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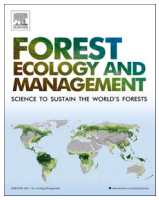

European beech decline in Slovenia is caused by a complex disease

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ABSTRACT

In recent decades, the average crown defoliation of European beech (*Fagus sylvatica*) in Central Europe has been steadily increasing, resulting in a decline in tree vitality. This study aimed to identify the key factors contributing to this deterioration. Forty healthy and 40 damaged European beech trees were felled on a systematic 16 × 16 km grid, and all tree parts were sampled for fungi and insects. Additionally, soil samples were collected for *Phytophthora* testing. Of 6400 cultured samples, 5828 fungal cultures were classified into 251 morphotypes. The twenty most frequent morphotypes from each tree part were selected for further molecular identification, revealing 44 different fungal taxa. The most frequently isolated fungal species were *Neonectria coccinea*, *Neohendersonia kickxii*, *Apiognomonia errabunda* and *Aureobasidium pullulans*—all well-known and common endophytes. Surprisingly, *Phytophthora* species were detected in only three of the 80 soil samples. The most frequent insect species were *Orchestes fagi*, *Phyllaphis fagi*, *Psilocorsis reflexella* and *Phyllonorycter maestingella*. The results indicate that the decline of European beech in Central Europe is driven by a multifaceted interplay of biotic and abiotic factors, with fungi playing the most significant role. Analysis revealed distinct differences in fungal and insect communities across sampled tree parts, but not between healthy and damaged trees. This finding is crucial, as it shows that healthy trees host endophytes that can exhibit pathogenic traits under external stress factors. Therefore, resilience and sustainability of beech will depend on mitigation of stressors and implementation of adaptive management strategies that address the evolving environmental challenges.

1. Introduction

European beech (*Fagus sylvatica* L.) is a prominent deciduous tree species with a broad and continuous natural range spanning from southern Scandinavia to the Mediterranean, and extending from the Spanish Pyrenees in the west to central Poland and western Ukraine in the east (Ellenberg, 1996; von Wühlisch, 2008; Tegel et al., 2013). From both ecological and socio-economic perspectives, *F. sylvatica* represents one of the most important and widely cultivated hardwood species in Europe, historically valued for its wood and ecological adaptability (von Wühlisch, 2008; Tegel et al., 2013).

In recent years, numerous reports from across Europe have highlighted a climate change-driven decline in several tree species, with European beech being particularly affected (Granata and Sidoti, 2004; Jung, 2009; Lakatos and Molnár, 2009; Rohner et al., 2021; Langer and Busskamp, 2023; Tropf et al., 2025). This ongoing decline is believed to be driven by climate change, characterized by rising temperatures, more frequent drought stress and increasingly irregular patterns of precipitation, both temporally and geographically. These environmental pressures, combined with the effects of facultative pathogens, endophytes and secondary pests, contribute to a complex disease syndrome that remains insufficiently understood. In particular, drought stress is considered a key trigger for vitality loss, while associated diseases play a central role in European beech mortality. Under projected climate change scenarios, the impact of facultative pathogens is expected to increase significantly due to shifts in climate patterns, including more frequent extreme weather events (Juroszek and von Tiedemann, 2013; Hunjan and Lore, 2020; Singh et al., 2023).

Increasing drought stress and temperature extremes weaken European beech trees, making them more vulnerable to different pests and pathogens, such as *Phytophthora* spp. (Cech and Jung, 2005; Jung, 2009; Jung et al., 2018; Jankowiak et al., 2022). *Phytophthora* species

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(Oomycota, Chromista) are renowned primary pathogens on numerous tree, shrub and crop species worldwide (Jung et al., 2018). *Phytophthora* epidemics in European countries are often driven by persistently wet growing seasons followed by extreme drought, either in the same year or the following one (Jung et al., 2018).

Another important fungus associated with European beech decline in European forests is *Biscogniauxia nummularia* (Bull.) Kuntze, the causal agent of European beech tarcrust (Granata and Sidoti, 2004; Lakatos and Molnár, 2009; Tropf et al., 2025). Although *Bi. nummularia* is considered an endophyte, under prolonged drought and high temperatures it exploits altered host physiology, displaying pathogenic traits such as elongated blackish bark lesions on the trunk and branches and wood decay in mature trees (Hendry et al., 1998; Granata and Sidoti, 2004; Luchi et al., 2015). It has also been proposed as a potential bioindicator of beech vitality (Luchi et al., 2015; Tropf et al., 2025). Other fungal diseases contributing to European beech decline include *Apiognomonia errabunda* (Roberge ex Desm.) Höhn., *Armillaria* spp., *Fomes fomentarius* (L.) Fr., *Kretzschmaria deusta* (Hoffm.) P.M.D. Martin and *Neonectria* spp. (Ogris et al., 2008).

European beech is also affected by abiotic factors such as wind and ice, as well as insect infestations. The following insects pose a long-term risk to European beech health: *Trypodendron domesticum* (Linnaeus, 1758), *Agrilus viridis* (Linnaeus, 1758), *Phyllaphis fagi* (Linnaeus, 1767), *Orchestes fagi* (Linnaues, 1758), *Elateroides dermestoides* (Linnaeus, 1761), *Cryptococcus fagisuga* (Lindiger, 1936) and *Taphrorychus bicolor* (Herbst, 1793) (Ogris et al., 2008). Non-native invasive species, such as non-native strains of *Phytophthora ramorum* Werres, De Cock & Man in 't Veld, *Phytophthora kernoviae* Brasier, Beales & S.A. Kirk, *Anoplophora chinensis* (Forster, 1771), *A. glabripennis* (Motschulsky, 1853) and *Litylenchus crenatae* ssp. *mccannii* Carta, Handoo, Li, Kantor, Bauchan, McCann, Gabriel, Yu, Reed, Koch, Martin, and Burke, 2020, also pose risks to future beech health.

All these harmful agents contribute to a complex disease affecting European beech, leading to long-term decline of trees and larger forested areas. Senf et al. (2018) analysed trends in forest canopy mortality between 1984 and 2016 across more than 30 million hectares of temperate forests in Europe and found that canopy mortality increased by 2.40 % per year, doubling the forest area affected since 1984. Similar trends have been observed in Slovenia, where average crown defoliation has steadily increased over the last three decades (Ogris and Skudnik, 2021). Since 2017, defoliation of European beech has exceeded 30 %, and even slightly defoliated trees (15 %) showed significant growth reduction (Ferretti et al. (2021). Recent monitoring indicates that diseases are among the primary drivers of European beech decline in Slovenia (Ogris and Skudnik, 2021).

In the context of Manion (1981) 'spiral of death' concept, this complexity can be viewed as the result of interacting predisposing, inciting and contributing factors. Predisposing factors are continuously present stressors that generally weaken the plant over a long period or throughout its life cycle, such as climate change, air pollution, *Phytophthora* spp., persistent pests or seed origin. Inciting factors last only a short period but have a strong, often acute impact on the tree, such as frost, drought or defoliators. Affected trees attempt to recover from the damage caused by inciting factors but are usually unsuccessful due to the persistent predisposing factors. Contributing factors (e.g. bark beetles, decay fungi, blue stain fungi, facultative pathogens) then exacerbate the decline. Trees are subjected to constant pressure from these interacting factors, creating a spiral that ultimately results in the general decline of affected European beech trees.

This study aimed to identify the key factors involved in European beech decline in Central Europe. The roles and importance of fungi, abiotic stressors (wind, snow, ice, late frost, etc.), insects and *Phytophthora* species were examined to assess their impact on European beech health and implications for long-term forest management. Based on these objectives, we tested the following hypotheses: (i) Multiple harmful agents collectively contribute to a complex disease causing European beech decline in Slovenia; (ii) On average, diseases cause greater damage to European beech in Slovenia than insects or other harmful agents; (iii) *Phytophthora* species are present in the soil of more than half of the sampled damaged European beech trees, highlighting their significant role in the decline of these trees; (iv) Fungal and insect communities differ between healthy and damaged trees.

2. Materials and Methods

2.1. Area description

In Slovenia, European beech is widespread and occurs across a wide range of site conditions (Dakskobler, 2008; Ficko et al., 2008), typically at elevations between 500 and 1600 m a.s.l. (Brus, 2008). European beech is the most important broadleaved tree species in Slovenia in terms of wood stock share within natural woodland vegetation. In 2023, it accounted for 119 million m^3, representing 33.4 % of the total wood stock in Slovenian forests (Forest funds 2023). European beech exhibits a broad ecological range, adapting to diverse climatic and geological conditions, and is characterized by high shade tolerance and strong growth capacity (Ellenberg, 1996).

2.2. Sampling plots, damage assessment and sample collection

ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) permanent sampling plots on a systematic 16 × 16 km grid (Kovač, 2014; Eichhorn et al., 2016) were used as a starting point for selecting 40 plots. These plots are annually monitored for forest condition using defoliation indicators and tree damage assessments, according to modified ICP Forests methodology. If European beech trees were absent on a plot or destructive sampling was not permitted on a plot, the nearest suitable location was selected instead. This approach resulted in 39 sampling plots near permanent plots. One additional plot was selected in the Alps to reach the goal of 40 plots and to strengthen representation in this region (Fig. 1). On average, the centroid of the sampling plot was 459 m from the original grid point, with a maximum distance of 1744 m.

Sampling occurred between end of May and September in 2021 and 2022 in accordance with ICP Forest guidelines, i.e. between the end of the first flush of foliage (when the leaves were fully developed) and the beginning of autumnal senescence (Eichhorn et al., 2016). On each plot, two trees were felled, totalling 80 trees: one visually healthy (defoliation less than 20 %, designated as "healthy") and one damaged (defoliation at least 20 %, designated as "damaged"). In two cases, no trees with less than 20 % defoliation were present on the plot. Consequently, a tree with 25–30 % defoliation was selected as the "healthy" tree, and a tree with 45–60 % defoliation was selected as the "damaged" tree, respectively. Trees selected were dominant or codominant to minimize

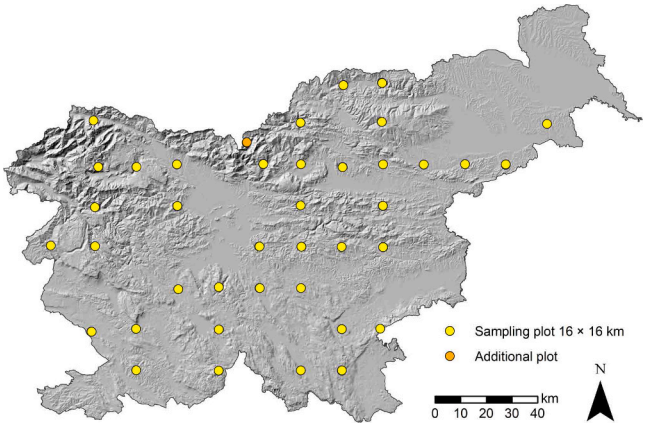

Fig. 1. Locations of sampling plots in the study in Slovenia (n = 40).

competition effects. The average distance between healthy and damaged trees was 42 m (range 6–144 m). For each tree, circumference at breast height, height, coordinates and defoliation were recorded. Diameter at breast height (DBH) was calculated from the circumference at breast height using equation DBH = c/π, where c is the circumference. Tree height was measured using a Vertex III (Haglöf, Sweden), and coordinates were recorded with a handheld GPSMAP 64 s GPS (Garmin, USA). Defoliation, defined as leaf loss in the assessable crown relative to a reference tree (Eichhorn et al., 2016), was assessed in 5 % steps. The reference tree was chosen as the healthiest local tree with full foliage, capable of thriving at the site, taking into account factors such as altitude, latitude, age, site conditions and social status.

Each tree was felled and carefully inspected for any symptoms and signs of disease, insects, abiotic agents, game and grazing, direct action of man or other damage agent (e.g. competition). The crown condition and the presence of damaging agents were visually assessed following the methods and criteria for harmonized sampling, assessment, monitoring and analysis of air pollution effects on forests, developed under the Convention on Long-Range Transboundary Air Pollution (CLRTAP) and the ICP Forests (Jurc and Jurc, 2014; Eichhorn et al., 2016). The following information was recorded: affected part of the tree, specification of the affected part, location in the crown, age of damage, main category of causal agent or factor, scientific name of the cause and extent of damage (%). The extent of damage was defined as the proportion (%) of affected leaves, branches or stem due to the action of the causal agent or factor (Eichhorn et al., 2016). Branch damage was expressed as the percentage of affected branches, and stem damage as the percentage of the stem circumference (Eichhorn et al., 2016).

Five tree parts were sampled for fungal isolation: leaves, twigs (up to 20 mm in diameter, see Supplementary Table S1), branches (over 20 mm in diameter, see Supplementary Table S1), trunk, surface roots and root collar (up to 25 cm from the ground). At least four samples from each tree part were collected, prioritising damaged tissue. If damage was not observed, healthy tissue was collected instead. In total, 20 samples per tree and 40 samples per plot were collected, resulting in 1600 samples.

Felled trees were also systematically surveyed for insects, which were collected and recorded according to the tree and tree part on which they were found. Furthermore, the percentage of defoliation caused by insects was estimated for every tree.

For the *Phytophthora* baiting assay, rhizosphere soil was collected from three to four points within a 1 m radius of each sampled tree. Prior to sampling, the upper humus and organic layers were removed, and soil was taken from a depth of 10–20 cm. A minimum of 1 kg of soil was collected per sample. Soil samples were marked, stored in a cooling box and transferred to the Diagnostic Laboratory of the Plant Protection Department at the Agricultural Institute of Slovenia within 24 h of collection.

2.3. Isolation of fungi

Samples, collected as described above for the purpose of fungal isolation, were labelled, stored in a cooling box and transferred to the Laboratory of Forest Protection at the Slovenian Forestry Institute, where they were stored in a refrigerator at 4 °C until processing. All samples were processed in 24 h. The samples were surface sterilized following this procedure: epiphytes were scrubbed off under tap water for approx. 1 min, dipped in 70 % ethanol for 60 s, 1 % commercial bleach for 30 s, 70 % ethanol for 60 s, rinsed in distilled water, and air-dried on clean paper towels. Subsamples from each sample were cut from the edge of discoloured wood or from the leading edge of necrosis in the bark/leaf. A thin outer layer of bark was removed to reach the leading edge of necrosis. When no damaged part was present, a subsample was taken from healthy tissue. The designations of subsamples are described in Table 1. Four subsamples were collected from each sample, totalling 6400 subsamples/tissue pieces (Table 1). Four subsamples were plated on a growth medium containing 3.9 % (w/v) potato dextrose agar (PDA; Becton Dickinson, Sparks, MD, USA) supplemented with streptomycin (Sigma-Aldrich, Saint Louis, MO, USA) and incubated in darkness at 21.1 ± 0.01 °C. The plates were regularly checked, and any outgrowing mycelium was transferred to new PDA plates. Isolates were classified into fungal morphotypes according to visual morphological characteristics of the cultures. The twenty most frequent fungal morphotypes per tree part considering all trees were selected for identification. After the identification of fungi was completed (see 2.4), the frequency of the fungal species was calculated based on the fungal morphotype to which the species belonged, as well as the number of isolates classified under that morphotype. Representative cultures were deposited in the culture collection of the Laboratory of Forest Protection (ZLVG) at the Slovenian Forestry Institute (Supplementary Table S2).

2.4. Identification of fungi

Total fungal DNA was extracted from mycelium scraped from PDA plates using the Nucleospin Plant II (Macherey-Nagel, Düren, Germany), following the manufacturer's instructions, except that Lysing Matrix A tubes (MP Biomedicals, Solon, OH, USA) and the Precellys Evolution homogenizer (Bertin Technologies, Montigny-le-Bretonneux, France) were used for homogenization. When the ITS region alone was insufficient for species identification, additional genetic markers were amplified to improve taxonomic accuracy. For amplification of selected DNA regions, we used combinations of primer oligonucleotides and

Table 1
Number of samples per tree class, tree part and sample location.

Tree class	Tree part	Discoloured wood (WD)	Healthy wood (WH)	Outer bark (BO)	Inner bark (BI)	Healthy bark (BH)	Diseased leaf (LD)	Healthy leaf (LH)
Damaged	Leaves	0					159	1
	Twigs (< 2 cm)	14			146			
	Branches (> 2 cm)	75		1	84			
	Trunk	68		78	2	12		
	Roots and collar (≤ 25 cm height)	108	1	48		3		
Total Damaged		265	1	127	232	15	159	1
Healthy	Leaves	0					151	9
	Twigs (< 2 cm)	18		1	137	4		
	Branches (> 2 cm)	74		2	84			
	Trunk	69	1	76	5	9		
	Roots and collar (≤ 25 cm height)	99		50	3	8		
Total Healthy		260	1	129	229	21	151	9
Grand Total		525	2	256	461	36	310	10

conditions as specified in Table 2.

PCR products were cleaned using a Wizard SV Gel and PCR Clean-Up System (Promega, Madison, WI, USA) and sequenced at a sequencing facility (Eurofins, Köln, Germany) in both forward and reverse directions using the same primers as for the PCR. Sequences were visualized and manually edited using Geneious Prime v.2019.0.3. (Biomatters Ltd., Auckland, New Zealand). Consensus sequences were subjected to individual nucleotide-nucleotide searches using the megablast algorithm on NCBI (http://www.ncbi.nlm.nih.gov/BLAST/, accessed on different dates 20 January 2023–9 October 2023). Sequences were deposited in GenBank (Supplementary Table S2). Species identification was based on a combination of BLAST search results, phylogenetic tree placements and relevant data from the literature.

2.5. Identification of insects

Insects were identified based on their morphological characteristics. Adult specimens were identified to the species level, while juvenile specimens were identified to the lowest possible taxonomic level (family or genus). When identification was not possible, species were inferred based on the type of damage (e.g. mines, galls or galleries), otherwise a higher taxonomic level was assigned.

2.6. Isolation of Phytophthora spp.

Isolations of *Phytophthora* spp. from soil samples followed the procedure described by Corcobado et al. (2020) with some modifications. Approximately 1 kg of each soil sample was carefully mixed, divided into two plastic containers and carefully flooded with distilled water so that the soil was covered by 2–3 cm of water. Floating particles were removed either with tweezers or a small sieve, and the soil was allowed to settle for at least two hours. Fresh, healthy leaves were floated on the water surface to cover it completely. Baiting material included young and mature leaves of *Rhododendron catawbiense* cv. 'Cunningham's White', cotyledons and young leaves of *F. sylvatica*, and young leaves of *Quercus rubra* L., *Q. petraea* (Mattuschka) Liebl., *Castanea sativa* Mill., *Carpinus betulus* L., and *Vaccinium myrtillus* L. Baits were incubated for 3–7 days at 20–22 °C under daylight conditions. Leaves exhibiting necrotic lesions were examined under a light microscope (Zeiss, Oberkochen, Germany) at 60 × magnification. Infected tissue was briefly washed with distilled water and dried under laminar airflow, and pieces of necrotic spots were plated onto P_5ARPH selective agar media (EPPO, 2006) and incubated at 21 °C in the dark (Corcobado et al., 2020). Plates were regularly checked from 24 h after plating (Jung et al., 2016). Developing colonies were transferred onto carrot piece agar (CPA; Werres et al., 2001; agar 22 g, carrot pieces 50 g, distilled water 1000 ml), and after three weeks of growth at 21 °C, isolates were inoculated onto CPA slants and stored in sterile water at 8 °C until further processing.

Table 2
Primer oligonucleotide combinations and PCR conditions.

DNA region	Primers used	Annealing T (°C)	Reference of primers used
ITS rDNA	ITS1 / ITS4	55	White et al. (1990)
Calmodulin (CAL)	CAL-228F / CAL-737R	48	Carbone and Kohn (1999)
Translation elongation factor 1-alpha (EF-1α)	EF1-728F / EF1–986R	58 66 (9x) and 56 (35x)	Carbone and Kohn (1999)
	EF1-728f / EF1–1567r	55	Carbone and Kohn (1999); Rehner and Buckley (2005)
	EF1f / EF2r	57	O'Donnell et al. (1998)
	ARMEF-F3a / ARMEF-R		Elías-Román et al. (2013)
RNA polymerase II largest subunit (rpb2)	RPB2–5f2 / RPB2–7cr	60 (5x), 58 (5x) and 54 (30x)	Liu et al. (1999)
Beta-tubulin (β-tubulin)	BT2a / BT2b	55	Glass and Donaldson (1995)
	BT-CadF / BT-CadR	56	Travadon et al. (2015)
Actin (ACT)	ACT-512F / ACT-783R	61	Carbone and Kohn (1999)

2.7. Identification of Phytophthora spp.

DNA was extracted from ca. 100 mg of 14-day-old mycelium scraped from CPA using a DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. *Phytophthora* species were identified by amplifying the ITS-rDNA region using primers ITS5/ITS4 (White et al., 1990), COX1 using primers OomCoxI-Levup/OomCoxI-Levlo (Robideau et al., 2011) and β-tubulin using primers TUBUF2/TUBUR1 (Kroon et al., 2004). PCR amplifications of ITS1 and COX1 followed EPPO PM7/129 (EPPO, 2021), whereas β-tubulin was amplified as follows: initial denaturation at 95 °C for 1 min; 35 cycles consisting of denaturation at 95 °C for 15 s, annealing at 65 °C for 15 s and extension at 72 °C for 60 s; and final extension at 72 °C for 3 min. All reactions were done on a Veriti 96-Well Thermal Cycler (9902, Applied Biosystems, Waltham, MA, USA) using MyFi Mix (Bioline, Meridian Bioscience, Cincinnati, OH, USA) and 10–20 ng of template DNA. PCR products (ca. 1000 bp for ITS and β-tub, 800 bp for COX1) were purified and Sanger sequenced at a commercial service provider (Macrogen Europe Ltd., Amsterdam, Netherlands). Sequences were visualized and manually edited using Geneious Prime v. 2024.0.3 (according to EPPO PM7/129 (EPPO, 2021). Consensus sequences were used to perform an individual nucleotide-nucleotide search with the megablast algorithm on the NCBI website (http://www.ncbi.nlm.nih.gov/BLAST/, accessed on 5 May 2025). Sequences were deposited in GenBank.

2.8. Data analysis

Statistical analyses were performed in R (R Core Team, 2022). Differences in the percentage of damage by different agents were tested with a Friedman test using the sampling plots as a block. Additionally, the Wilcoxon signed-ranked test for pairwise multiple comparisons was used to identify statistical differences between the groups. Differences in total damage and per agent between the two tree classes were tested using the Wilcoxon signed-rank test.

Differences in the community structure of fungal morphotypes and insect taxa between different tree classes and tree parts were tested using analysis of similarities (ANOSIM) with the "vegan" library (Clarke, 1993; Oksanen et al., 2022) based on Jaccard dissimilarities (Magurran, 2004) and visualized with the NMDS function (Nonmetric Multidimensional Scaling). Additionally, the Dunn's posthoc test with Bonferroni correction was used for pairwise multiple comparisons.

3. Results

3.1. Sampled trees and extent of damage

The sampled trees had an average diameter at breast height of 39.9 cm and a height of 26.4 m (Table 3). No completely healthy European beech trees were observed. Trees classified as healthy had an average defoliation of 12.3 % (Table 3), while damaged trees had a significantly higher average defoliation ($p < 0.001$). A significant difference in total damage was observed between damaged and healthy trees ($p < 0.001$). Significantly more damage was observed in damaged trees compared to healthy trees for fungi ($W = 10964$, $p < 0.001$, $n_H = 123$, $n_D = 129$), abiotic agents ($W = 245$, $p < 0.01$, $n_H = 20$, $n_D = 15$) and insects ($W = 3026$, $p < 0.01$, $n_H = 65$, $n_D = 72$), but not for the direct action of man ($W = 388$, $p = 0.08$, $n_H = 25$, $n_D = 25$) or game and grazing ($W = 0.5$, $p = 0.64$, $n_H = 3$, $n_D = 1$) (Table 4).

We found a significant difference between damaging agents

Table 3
Diameter at breast height, height and defoliation of sampled trees by tree class (n = 40).

Tree class	Number	Diameter at breast height (cm)			Height (m)			Defoliation (%)		
		Avg	Min	Max	Avg	Min	Max	Avg	Min	Max
Damaged	40	40.5	19.1	59.8	27.2	15.8	35	37.5	20	65
Healthy	40	39.3	24.8	67.5	25.5	15.3	39.5	12.3	5	30

Table 4
Damage extent by agent group and tree class.

Agent group	Average damage extent (%)[a]	No. of records	Tree class	Damage extent (%)		No. of records
				Avg	Max	
Game and grazing	0.8^{ac}	4	Damaged	0.0	0	1
			Healthy	1.0	2	3
Insects	2.1^{a}	137	Damaged	2.9	24	72
			Healthy	1.2	5	65
Fungi	5.3^{b}	252	Damaged	7.9	50	129
			Healthy	2.6	20	123
Abiotic agents	3.2^{b}	35	Damaged	4.8	15	15
			Healthy	2.1	5	20
Direct action of man	1.2^{c}	50	Damaged	1.9	10	25
			Healthy	0.5	4	25
Other	0.2^{ac}	4	Damaged	-	-	0
			Healthy	0.3	1	4

[a] Means with the same letter are not significantly different ($p > 0.05$).

($p < 0.001$). Fungi caused the highest average damage (5.3 %, Table 4), followed by abiotic agents (3.2 %) and insects (2.1 %). Three statistically distinct groups of damaging agents were identified: fungi and abiotic factors (shown as group "b" in Table 4) caused the highest damage to European beech, insects (group "a") caused intermediate damage and direct human activity (group "c") was associated with lower damage levels ($p < 0.001$ for comparisons between groups "a" and "b", and "a" and "c"; $p < 0.01$ between groups "b" and "c").

Fungi were the most frequently recorded damaging agent group and caused the highest extent of damage in both tree classes (i.e., damaged and healthy) amongst all agent groups (Table 4). Game and grazing and the "other" agent group had the lowest frequency and caused the lowest damage. Insects were the main damaging agent on leaves, causing greater damage than fungi or other agents (Supplementary Table S3). Fungi were the predominant damage agent on trunks, collars, branches and twigs. Abiotic agents were the second most important damaging agent on these parts, except on the branches and twigs of damaged trees, where insects were ranked second.

3.2. Damaging agents

3.2.1. Fungi

From a total of 1600 beech samples, 6400 pieces were cultured on agar plates, yielding 5828 fungal isolates classified into 251 morphotypes. Damaged trees yielded 2920 isolates representing 219 different morphotypes, while healthy trees yielded 2908 isolates representing 224 morphotypes.

Morphotype diversity was highest on the trunk, with roots and collar displaying similar diversity levels (Table 5). Branches and twigs ranked second in terms of morphotype diversity. Leaves had the lowest number of morphotypes.

Based on a subsample location the greatest fungal diversity was observed on outer bark (Table 6). Isolations from inner bark ranked second and isolations from discoloured wood ranked third in terms of fungal diversity. Healthy leaves and healthy bark yielded less morphotypes and isolates, because of lower numbers of samples (Table 1).

The average Jaccard similarity index between sampling plots was 0.18, with a maximum of 0.38. Similarity for fungal communities was highest between twigs and branches and lowest between leaves and the other parts (Table 7).

ANOSIM results indicated that fungal morphotypes differed significantly between the five tree parts ($p = 0.001$, Fig. 2), but not between the two tree classes ($p = 0.511$, Fig. 3). Pairwise comparisons revealed that fungal communities differed significantly between all analysed tree parts ($p < 0.001$ for all significant comparisons), except between branches and the trunk ($p = 1$) (Fig. 2).

For further fungal identification, the 20 most frequent morphotypes per tree part considering all trees were selected, totalling 100 morphotypes. After removing duplicates across parts, 72 morphotypes were retained, representing 3830 isolates (65.7 % of all isolates). Forty-four taxa were identified.

Cadophora spadicis Travadon, D.P. Lawr., Roon.-Lath., Gubler, W.F. Wilcox, Rolshausen & K. Baumgartner was the most common fungal species on tree collars (Supplementary Table S2). Other species on tree collars appeared three times less frequently than *Ca. spadicis*. Among those with a frequency greater than 20 were *Neonectria coccinea* (Pers.) Rossman & Samuels, *Clypeosphaeria* sp. and *Cosmospora* sp. The three most common fungal species on the trunk were *Ne. coccinea*, *Cytospora hippophaicola* Špetík, Eichmeier, Gramaje, Stuskova & Berraf-Tebbal, and *Neocosmospora quercicola* Sand.-Den. & Crous (Supplementary Table S2). Fungi on the trunk with an isolation frequency above 20 also included *Ca. spadicis*, *Pezicula* sp., *Aureobasidium pullulans* (de Bary & Löwenthal) G. Arnaud, *Clonostachys* sp. and *Neohendersonia kickxii* (Westend.) B. Sutton & Pollack. On twigs, two species, *N. kickxii* and *Ne. coccinea*, were notably dominant (Supplementary Table S2), while all other species or taxa appeared more than three times less frequently. On branches, similar to twigs, *Ne. coccinea* and *N. kickxii* were dominant, but in reverse order (Supplementary Table S2). Other fungal species on branches appeared at least two times less frequently. The three most common fungi species on leaves were *Apiognomonia errabunda* (Roberge ex Desm.) Höhn., *Au. pullulans* and *Didymosphaeria* sp. (Supplementary Table S2). Species with an isolation frequency above 20 also included *Petrakia liobae* Beenken, Andr. Gross & Queloz and *Alternaria* sp.

We also conducted a frequency analysis based on the subsample isolation location (Supplementary Table S2). The most common species in the inner bark were *N. kickxii* and *Ne. coccinea*. Other taxa were at

Table 5
Number of fungal morphotypes and isolates by tree part.

Tree part	Morphotype count	Isolate count
Trunk	153	999
Roots and collar	152	875
Branches	138	1177
Twigs	132	1365
Leaves	119	1412

Table 6
Number of fungal morphotypes and isolates by subsample location.

Subsample location	Fungal morphotype count	Isolate count
Healthy bark (BH)	2	2
Inner bark (BI)	161	2013
Outer bark (BO)	164	1113
Damaged leaf (LD)	118	1394
Healthy leaf (LH)	14	18
Discoloured wood (WD)	151	1288

Table 7
Jaccard similarity index for fungal community between tree parts.

Tree part	Leaves	Twigs	Branches
Twigs	0.31		
Branches	0.34	0.57	
Trunk	0.34	0.44	0.48

least four times less common. In the outer bark, the most common fungi were *Cy. hippophaicola* and *Ne. coccinea*. Only one taxon, the genus *Clypeosphaeria*, was identified from healthy bark. From discoloured wood, the most frequently isolated fungi were *Ne. coccinea*, *Ca. spadicis* and *N. kickxii* (Supplementary Table S2). Other taxa had significantly lower frequencies (three times or more). From diseased leaves, the most frequently isolated fungi were *Ap. errabunda*, *Au. pullulans* and *Didymosphaeria* sp. (Supplementary Table S2). Among the more common species were also *P. liobae* and *Alternaria* sp. From healthy leaves, the most frequently isolated fungus was *Ap. errabunda*.

3.2.2. Insects

A total of 71 insect taxa were identified. The number of insect species per tree ranged from 3 to 15, with an average of 7 species per tree. Within the sampling plots, the number of insect species ranged from 8 to 25, with an average of 15 species per plot.

The most frequently observed insects were *Mikiola fagi* (Hartig, 1839), *Orchestes fagi* (Linnaeus, 1758) and *Phyllonorycter maestingella* (Müller, 1764) (Table 8). The most damaging insects, recorded more than ten times, were *O. fagi*, *Phyllaphis fagi* Richards, 1973, *Psilocorsis reflexella* Clemens, 1860 and *P. maestingella* (for both damaged and healthy tree classes). However, their contribution to damage extent was low; for example, *O. fagi* caused on average 1.6 % damage in damaged trees and 0.9 % in healthy trees. The ten most frequently recorded insect species were all leaf feeders.

Amongst the less frequently observed insects (less than 10 records), the most damaging were ambrosia beetles *Xyleborus* sp. and *Anisandrus dispar* (Fabricius, 1792) (Table 9).

The average Jaccard similarity index for insect communities between sampling plots was 0.27, reaching a maximum of 0.80. Similarity was highest between branches and the trunk, and the lowest between twigs

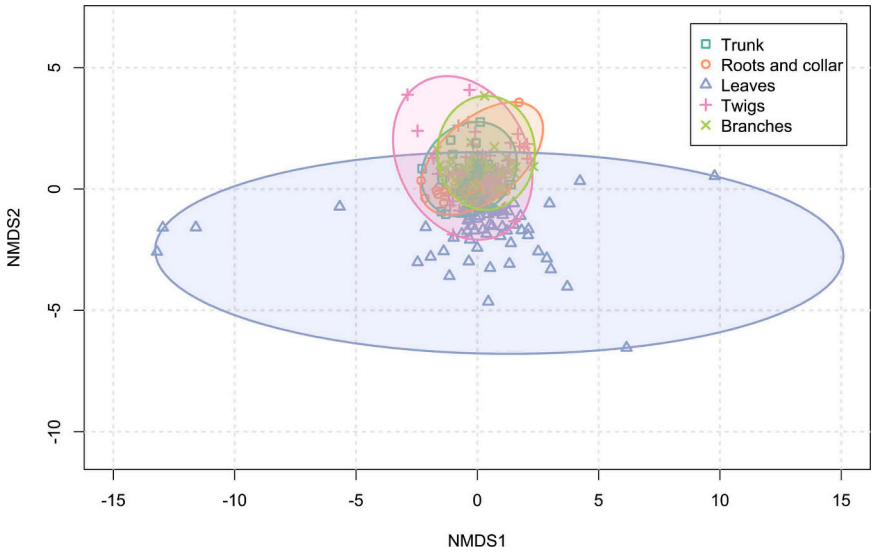

Fig. 2. NMDS analysis of fungal morphotype similarity between different tree parts (trunk, roots and root collar, leaves, twigs, branches).

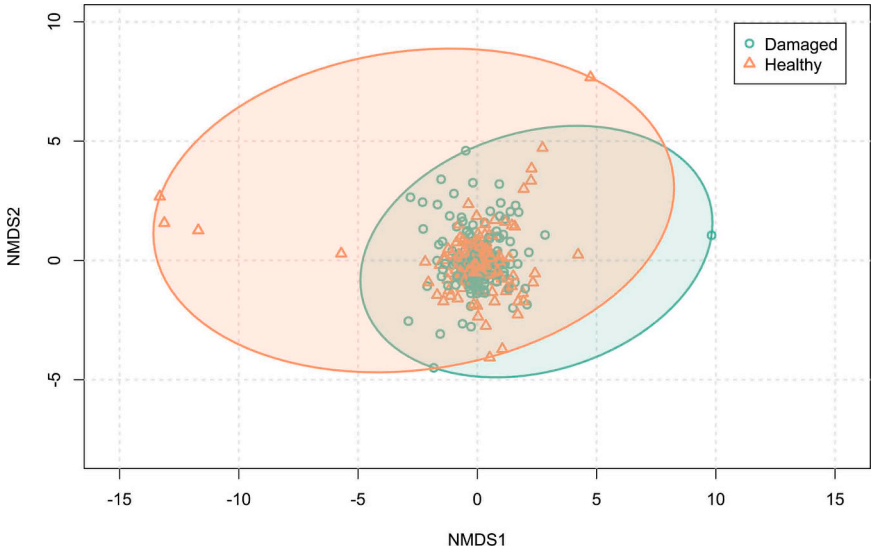

Fig. 3. NMDS analysis of fungal morphotype similarity between healthy trees (red triangles) and damaged trees (green circles).

Table 8
Most frequently recorded[a] insects (n > 10).

Tree class	Agent	Damage extent (%)		No. of records
		Avg	Max	
Damaged	*Orchestes fagi* (Linnaeus, 1758)	1.6	10	37
	Phyllaphis fagi Richards, 1973	1.1	5	19
	Psilocorsis reflexella Clemens, 1860	0.5	2	23
	Phyllonorycter maestingella (Müller, 1764)	0.5	1	23
	Mikiola fagi (Hartig, 1839)	0.3	1	37
	Hartigiola annulipes (Hartig, 1839)	0.2	1	14
	Phyllonorycter sp. Hübner, 1822	0.0	0	13
Healthy	*Orchestes fagi* (Linnaeus, 1758)	0.9	10	34
	Phyllaphis fagi Richards, 1973	0.5	2	21
	Psilocorsis reflexella Clemens, 1860	0.5	3	18
	Phyllonorycter maestingella (Müller, 1764)	0.4	2	19
	Mikiola fagi (Hartig, 1839)	0.3	3	39
	Hartigiola annulipes (Hartig, 1839)	0.3	1	16
	Phyllonorycter sp. Hübner, 1822	0.0	0	11
	Lepidoptera Linnaeus, 1758	0.0	0	12

[a] Complete list of recorded insects is available in Supplementary Table S4.

Table 9
Less frequently recorded insects with higher average damage extent (n ≤ 10; average damage extent ≥ 0.2).

Agent	Damage extent (%)		No. of records
	Avg	Max	
Xyleborus sp. Eichhoff, 1864	3.0	10	4
Anisandrus dispar (Fabricius, 1792)	2.4	10	7
Phyllonorycter messaniella (Zeller, 1846)	1.0	1	3
Auchenorrhyncha Duméril, 1805	1.0	1	2
Cercopoidea Leach, 1815	1.0	1	2
Tortricidae Latreille, 1803	1.0	1	1
Chrysomellidae Latreille, 1802	1.0	1	1
Elateridae Leach, 1815	1.0	1	1
Membracidae Rafinesque, 1815	1.0	1	1
Cicadellidae Latreille, 1802	0.9	5	10
Incurvaria koerneriella (Zeller, 1839)	0.9	1	8
Parornix fagivora (Frey, 1861)	0.6	1	7
Pentatoma rufipes (Linnaeus, 1758)	0.5	1	10
Miramella irena (Fruhstorfer, 1921)	0.5	1	2
Sessiidae Boisduval, 1828	0.5	1	2
Agrilus sp. Curtis, 1825	0.3	1	3
Orgyia antiqua (Linnaeus, 1758)	0.2	1	5

and the trunk. No species were shared between leaves and twigs (Table 10).

Insect communities differed significantly between tree parts ($p = 0.001$) but not between tree classes ($p = 0.768$), based on ANOSIM results (Fig. 4, Fig. 5). Pairwise comparisons revealed significant differences between all analysed tree parts ($p < 0.001$ for all significant comparisons), except between leaves and twigs, where no significant difference was observed ($p = 0.769$) (Fig. 4).

3.2.3. *Phytophthora* species

From a total of 80 soil samples, *Phytophthora* species were isolated from only three samples. The isolated species were *P. gonapodyides* (H.E. Petersen) Buisman, *P. hedraiandra* De Cock & Man in 't Veld, and *P. cactorum* (Lebert & Cohn) J. Schröt. (Supplementary Table S5). These isolates were obtained from soil samples collected near two damaged trees (*P. gonapodyides* and *P. hedraiandra*) and one healthy tree (*P. cactorum*). The remaining 25 samples contained only *Pythium* species, which were not further identified.

Table 10
Jaccard similarity index for insect community between tree parts.

Tree part	Leaves	Twigs	Branches
Twigs	0		
Branches	0.15	0.08	
Trunk	0.07	0.06	0.24

4. Discussion

European beech decline, a progressive trend observed across European beech forests, raises concerns throughout Europe (Senf et al., 2018). Several studies showed that *Phytophthora* spp., prolonged periods of excessive rainfall and droughts are associated with European beech decline (Vettraino et al., 2008; Jung, 2009; Jankowiak et al., 2022). In addition to drought stress, the endophytic fungus *Bi. nummularia* (Granata and Sidoti, 2004; Langer and Busskamp, 2023; Tropf et al., 2025), *Ne. coccinea* (Langer and Busskamp, 2023; Tropf et al., 2025) and other organisms (Lakatos and Molnár, 2009) contribute to beech decline. Due to climate change and the increasing frequency of drought stress, latent and opportunistic pathogens are becoming a growing threat to European beech. In this context, members of the Botryosphaeriaceae family are considered capable of playing a primary role in the progression of beech vitality loss under climate change conditions (Langer and Busskamp, 2021, 2023). Notably, *Botryosphaeria corticola* A. J.L. Phillips, A. Alves & J. Luque, identified by Langer and Busskamp (2021) as the most aggressive species in pathogenicity tests, was not detected in our study. Similarly, *Diplodia corticola* A.J.L. Phillips, A. Alves & J. Luque and *D. mutila* (Fr.) Fr., recognized as frequent potentially severe pathogens by Langer and Busskamp (2023), were also absent from our findings.

Our results indicate that European beech vitality loss is associated with multiple damaging factors, resulting in a complex disease. Fungi caused the highest average extent of damage, followed by abiotic agents, with insects ranking third. These results align with the annually monitored condition of Slovenian forests on a systematic 16 × 16 km grid (Ogris and Skudnik, 2022). Fungi were the most important damaging factor for twigs, branches, trunk, and roots and collar in healthy trees. Abiotic agents were the most important on trunk and roots and collar of damaged trees, while insects were the most important group only on leaves, where they caused greater damage than other agents.

Fungal and insect communities did not significantly differ between "damaged" and "healthy" trees, which suggests that the communities identified in declining trees are also present in apparently healthy individuals. Similarly, Tropf et al. (2025) found that vitality status did not affect the fungal community in asymptomatic European beech tissues. This implies that external stressors, rather than the mere presence of these organisms, play a key role in triggering pathogenic activity. Given the observed trends, we anticipate that defoliation and vitality loss in European beech will continue to worsen.

Fungal and insect communities differed significantly between tree parts. The greatest diversity of fungal morphotypes was found in older tree parts, namely the trunk and roots and collar. These findings indicate that older tree parts host a greater diversity of fungal species, which is consistent with previous studies demonstrating the influence of stand age on fungal community structure and the successional development of these communities, particularly on decaying and dead wood (Odriozola et al., 2020; Lepinay et al., 2022; Castillo et al., 2023). Similarly, the outer bark exhibited the highest fungal diversity, likely due to its direct exposure to the environmental conditions and its role as a first barrier accumulating a diverse assemblage of organisms, which is consistent with the findings of Pellitier et al. (2019).

Isolations from different tree parts yielded a wide variety of fungal species. On twigs and branches, *Ne. coccinea* and *N. kickxii* were most frequently isolated, while on leaves, *Ap. errabunda*, *Au. pullulans* and *Didymosphaeria* sp. were the most abundant. From roots and collar, *Ca. spadicis*, *Ne. coccinea* and *Clypeosphaeria* sp. were the most frequently isolated, whereas on the trunk, *Ne. coccinea*, *Cy. hippophaicola* and *Neo. quercicola* predominated. Altogether, we identified 44 fungal taxa with

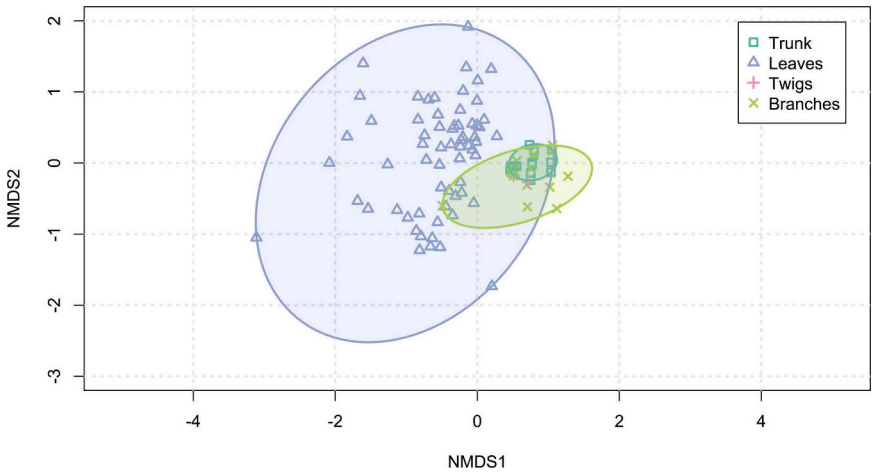

Fig. 4. NMDS analysis of the similarity of insect taxa between different tree parts (trunk, leaves, twigs, branches).

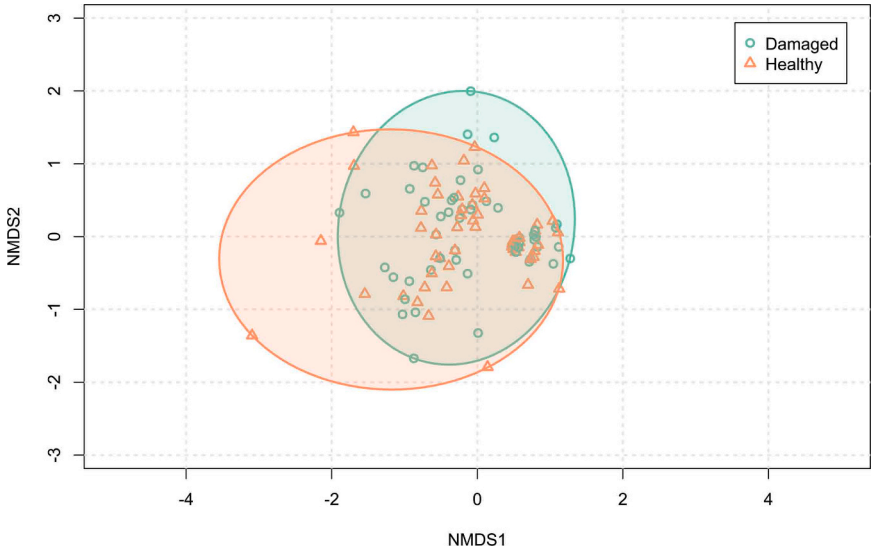

Fig. 5. NMDS analysis of the similarity of insect taxa between healthy trees (red triangles) and damaged trees (green circles).

diverse life traits, including endophytes, saprophytes and facultative pathogens. Some species, such as *N. kickxii* in twigs, *Ne. coccinea* in wood and *Ap. errabunda* in leaves, are known endophytes in healthy tissues (Kowalski and Kehr, 1992; Danti et al., 2002; Sieber, 2007; Langer and Busskamp, 2023; Tropf et al., 2025). Under host stress, these endophytes can become opportunistic pathogens. For example, *Ap. errabunda* is known to be stimulated by insects such as *M. fagi* and *H. annulipes* or by late frost (Pehl and Butin, 1994), while *Ne. coccinea* responds to host stressors such as wounding or fungal inoculation and has been recognized as the main fungal species causing bark necroses and vitality loss in European beech (Langer and Busskamp, 2021; Tropf et al., 2025). *Au. pullulans* and *Didymosphaeria* sp. are ubiquitous species with broad substrate associations (Andrews et al., 2002; Ariyawansa et al., 2014). While *Au. pullulans* is a well-known epiphyte or endophyte (Andrews et al., 2002), the genus *Didymosphaeria* includes saprobic, endophytic and pathogenic species (Ariyawansa et al., 2014). In contrast, *Ca. spadicis*, *Cy. hippophaicola* and *Neo. quercicola* are mainly reported as pathogens responsible for wood decay, cankers and tree decline (Travadon et al., 2015; Sandoval-Denis et al., 2019; Frascella et al., 2024; Lin et al., 2024). However, in our study they were isolated mainly from outer bark, suggesting a secondary role. These findings support the hypothesis that facultative, opportunistic and latent pathogens play an important role in European beech decline, acting as dormant mechanisms activated by stress. This is in agreement with the findings of Langer and Busskamp (2021), who reported that elevated temperatures favoured the establishment and growth of early colonising species such as *Ne. coccinea* and *Bi. nummularia*, as well as plant pathogens including *Bo. corticola*, *Nectria cinnabarina* (Tode) Fr., and *Eutypella quaternata* (Pers.) Rappaz.

Abiotic agents were identified as the second most damaging factor. Trunks showed the highest extent of abiotic damage, although these events were rare (only two records). Branches and twigs also exhibited substantial damage, ranking second in severity among all damage types. Most of this damage was old, primarily resulting from the catastrophic 2014 ice storm (Nagel et al., 2016; de Groot et al., 2018). Wind was also identified as an important abiotic damaging agent, though only old damage was observed. Due to their predominantly historical nature, abiotic agents were not examined in detail, yet they can cause acute, large-scale disturbances and may trigger secondary outbreaks of pests and diseases. Our study did not address drought, high temperatures or frost—despite their likely critical roles—due to limited project resources. These agents can have profound effects on host physiology and vitality, as well as on pests and diseases. Therefore, we refer to abiotic agents primarily as a tool for the possible explanation of ecological processes underlying European beech decline.

We identified 71 insect taxa, representing 35.9 % of all insects

associated with European beech in Slovenia (Jurc, 2012). Insects ranked third in terms of average damage but were the primary damaging agents affecting leaves, causing more damage than fungi or other agents. In certain cases, insects can cause complete or early defoliation of European beech, resulting in reduced vitality and increased stress for the tree. Therefore, insects can play an important indirect role in facilitating facultative pathogens and secondary pests, which target already weakened trees. The most frequently observed insect species in our study were leaf-feeders *O. fagi* and *Ph. fagi*. Both species were extremely abundant nationwide in 2022 (Kavčič, 2022), corresponding to the high frequency specimens we recorded. Among the less frequently observed insects, the most damaging were ambrosia beetles *Xyleborus* sp. and *A. dispar*, contrary to initial expectations that *T. bicolor* and jewel beetles would be the primary damaging agents. Both *Xyleborus* sp. and *A. dispar* are well-known ambrosia beetles, predominantly attacking damaged or weakened hosts and causing substantial damage, such as technical devaluation, reduced fruit production and tree decline (Tanasaković et al., 2016; Rizzo et al., 2023).

Despite the well-documented association of *Phytophthora* species with declining European beech trees, our study revealed an unexpectedly low diversity and abundance of this genus in Slovenian forest soils. Of the 80 soil samples collected, *Phytophthora* spp. were isolated from only three. In contrast, the majority of samples yielded isolates belonging to the genus *Pythium*, which were not identified to the species level. The *Phytophthora* species recovered in our study (*P. gonapodyides*, *P. hedraiandra* and *P. cactorum*) differed from those most commonly reported in similar European forest surveys, which have consistently identified *P. plurivora*, *P. cambivora*, *P. citricola* and *P. cactorum* as dominant species in beech-associated ecosystems (Jung, 2009; Corcobado et al., 2020).

The low diversity of *Phytophthora* species observed is unlikely to be due to the timing of sampling or the methodology used, as we applied the same baiting approach under comparable environmental conditions in soils from tree nurseries and a botanical garden, where we successfully recovered a much greater diversity of *Phytophthora* and *Phytopythium* species. To address the potential limitations of baiting—particularly its reliance on the active sporulation of pathogens—a metabarcoding approach could be employed (Sarker et al., 2023). This molecular method enables detection of *Phytophthora* DNA even when the pathogen is not actively growing or producing spores and thus may escape traditional isolation techniques.

Taken together, these findings suggest that *Phytophthora* species may play a limited role in beech decline in Slovenian forests, except in specific cases previously reported (Munda et al., 2007). Furthermore, symptoms of *Phytophthora* infection on forest trees in Slovenia are rarely observed in areas with no afforestation or distant from frequently visited trails. This spatial pattern supports the hypothesis that human activity—particularly the introduction of contaminated planting material—plays a key role in the initial entry of *Phytophthora* species into forest ecosystems, with subsequent local spread likely facilitated via soil or water movement along transport routes and hiking paths.

Our study focused on the key factors involved in European beech decline. Therefore, samples were collected primarily from damaged parts of the trees. Healthy parts were collected only when no damaged parts were present, resulting in small numbers of visually healthy samples. Consequently, results from healthy samples are biased due to their limited numbers. Unfortunately, the limited project resources did not allow to sample an equal number of visually healthy tree parts. However, other studies have focused on endophytic mycobiota in healthy tissues of European beech (Kowalski and Kehr, 1992; Danti et al., 2002; Sieber, 2007; Langer and Busskamp, 2023; Tropf et al., 2025).

Based on our findings, we confirmed the first two hypotheses: (i) that multiple harmful agents contribute to the decline of European beech in Slovenia, collectively forming a complex disease; and (ii) that diseases, on average, cause more severe damage than insects and other harmful agents. In contrast, the third hypothesis (iii)—that *Phytophthora* species are present in the soil of more than half of the damaged beech trees—was not supported by the data, suggesting that *Phytophthora* species may not have played a major role in the observed decline in our study area. Similarly, the fourth hypothesis (iv) was rejected because fungal and insect communities did not differ significantly between healthy and damaged trees.

The observed increase in European beech canopy damage in Slovenia since the 1990s is consistent with broader European trends. Senf et al. (2018) found that, on average, 0.79 % of European temperate forest area experienced canopy mortality each year between 1984 and 2016, with annual rate increasing by 2.4 %—effectively doubling over the study period. Similarly, Ognjenović et al. (2020) observed a significant increase in European beech defoliation in Croatia between 1996 and 2007, identifying extreme summer temperatures and low June precipitation in the previous year as key drivers of defoliation, suggesting a one-year lag effect. Similar patterns were found in foliar nutrient concentrations, where high summer temperatures reduced nutrient uptake. Overall, these findings highlight that heat and drought not only affect beech vitality in the current year but also have lasting effects in subsequent years (Ognjenović et al., 2020).

This is further reflected in reduced radial growth observed in various parts of Europe since the 1980s (Dulamsuren et al., 2017; Knutzen et al., 2017; Levanič et al., 2023). As tree-ring widths are strongly influenced by climatic events, they serve as valuable indicators of environmental change and tree response to shifting conditions (Levanič et al., 2023). European beech exhibits a strong climate signal in tree-ring data and responds distinctly to extreme weather events, such as extremely hot and dry years (Arnič, 2023; Levanič et al., 2023). Several studies have shown that above-average summer temperatures and reduced precipitation negatively affect radial growth, whereas high spring temperatures tend to enhance it (Knutzen et al., 2017; Prislan et al., 2019; Adamič et al., 2023; Arnič, 2023; Levanič et al., 2023). Moreover, within the centre of the European beech distribution range, *F. sylvatica* forest stands show contrasting growth trends depending on elevation—growth decline is observed at lower elevations, while growth increases at higher ones (Dulamsuren et al., 2017). These patterns are consistent with findings of Levanič et al. (2023), who suggested that environmental conditions in alpine regions are more favourable for European beech growth than those in the continental regions.

Altered growing conditions may affect not only tree-ring width but also wood anatomical structure, physical characteristics and practical applicability. A significant correlation between tree-ring width, vessel density and relative conductive area was demonstrated by Arnič (2023). In addition to the projected changes in radial growth over the coming decades, the model developed by Prislan et al. (2019) predicts longer growing seasons driven by rising air temperatures and reduced precipitation during the vegetation period.

All evidence suggest that European beech is becoming increasingly vulnerable due to drought and a warmer climate (Chakraborty et al., 2021), which aligns with the results of our study. However, unlike the above-mentioned European studies, our research did not identify a significant impact of *Phytophthora* species and *Bi. nummularia*. Considering that drought is a triggering factor of European beech decline and that a warmer climate is a predisposing factor, we expected higher occurrences of *Bi. nummularia,* fungi from the *Botryosphaeriaceae* family, jewel beetles and bark beetles. These expectations were not met. Instead, the fungi *N. kickxii*, *Ne. coccinea* and *Ap. errabunda* were predominant, which are well-known and very common endophytes of European beech.

Our study revealed that fungal and insect communities did not differ between healthy and damaged trees, indicating that all harmful organisms found in damaged trees are already present in or on healthy ones. Therefore, external triggering factors that stimulate the pathogenic activity of these species are crucial, which is in agreement with Langer and Busskamp (2021). This finding has important implications for the management of European beech forests. Damage could be reduced by providing an environment with minimal stressors and triggering factors.

In this context, proactive adaptation to climate change and strategic adjustments to forest management plans are essential. Ensuring the long-term resilience and sustainability of European beech forests will depend on our ability to mitigate stressors and implement adaptive management strategies that address the evolving environmental challenges.

CRediT authorship contribution statement

Nikica Ogris: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ana Brglez:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Andreja Kavčič:** Writing – review & editing, Investigation, Formal analysis. **Janja Zajc Žunič:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Maarten de Groot:** Writing – review & editing, Investigation, Formal analysis. **Barbara Piškur:** Writing – review & editing, Methodology, Formal analysis.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123464.

Data Availability

Data are available at https://dx.doi.org/10.20315/Data.0007 Agents of European beech decline (Digital Repository of Research Organizations of Slovenia (DiRROS))

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