surface of PDA non-amended medium in a 9 cm-Petri dish medium).

Fungal species	Isolation organ	Tree species	Location	Growth rate (days)
Ambrosiella xylebori	Mature female	*Ceratonia siliqua*	Nahal Betset	7
Fusarium solani	Active gallery	*Quercus infectoria*	Adamit	10
Thyridium lauri	Active gallery	*Cercis siliquastrum*	Evron	25

Table 3. Species of woody plants attacked by *Xylosandrus compactus*, in the Western Galilee, Israel, and severity of damage according to the tree species (presented in alphabetical order). In each of the species listed, branches actively populated by *X. compactus* were identified. The severity of damage refers to the years 2022-2024 during the outbreak period of BTB populations.

Species	**Botanical family**	**Damage severity index**
Acer obtusifolium	Sapindaceae	2
Arbutus andrachne	Ericaceae	**3
*Carya illinoinensis**	Juglandaceae	1
*Celtis australis**	Cannabaceae	1
Ceratonia siliqua?*	Fabaceae	**3
Cercis siliquastrum	Fabaceae	3
*Fraxinus uhdei**	Oleaceae	1
Laurus nobilis	Lauraceae	3
*Magnolia grandiflora**	Magnoliaceae	1
Nerium oleander	Apocynaceae	1
Olea europea	Oleaceae	1
Pistacia lentiscus	Anacardiaceae	1
Pistacia palaestina	Anacardiaceae	2
Platanus orientalis	Platanaceae	2

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Quercus calliprinos	Fagaceae	1
*Quercus ilex**	Fagaceae	2
Quercus infectoria	Fagaceae	2
Quercus ithaburensis	Fagaceae	2
*Quercus suber**	Fagaceae	2
Smilax aspera	Smilacaceae	**3
*Tecoma stans**	Bignoniaceae	1
Viburnum tinus	Adoxaceae	1

* Introduced (non-native)

** Significant tree mortality was recorded in some locations

Table 4. Concentration of the population success test of *Xylosandrus compactus* from different sampling events. The values indicate % *X. compactus* infested twigs with live immature stages of the borer. Most of the twigs were sampled in the experimental plot at KKL- Cabri plot, other twigs were sampled from mature trees in Yechiam and Ga'aton.

Tree species (number of sampling events)	% twigs with live immature stages of BTB (number twigs examined)
Acer obtusifolium (4)	25.0 (32)
Arbutus andrachne (2)	64.4 (59)
Ceratonia siliqua (5)	29.9 (117)
Cercis siliquastrum (6)	49.5 (245)
Laurus nobilis (5)	24.5 (159)
Pistacia palaestina (4)	51.5 (66)
Quercus calliprinos (4)	16.7 (102)
Quercus ithaburensis (2)	14.3 (28)
Total	37.0 (817)

Table 5. Presentation of the % mean ± SD of inhibition by 21 systemic fungicides at a dose of 0.1 PPM on the development of the two symbiotic fungal species *Ambrosiella xylebori* and *Thyridium lauri*, and one of the common worldwide associates *Fusarium solani* (previously suspected of being a symbiotic species). The values in bold indicate an average inhibition of fungal development greater than 85%.

The preparation	The fungus (and isolate number)		
	A. xylebori (15-2)	*T. lauri* (16-5)	*F. solani* (1-1)
Acanto Plus	44.6 ± 0.64	83.8 ± 0.55	66.3 ± 2.03
Amistar	31.8 ± 3.5	93.8 ± 1.7	95.7 ± 0.9
Beltanol	96.7 ± 1.39	90.1 ± 5.17	95.6 ± 0
CeraMax	101.7 ± 1.13	101.7 ± 3.52	100 ± 0.81
Dodine	105.5 ± 0.47	100.5 ± 2.01	100.4 ± 0
Elatus Plus	37.1 ± 2.58	101 ± 1.42	100 ± 0.83
Hosen	21.2 ± 1.19	101.6 ± 1.94	97.5 ± 1.09
Kenja	97 ± 0.42	101.7 ± 3.2	96 ± 0.4
Luna experience	**10.6 ± 0.15**	99.9 ± 1.08	71.2 ± 0.35
Luna Sensation	**14.7 ± 1.55**	99.9 ± 0.54	67.7 ± 0.34
Luna Tranquility	90.4 ± 1.13	115.2 ± 1.54	100 ± 0.42
Mirage	27.1 ± 2.8	27.56 ± 0.4	**10.9 ± 0.1**
Miravis Solo	92.9 ± 1.33	100.5 ± 3.18	41.6 ± 0.81
Parade	99 ± 0.95	85.8 ± 7.86	96 ± 0.8
Primium	44.7 ± 1.58	107.1 ± 2.03	97.9 ± 0.71
Serenade	**8.3 ± 0.36**	**0.5 ± 0.12**	**4.1 ± 0.17**
Shido	97.8 ± 3.16	100 ± 0.53	99.6 ± 0.72
Switch	70.1 ± 2.5	80.06 ± 2.3	52.9 ± 2.8
Tachigaren	103.2 ± 0.93	100 ± 3.87	100.4 ± 0
Tecto	91.6 ± 2.73	90.6 ± 2.81	101.7 ± 1.11
Twist	97.8 ± 0.77	104.4 ± 2.88	85.2 ± 1.68

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Fig. 1

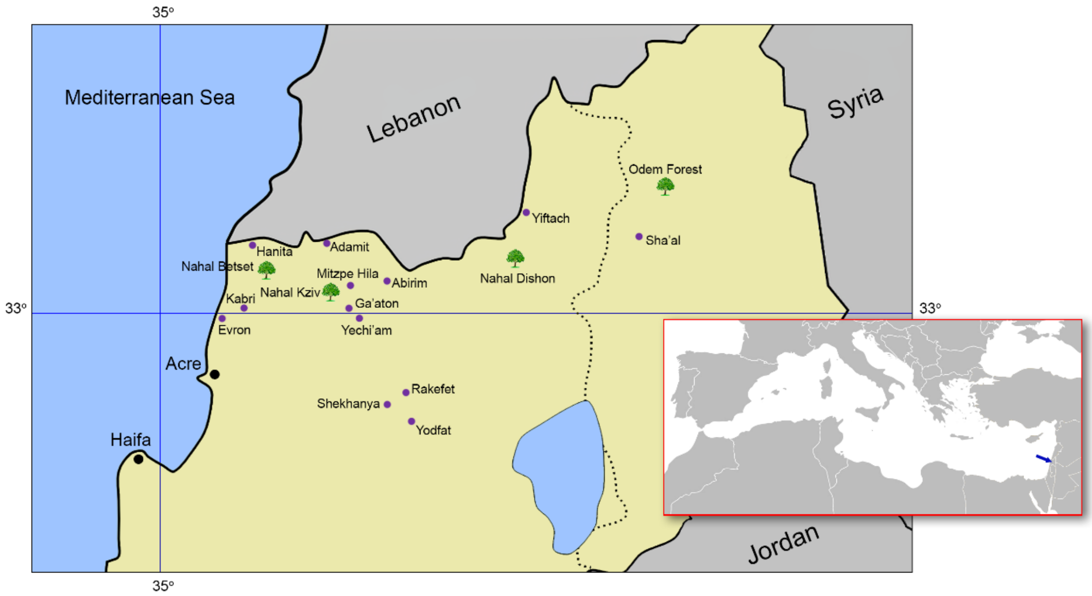

Fig. 2

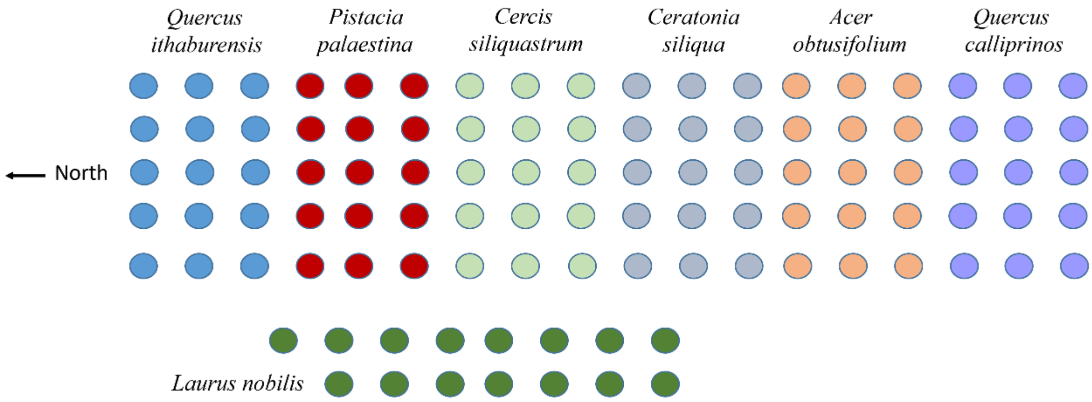

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Fig. 3

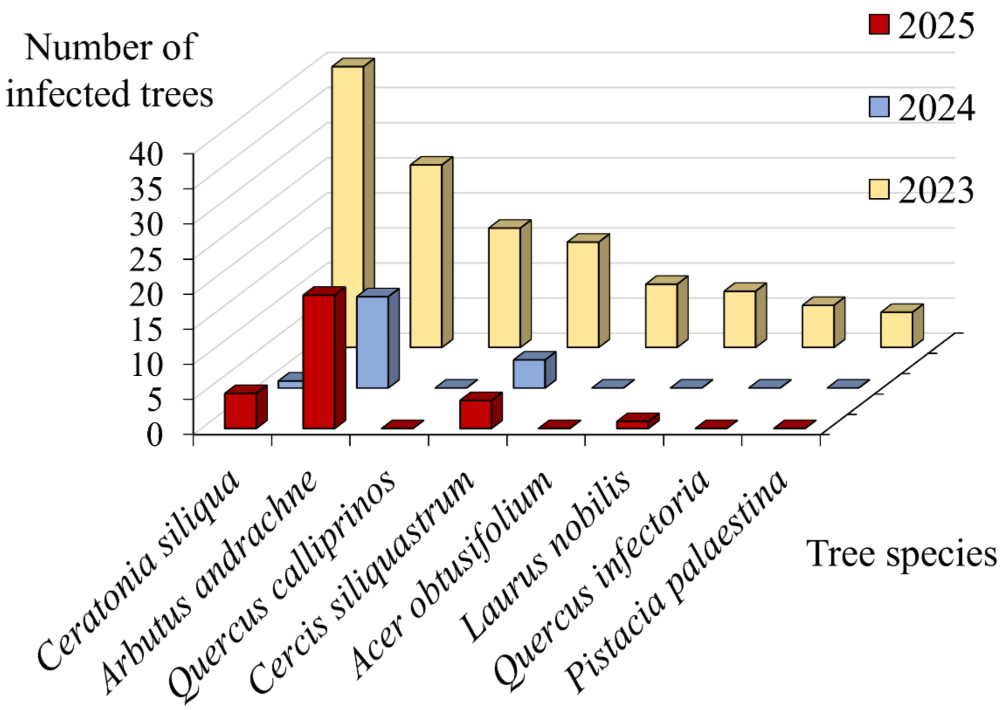


Fig. 4

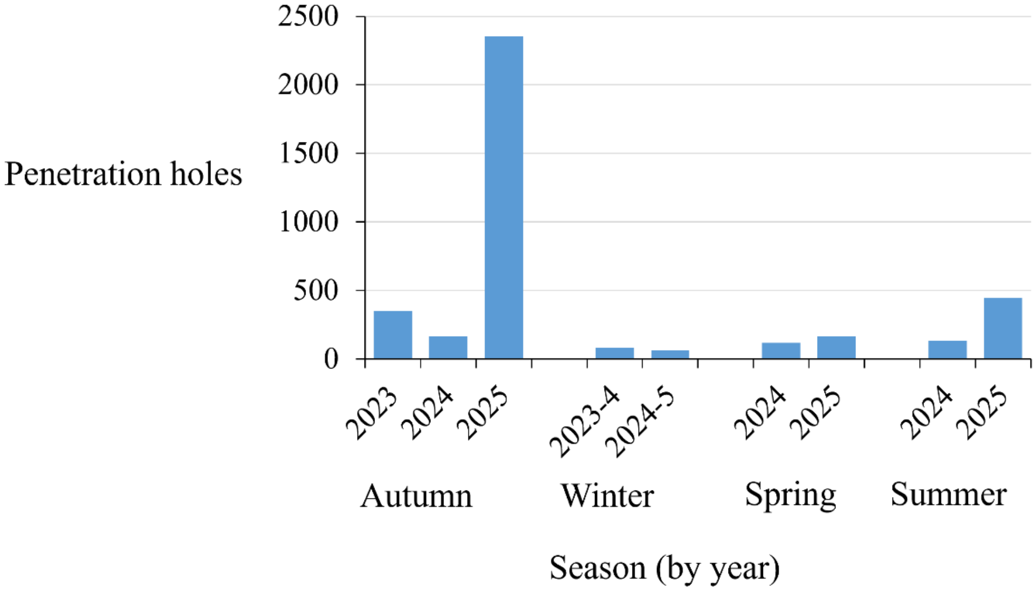
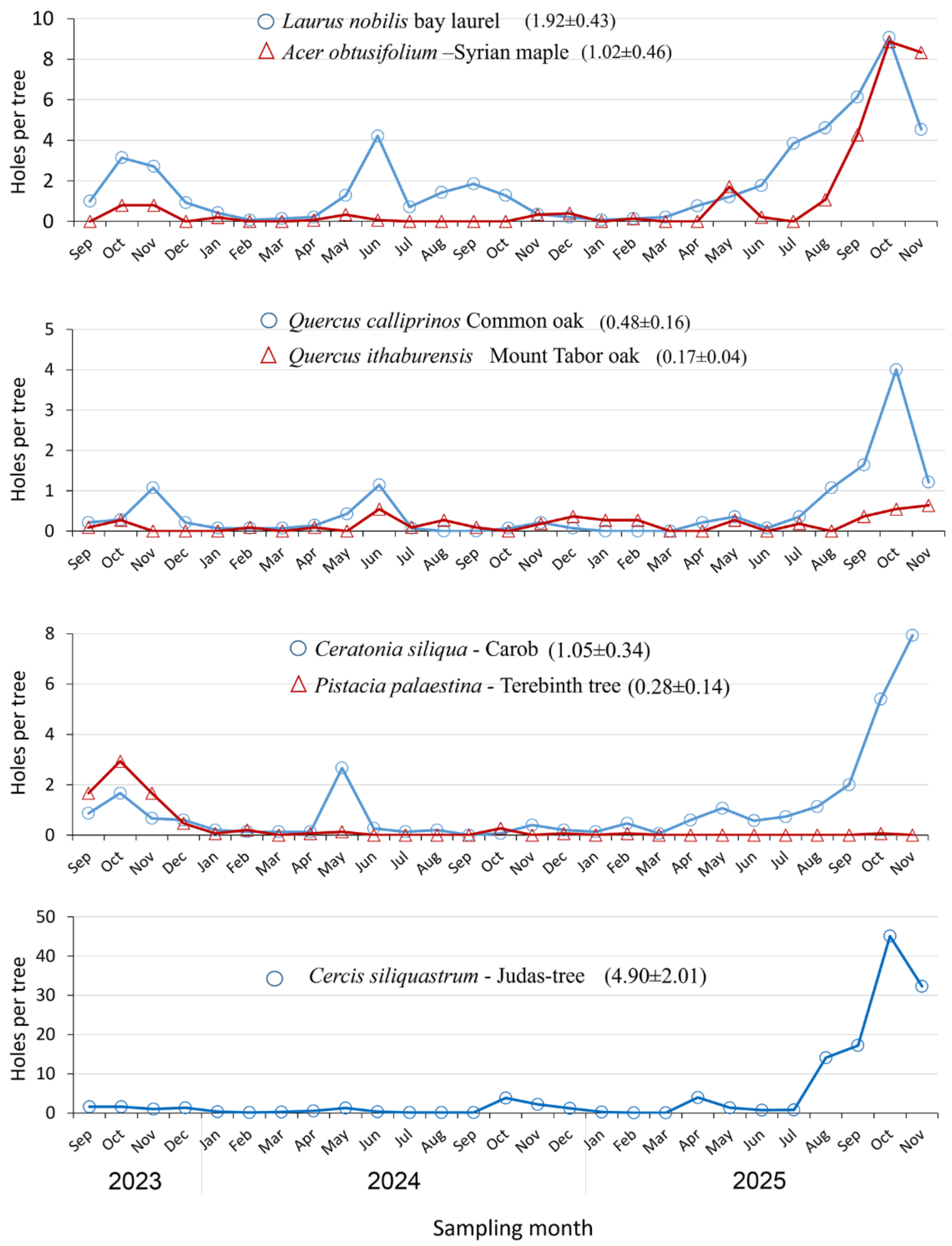


Fig. 5



Laurus nobilis bay laurel (1.92±0.43)
Acer obtusifolium –Syrian maple (1.02±0.46)
Quercus calliprinos Common oak (0.48±0.16)
Quercus ithaburensis Mount Tabor oak (0.17±0.04)
Ceratonia siliqua - Carob (1.05±0.34)
Pistacia palaestina - Terebinth tree (0.28±0.14)
Cercis siliquastrum - Judas-tree (4.90±2.01)
Holes per tree
Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov
2023
2024
2025
Sampling month

Fig. 6

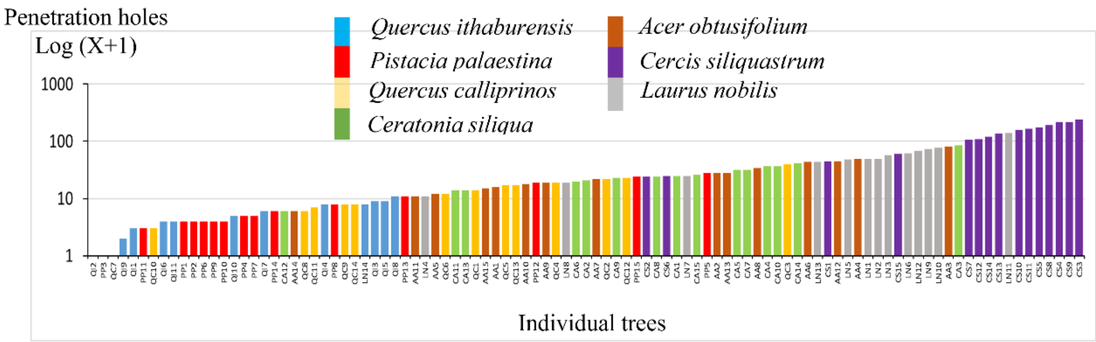

Penetration holes
Log (X+1)
1000
100
10
1
Quercus ithaburensis
Pistacia palaestina
Quercus calliprinos
Ceratonia siliqua
Acer obtusifolium
Cercis siliquastrum
Laurus nobilis
Individual trees

Fig. 7

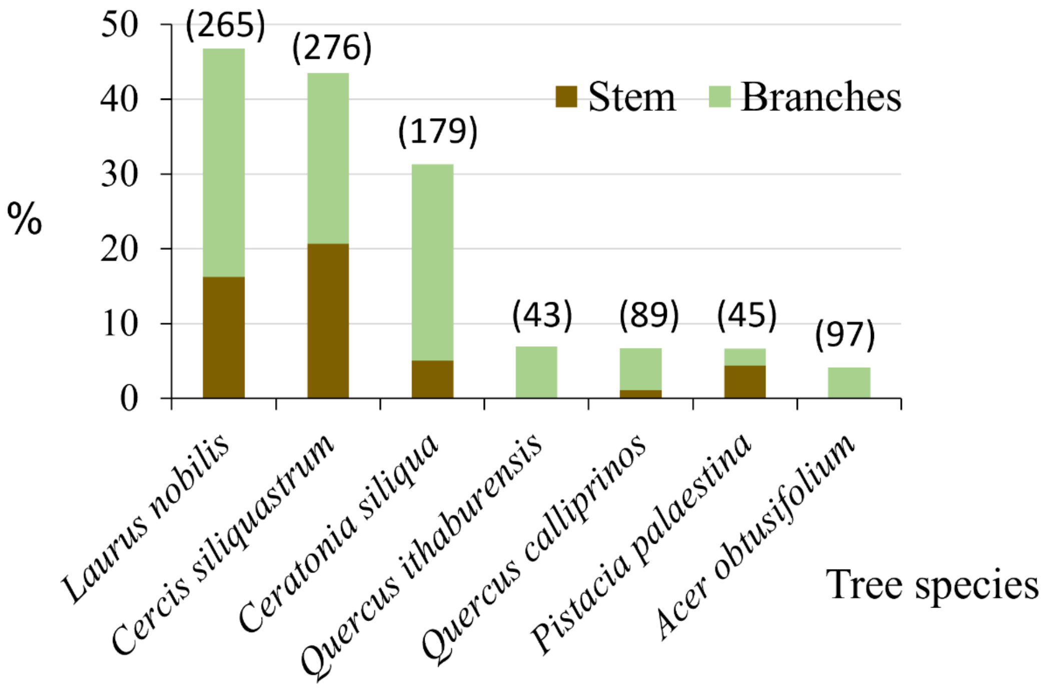
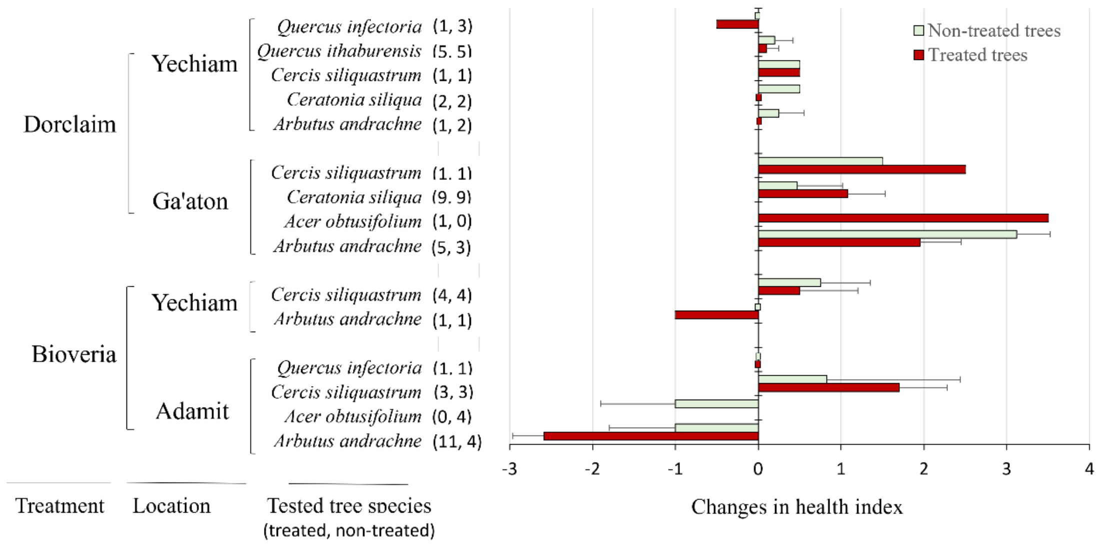

%
50
40
30
20
10
0
(265)
(276)
(179)
(43)
(89)
(45)
(97)
Stem
Branches
Laurus nobilis
Cercis siliquastrum
Ceratonia siliqua
Quercus ithaburensis
Quercus calliprinos
Pistacia palaestina
Acer obtusifolium
Tree species

Fig. 8



Dorclaim
Yechiam
Quercus infectoria (1, 3)
Quercus ithaburensis (5, 5)
Cercis siliquastrum (1, 1)
Ceratonia siliqua (2, 2)
Arbutus andrachne (1, 2)
Ga'aton
Cercis siliquastrum (1, 1)
Ceratonia siliqua (9, 9)
Acer obtusifolium (1, 0)
Arbutus andrachne (5, 3)
Bioveria
Yechiam
Cercis siliquastrum (4, 4)
Arbutus andrachne (1, 1)
Adamit
Quercus infectoria (1, 1)
Cercis siliquastrum (3, 3)
Acer obtusifolium (0, 4)
Arbutus andrachne (11, 4)
Non-treated trees
Treated trees
-3
-2
-1
0
1
2
3
4
Treatment
Location
Tested tree species
(treated, non-treated)
Changes in health index