The importance of veteran trees is well recognised nowadays. The sudden breakdown of some veteran trees reported in the last years in Trentino (Northeastern Italy) raised concerns about the health status of the recorded veteran trees. Particularly, the constant presence (100%) of Kretzschmaria deusta (Hoffm.; Fr.) P.M.D. Martin on the more recently fallen trees suggested a possible direct role of this pathogen in the decaying process. It is to remember that the decay caused by K. deusta is particular because the fungus degrades cellulose creating holes in cell secondary walls. This degradation reduces the tensile strength of wood that becomes brittle and easy to snap off with a characteristic fracture (Luly 2017). Moreover, the presence of dark lines due to the fungus in the decayed wood is considered a typical characteristic of K. deusta (Wilkins 1934). To investigate this subject, a complete survey of veteran beech (Fagus sylvatica L.) trees, among the most endangered in recent years, was carried out. The main goal of this study was to estimate whether and how much the presence of K. deusta could be related to the damages and to the failure risk conditions of the surveyed trees.
Moreover, the effect of some environmental and meteorological conditions on pathogen behaviour have been also considered in order to enhance the management practices.

Materials and methods

Field investigations

Veteran beeches in Trentino

In 2015, the Forest and Fauna Service of the Autonomous Province of Trento carried out a complete revision of the veteran trees defined as “monumental”, aiming to harmonize the previous inventory of 2003 with the more recent criteria proposed by the national law. Dead and fallen trees as well as the smallest ones were removed from the record. The criteria followed were: 1. age and size (with species-specific trunk circumference thresholds, for beech 400 cm); 2. peculiar shape; 3. ecological value; 4. botanic rarity; 5. plant architecture; 6. landscape value; 7. historic-cultural-religious aspects.

In each administrative forest district, surveys were carried out aimed to identify the most representative single trees or groups that were mapped and geo-localized. Of these, 115 beech trees were selected for this specific investigation.

Visual Tree Assessment (VTA) of identified veteran trees

The selected trees were examined during field surveys carried out in March and April 2016.

According to Pezzi et al. (2020), diameter at breast height (DBH) and tree height were measured on each selected tree. Vitality, presence of pathogens and pest, structural condition and failure risk were then evaluated. Vitality was expert-based assessed on crown condition (transparency or death of branches), adopting the following scale modified from Müller & Stierlin (1990): (i) slightly suffering, defoliation or death of branches up to 20% of the whole crown; (ii) suffering, defoliation or death of branches from 20% to 50% of the whole crown; (iii) declining defoliation or death of branches from 50% to 75% of the whole crown; (iv) dead, defoliation or death of branches over 75% of the whole crown. Moreover, the presence of other fungal attacks on the collars or stems was assayed.

The conditions of the trees was evaluated considering the presence of damage and structural anomalies in the different tree parts; (i) crown: asymmetry, death of branches, signs of pruning, other wounds, decaying wood with rot and/or cavities on branches, fungal fruiting bodies; (ii) trunk: leaning, wounds, decaying wood with rot and/or cavities (% of diameter), fungal fruiting bodies; (iii) collar and root: wounds with decaying wood, rot and/or cavities (% of diameter), fruiting bodies, excavation or soil movement in the root area, soil cracking.

Site conditions (wind exposure and natural or altered soil condition) and surrounding type of environment (wood, pastures, or urban area) were recorded. Target rating was assessed considering the occurrence of potential targets (structures or human occupancy of the area) under or in proximity to the trees (Matheny & Clark 1994): absence, occasional or intermittent presence; frequent or constant presence.

The level of damage and related failure risk was assessed by adapting the risk classes reported by Smiley et al. (2017): low risk (no damage); moderate risk (low level of damage, management needed); high risk (medium level of damage, problems for tree stability and need for constant management); extreme risk (high level of damage, tree stability strongly affected and few or no possibilities of management).

A specific observation on fruiting bodies belonging to K. deusta (Fig. 1) and related decay attacks was carried out recording their presence and extent on the tree. The occurrence of other fungal fruiting bodies was also recorded.

A buffer area of 50 m around the examined trees was surveyed aiming to detect both allocation of the tree (roots, stumps and, particularly, to find the presence of K. deusta fruiting bodies and related damage.

Laboratory test

Morphological characterization

Parts of trunks of infected trees containing xylariaceous stromata were transferred to the laboratory. Single ascospore cultures were obtained from ascomata based on the method described by Rogers & Ju (1998). Morphological observation of colonies growing in Malt Extract Agar (MEA) dishes at 25 °C was carried out with an SMZ1000® stereomicroscope (Nikon, USA), while microscopic features, such as size, shape, colour and arrangement of conidia, were observed with an Eclipse 80i® microscope (Nikon) dotted with a digital sight images (DS-L2 imaging controller, Nikon). Light microscope observation of ascospores was done in distilled water and measurements were determined.

Molecular identification

Genomic DNA was extracted directly from stromata. Each sample was frozen with liquid nitrogen and ground using a sterile mortar and pestle. DNA was extracted using 200 mg of the fine powder obtained from the frozen stromata using a DNeasy® Plant Mini kit (Qiagen, Hilden, Germany) according to the manufacturer’s instructions. DNA samples were stored at -20 °C. The DNA amplification was obtained by polymerase chain reaction (PCR) using the primers pair ITS5′ (5′-CAAAGTAAAGATTCG-TAACACG-3′) and ITS4′ (5′-TCTCCGCTATTGATATGC-3′) to amplify ribosomal ITS1 and ITS2 (White et al. 1990). The PCR mixture comprised 12.5 µl of GoTaq® Green Master Mix (Promega), 10.5 µl of water supplied with the GoTaq, each primer at 0.2 mM (Sigma-Aldrich) and 1 µl of DNA. A Biometra T1 Thermocycler (Whatman Biometra, Gottingen, Germany) was used for PCR with the following protocol: 5 min at 95 °C; 35 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 45 s and extension at 72 °C for 1 min; and a final extension step at 72 °C for 10 min. PCR fragments were analysed using 1% agarose gel electrophoresis in 1× Tris-boric-acid-EDTA buffer (TBE), stained with SYBR Safe® (Life Technologies, Milan, Italy) and visualized under UV light. As a size standard, the GeneRuler® DNA

![Fig. 1 - Fruiting bodies of Kretzschmaria deusta, sexually reproductive black charcoal-like crusts and white/grey asexual stage, on a degraded beech trunk.](image-url)
Effect of temperature on mycelial growth

The influence of temperature on mycelial growth was assessed in vitro. To evaluate the possible difference of behaviour between the strains of the fungus, three isolates of *K. deusta*, one obtained from a decayed stump and two others from living declining trees, were selected for growth assay. Mycelia plugs 5 mm in diameter were cut from 10-day-old colonies and transferred onto Petri dishes containing Potato Dextrose Agar (PDA, Oxoid, UK). Three replicate dishes were incubated in the dark at 0, 5, 10, 15, 20, 25, 30 and 35 °C. The rays of the resulting colonies were measured at 1, 3, 7, 10 and 14 days from inoculation. Differences in isolates and replication were compared with ANOVA using STATISTICA® v.13.3 (StatSoft Inc., Tulsa, OK, USA). Fisher’s least significant difference was used to test for significant differences among the means (α = 0.05). The experiment was repeated twice and the mean data was presented.

Meteorological data

Yearly and daily mean temperatures for the period 1983 to 2020 were obtained from the meteorological station at San Michele all’Adige (209 m a.s.l., FEM agrometeorological network), located in central Trentino. We used freely available meteorological data series of daily average, minimum and maximum temperatures to obtain the yearly and daily average values. The provider does not directly provide climatic (or aggregated) data but guarantees the correctness of the measurements and their elimination in instances of instrument malfunction. Moreover, the provider does not supply information regarding data validation procedures.

Statistical analysis

The collected data were processed in order to find a relationship between the occurrence of the disease and alternatively the occurrence in the area (dependent variables) and the measurements collected in the field (independent variables). The analysis led to the definition of two possible models based on the relevant variables for this specific domain knowledge: (i) disease presence = area presence + elevation + position + circumference + age; (ii) area presence = disease presence + elevation + circumference + age + rot.

All those variables that were collinear to the combination of the independent variables and the variables already present in the model were excluded.

Once the candidate variables for the model had been identified, the most parsimonious model (lowest complexity, i.e., using the fewest variables) was sought, without compromising the predictive ability. Stepwise model selection based on the Akaike Information Criterion (AIC) was used.

Results

Field investigations

Veteran beeches in Trentino

Overall, 40 sites were considered of interest by the Forest Service for the presence of veteran beech (Tab. S1 in Supplementary material). In 10 sites, the identified trees were single trees on pastures or meadows, probably left as shade for the livestock or near huts or private houses. In 19 sites the surviving giants are old trees in a woodland context either as released standards in coppices or isolated trees surrounded by new trees or on the edge of younger woodlands.

In six sites the survey selected groups of trees scattered or in rows on pastures. In other three sites the signalled groups were reported as old rows on the edge of a woodland, while the last two sites were located in an urban context. A total of 115 trees were evaluated, 31 as isolated and 84 as being at extreme risk was found to have recently failed at the time of the survey because of evident root rot, while the other had a complete breakdown exactly 15 days after the evaluation (Fig. 2). The 43% of the trees showed significant defects or problems in need of management and 6% had a high level of risk because of the presence of several structural problems. The 54% of trees showed damage or presence of rot at collar level, while 30% had wounds and rot on the trunk. The 11% of trees had a crown with broken or dead branches. Only 2% trees had significant damage, mainly wounds, on the roots.

The presence of *K. deusta* was recorded on 50.4% of the examined trees, mainly as characteristic fruiting bodies or typical wood degradation. The affected trees were present in each of the site conditions: 58% of the single trees in a woodland, 42% of the single trees in pastures or gardens, 49% of trees growing as a group in woodlands and 52% of those living as a group in a woodland. One tree showed only a well-developed typical rot of the trunk, while in all the others the presence of the fungus was clearly identified by the fruiting bodies. In
14 trees these were observed on less than 10% of the collar circumference; in other 29 the colonization involved less than 50% of the circumference and in the remaining 15 it ranged between 60% up to 80%. The fruiting bodies or evident rot was limited to the base of the trunk (up to 1 m) in 20 trees, while on other 23 the fungus colonized up to 2 m. Fifteen trees showed colonization between 2 up to 6 m; 5 or 6 m of infected tissues were detected on 3 of these latter. On 22 trees other fungi were observed and identified by means of morphological observation. On 12 trees, **Armillaria** spp. was present both as old fruiting bodies or mycelium, while on the roots of other 5 trees the fruiting bodies of **Meripilus giganteus** (Pers.) Karst were evident. **Ganoderma** resinaceum Boud. was present on other 5 trees, while **Schizophyllum commune** Fr. colonized part of one of the **K. deusta** affected trees.

**K. deusta** was detected in 21 areas on living beeches or in the stumps around the surveyed trees. In 8 of these areas the fungus was present only in the surroundings but not on the veteran trees. In 7 areas **K. deusta** was not observed either on the veteran trees or nearby.

**Laboratory tests**

**Morphological and molecular identification**

Species identification combines sequence information for the internal transcribed spacer (ITS) of rDNA with morphology of stromata sampled at the trunk base of infected trees and microbiological characteristics. Mature stromata appear as black charcoal-like crusts with an irregularly rugose surface dotted with inconspicuous perithecial mounds. The ascospores are fusiform, brown to dark brown, smooth, non-septate, 24-33 µm × 6.5-8.5 µm, on the average 29±7.5 µm.

Cultures on MEA at 25 °C reached more than 70 mm in diameter in 18 days, first whitish, feltly and zonate, then becoming grey from the centre outwards with concentric zones. Amplification of the ITS loci yielded fragments of approximately 600 bps. The sequences obtained 100% of similarity with **K. deusta** using the basic GenBank local alignment search tool program (BLAST). At least one sequence obtained from each site was published in Genbank (accession numbers from MT573939 to MT573952). Moreover, two sequences resulted as having 100% homology with the mycoparasite **Cosmopora berkeleyana** (P. Kars.) Gräfenhan, Seifert & Schroers. (accession number MT626674-75). In fact, the presence of reddish pear shape perithecia was observed on the surface of the fruit bodies of **K. deusta** (Fig. S2 in Supplementary material), suggesting that this fungus is parasitized by other fungi. Indeed, Herrera et al. (2016) demonstrated that most host-parasite links considered coevolutionary included **Cosmopora** associated with **Kretzschmaria**, **Stilbohypoxylon**, and **Xylaria** hosts.

**Effect of temperature on pathogen mycelial growth**

No significant differences (p>0.05) were found between the growth of the **K. deusta** isolates from living declining trees and decayed stumps. As shown in Fig. 3, the three isolates were able to grow in a range of temperatures varying from 10 to 30 °C, whereas no growth was observed at 0 °C and 35 °C, while at 5 °C a reduced initial growth was observed only at the end of the observation period. In general, the rate of mycelial growth increased as temperature increased up to 25 °C and then decreased rapidly as further increased. At 10 °C, mycelial growth of all isolates was slow with an average rate of 0.6 mm day⁻¹ compared to significantly higher rates of 1.9, 3.3 and 4.1 mm day⁻¹, noted at 15 °C, 20 °C and 25 °C, respectively. Optimum growth occurred at 25 °C for all isolates. A temperature of 35 °C devitalized the fungus, while at 0 °C it was able to grow again when exposed to the optimal temperature.
Meteorological data
Data obtained from the meteorological station at S. Michele all’Adige are reported in Fig. 4 and Fig. 5. The anomalies of mean annual temperature showed a clear slight increase in the considered period, with a rise of almost 0.5°C in the last years. Moreover, this trend is emphasised by the anomalies in the number of days with mean temperature above 18°C, which in the last year was 10 to 20 days above the average value.

This is in accordance with what was reported by Tudoroiu et al. (2016), who recognised the same trend of temperature increase in Trentino and the Eastern Alps, despite the mitigating effect of elevation.

Statistical analysis
The analysis led to the definition of two different possible models based on the relevant variables for this specific domain knowledge. In both cases, no statistical significance was found between the presence of the disease and the independent variables.

Discussion and conclusion
The survey clearly demonstrated the abundant presence of K. deusta in Trentino and its possible and effective role on the survival of the recorded veteran beeches. The presence and damage due to the pathogen was observed on 50.4% of the examined trees, in some cases associated with a highly degraded condition of the individual. In fact, a large number of evaluated trees showed a moderate or high failure risk related to root, collar and trunk degradation, mainly due to K. deusta, in a few cases associated with other wood and root rot agents. Because of the natural condition of almost all the sites, the majority of veteran trees are not threatened by bad management, though two of the worst trees (Cà vecia-4 and Villa Pia-15) were heavily pruned about 10-15 years ago. Therefore, the physiological processes of aging can be considered as the main driver of their health condition evolution; as suggested by the fungus mainly as saprotroph or preferential ways of colonization of the host (Guglielmo et al. 2010, Giordano et al. 2015) and it could also be adopted for veteran trees in more natural contexts. Anyway, the detection of the fungus only attests to its presence but the evolution and timing of wood colonization remain very difficult to forecast because of the multiple factors involved, such as plant status and environmental conditions.

K. deusta was present around the veteran trees in the investigated beech wood: the fungus was found in most of the areas (33 out of 40) as a quite common presence on both stumps and living trees. This observation confirms those of other authors who reported K. deusta as a common component of the mycflora of beech woods, especially in old growth stands both in Italy (Granito et al. 2015, Persiani et al. 2016) and Europe (Baldrian et al. 2016, Heine et al. 2019). These recent records do not consider the fungus mainly as saprotroph or debris colonizer, but its damaging potential as a pathogen had already been recognized in the past (Wilkins 1934). Moreover, the fungus was found to be damaging beech trees at a high rate both in Czechoslovakian and Yugoslavian woodlands (Prinjářová 1982), while more recently, its pathogenic role in urban tree management was enhanced (Guglielmo et al. 2010, Giordano et al. 2015). Thus, K. deusta can act as cause of damage on old trees, as observed in our survey, but it could also be considered as a more effective agent for the possible evolution of old growth beech stands.

Interestingly, the easily recognized K. deusta spores were considered in paleoecology a valid proxy to understand the evolution of forest cover; it should be remembered that K. deusta is common on Fagus, but can also affect other genera including Acer, Aesculus, Alnus, Betula, Carya, Castanea, Fraxinus, Populus, Quercus, Salix, Taxus, Tilia and Ulmus (Van Geel et al. 2013). The ascospores recovery in lake or moorland pollen deposits was correlated mainly to an increase or decrease in deciduous species in the surroundings woodland, but in some cases spore peaks were also associated to some particular extreme weather conditions such as rainstorms affecting beech woods (Van Geel et al. 2013) or to a drastic decline as reported for Ulmus sp. in northern Europe (Innes et al. 2006).

In this context, it is still difficult to assess a possible role of climate change in the development of infections and spread of the fungus. Anyway, the constant increase of temperature also in the Alpine region could suggest a longer favorable period for mycelium growth and also for germination of its spores (Wilkins 1934). In fact, data obtained in this study confirmed a positive growth range of the fungal isolates between 10-30 degrees with an optimum at 25°C, as reported in previous studies both in Europe and Italy (Wilkins 1934, Capretti et al. 2003). In addition, palaeoecological reconstructions of forest dynamics of Ulmus in the United Kingdom and Tilia in Poland (Innes et al. 2006, Latalowa et al. 2013), suggested a likely increase in the growth rate and success of K. deusta infection due to the rise of few degrees in the average annual temperature, and hypothesized an increased risk of K. deusta outbreaks in a warming climate condition.

The possible role of the multiple wounds on collar and roots of the assessed veteran trees could also be considered in the epidemiology of the parasite, because they are preferential ways of colonization of the host (Guglielmo et al. 2012). A stress condition due to meteorological events could also affect the callusing and compartmentalization ability of the trees.

K. deusta, considered up to now a minor parasite if not a saprotroph, could instead play a more incisive role both in the decline of old beech trees and in the natural evolution and aging process of woods. This possible role deserves more investigations, especially regarding the relationship with climate change. Moreover, the risk evaluation highlighted how the fungus presence along with other kinds of damage could affect the survival and safety of these veteran trees. On this subject, the obtained results emphasized the need for an appropriate management of the veteran trees, as already suggested by Lonsdale (2013) and Farina et al. (2019), aimed to preserve them as long as possible and assure the reduction of any risk for their fruition and enhancement.

Acknowledgements
The authors thank Stefano Corradini for

Kretzschmaria deusta on veteran beech

The authors thank Stefano Corradini for
his valuable technical support.

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Supplementary Material

Fig. S1 - Veteran beeches are keystones of the Trentino landscape.

Fig. S2 - Cosmospora berkeleyana perithecia growing directly above thestromata surface of K. deusta, and structure of asci and ascospore.

Tab. S1 - Surveyed veteran beech sites with K. deusta presence and risk status.

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