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Mistletoe on urban trees in the city of Vienna, Austria☆

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ABSTRACT

A study of mistletoe on urban trees was conducted in Vienna, Austria, with the aim to determine the degree of mistletoe infection, and to identify host species that are highly susceptible or alternatively, resistant to mistletoe parasitism. At the same time, the dependence of mistletoe (*Loranthus europaeus* L; *Viscum album* L) occurrence on various factors was investigated. For this purpose, the tree cadastre of the city of Vienna was evaluated (the record is about 213,841 trees) and the Botanic Garden of the University of Vienna was visited. New host trees, not known in the literature, were described for the first time. The apparent spreading of mistletoes cannot be traced to a single factor; several are important and interacting. It could be shown that the presence of mistletoe in cities is closely related to the species of host tree, the location, the growing density of the trees, the age of the trees, as well as tree height. The host trees often showed marked adaptation of native tree species to mistletoe (i.e., fewer infections) and significant infection in introduced tree species. In some species, certain cultivars may be resistant or less susceptible to mistletoe than others. Among the damage or diseases observed on trees infected by mistletoe, bark damage occurred most frequently. Determining the distribution of mistletoe and the underlying factors is of great importance for green space management in cities, especially in relation to climate change.

1. Introduction

Green spaces play an integral part in cities and have a positive impact on the urban environment. Compared to trees in natural areas, urban trees grow under more stressful conditions, which can make them more susceptible to pests, parasites and diseases (Díaz-Limón et al., 2016; Alvarado-Rosales and Saavedra-Romero, 2021; Walas et al., 2022; de Andres et al., 2024).

Mistletoe is a term for hemiparasitic plants belonging to several different taxa. In the order Santalales, they are presented by the families *Amphorogynaceae*, *Loranthaceae*, *Misodendraceae*, *Santalaceae* and *Viscaceae* (Nickrent et al., 2010; Ahmed and Dutt, 2015). Mistletoe establishes long-term (at least 20 years) relationships with various woody species. They obtain water and mineral nutrients from the host and can increase water stress, especially in arid regions (Zweifel et al., 2012; Sanguesa-Barreda et al., 2013; Ozturk et al., 2019; Lorenc and Vele, 2022). They can be one of the main reasons for the dieback of many forests, decorative and fruit crops (Mutlu et al., 2016).

Besides, mistletoes play an important ecological role by increasing biodiversity (Grundmann et al., 2011; Barbu, 2012; Watson, 2015; Griebel et al., 2017; Szmidla et al., 2019; Watson et al., 2023). They can produce large amounts of pollen, nectar or fruit, which is very important for many animal groups (Aukema, 2003; Mathiasen et al., 2008; Watson and Herring, 2012; Baltazár et al., 2013; Briem et al., 2016; Krasylenko et al., 2020; Briggs, 2021). Birds like to feed on the berries and sometimes build their nests in the middle of the mistletoe bush. Mushrooms, algae and lichens settle on different parts of the mistletoe.

The number of host species infected by mistletoe is one of the key factors that affect the prevalence, virulence and general distribution of the hemiparasite. Mistletoe species are known to have a variety of

☆ Note to editors: the Austrian Research Centre for Forests is the place where the work was performed. For Ukrainian scientists, the main place of work is the specified institutes in Ukraine.

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patterns of host specificity, from very narrow (only one species) to broad (hundreds of species) (Barney et al., 1998; Milner et al., 2020; Maul et al., 2019). In Vienna, two species widely distributed in Europe are found: *Loranthus europaeus* and *Viscum album*.

According to literature, *L. europaeus* can grow on *Castanea sativa,* Mill., *Olea europaea* L., *Carpinus betulus* L., *Betula pendula* Roth, *Acer campestre* L., *Crataegus monogyna* Jacq., *Prunus avium* L. (Krüssmann, 1977; Grazi, Urech, 1985; Eliás, 1985; Eliás, 2002; Zebec, Idžojtić, 2006; Kumbasli et al., 2011; Saraj et al., 2015; Glatzel et al., 2016; Krasylenko et al., 2019). However, the main host trees belong to the genus *Quercus: Q. robur* L., *Q. petraea* (Mattuschka) Liebl., *Q. cerris* L., *Q. pubescens* Willd., *Q. frainetto* Ten., *Q. rubra* L., *Q. palustris* Munchh., *Q. dalechampii* Ten., *Q. virgiliana* Ten.). In the early publication by Tübeuf (1923), several resistant species for *L. europaeus* were described, since attempts to artificially infect these tree species were unsuccessful: *Populus balsamifera* L., *Malus domestica* Borkh., *Prunus padus* L. and *Laburnum anagyroides* Medik.

Viscum album can settle on about 500 species of trees and shrubs (Mellado and Zamora, 2014; Krasylenko et al., 2020; Thomas et al., 2022). It is believed that when expanding its range, *V. album* prefers alien and introduced species (Zuber, 2004; Walas et al., 2022). In addition, *V. album* shows different specificity for the settlement of deciduous and coniferous species. Using a number of different genetic markers, the existence of three subspecies of mistletoe has been proven: *V. album* ssp. *abietis* (Wiesb.) Abromeit is found on silver fir (*Abies* sp.); *V. album* ssp. *austriacum* (Wiesb.) Vollmann mainly inhabits pine trees (*Pinus* sp.), and *V. album* ssp. *album* L. grows on a variety of deciduous woody species (Bilonozhko et al., 2019, 2021). All three subspecies are found in Austria. Another subspecies *V. album* ssp. *creticum* N. Böhling which grows only on *Pinus halepensis* ssp. *brutia* Ten. was described in Crete (Böhling et al., 2002). However, the principle by which some host plants are affected more abundantly than others has not yet been clarified, although instances where certain species are infected less often than others have been noted (Lech et al., 2020).

The aim of this study was to identify host species highly susceptible to mistletoe parasitism, assess the abundance of the different mistletoe species in Vienna and determine the intensity of the infection. In addition, the dependence of mistletoe distribution on various factors (location, tree density, age, height, trunk and crown size, tree disease, 'host quality' in the sense of Watson (2009) was studied and discussed. Our approach is different from other studies (based on direct observations by scientists) because of the availability of a unique tree database of the City of Vienna.

2. Materials and methods

This research is based on the analysis of the tree cadastre of the City of Vienna, as well as on personal observations by the authors. The data was provided by the municipal department Parks and Gardens ('Magistratsabteilung 42 Wiener Stadtgärten' or 'MA 42' for short) in November 2022. The municipal department is in charge of around 500,000 trees in the streets, parks and urban forests. The trees in streets have been completely recorded, as they serve as a working aid for MA 42. However, trees in parks and forest-like areas are only partially recorded. Further, the tree cadastre comprises only trees managed by the municipal department, but e.g., no trees in housing estates, industrial sites or the botanic garden. The Botanic Garden of the University of Vienna was visited and mistletoe infection assessed by the authors. The data is described in a separate subchapter.

The information provided for the Vienna tree cadastre contained data on tree species, age, height, crown and stem measurements, and diseases as well as records on the presence of disease, pests, mistletoes, pruning and other maintenance measures. In the tree cadastre, the records did not differentiate between the mistletoe species. Hence, an additional 750 trees that could theoretically be hosts for both *V. album* and *L. europaeus* were checked.

For convenience of analysis, the trees were placed in age groups (units of 20 years and separately old-growth trees) and trunk circumference groups (units of 50 cm). In the Vienna tree cadastre, the vitality categories are labelled as 'Exploration stage', 'Degeneration stage', 'Stagnation stage', 'Resignation stage' and 'dead'. Their classification is based on Roloff (2001).

Based on morphological descriptions, we identified fives types of bark (fissured, smooth, scaly, smooth-fissured, smooth-scaly). Smooth-fissured and smooth-scaly means that trees have smooth bark when they are young, but with age the bark becomes fissured or scaly.

In the tree cadastre, the indicators of damage for the crown, stem and root are recorded separately. The list of damages includes for the crown*: leaf necrosis/chlorosis, woodpecker holes, withered tips, branch breakage, bark-/wood damage, cancer, pruning site, cracks, rot, fungal infection, animal damage, reaction wood, leaf inhabiting fungi;* for the stem*: holes/ woodpecker holes, wood damage/rot cancer, fungus infection, inclusions, bark damage, reaction wood, cracks, leakage of tree sap, animal damage;* for the root*: holes, wood damage/rot, visible root damage, fungal damage, animal damage, insect holes, ground cracks*. For this study, the data on damage was only available for trees with mistletoes.

The data was analysed with Excel statistical functions using the Microsoft Office XP software, and Statistical Package for Social Sciences, version 11.5 (SPSS Inc., Chicago, 2002). To identify the relationship between the age of trees and mistletoe infection, as well as size characteristics of trees and mistletoe infection, the Pearson's chi-squared test (χ2-test) was used for independence (https://www.statgraphics. com/ resources-downloads). To complement the correlation analysis, all factors were included in a joint analysis by applying factorial analysis of mixed data (Pagès, 2004) using the FAMD function from the FactoMineR version 2.10 package in R version 4.3.3 (results in Supplementary Information, section A). For the spatial analysis of infection patterns, Moran's I statistic for spatial autocorrelation was first computed using the R package spdep (Bivand et al., 2017), while a 50 m radius around each tree was considered for the spatial weight matrix. Moran's I quantifies spatial autocorrelation by assessing the degree to which similar or dissimilar values are clustered or dispersed over a geographic area, and thus gives an idea of whether mistletoe-bearing trees tend to occur next to other mistletoe-bearing trees or not (more information and graphics in Supplementary Information, Section B). Nearest neighbour distances of all trees and mistletoe-bearing trees were calculated using the spatstat R package (Baddeley and Turner, 2005) and statistically compared using the Kolmogorov-Smirnov test. For the processing of GPS data, we used the program QGIS 3.22.12.

3. Results

3.1. Host species

In the tree cadastre, a total of 213,841 trees were analysed. The most common tree species in Vienna are *Acer*, *Tilia*, *Fraxinus*, *Aesculus* and *Populus.* They account for approximately 53,8 % of the trees. Mistletoe was observed on 6537 trees, representing 3.06 % of the total tree population. Out of 546 taxa of woody species, 114 are affected by mistletoe. The level of infection can vary from 1 to 30 mistletoe bushes per tree.

Two different species of mistletoes are found – *V. album* and *L. europaeus*. *V. album* ssp. *album* occurs on the vast majority of host tree species (97 %). *V. album* ssp. *austriacum* occurred on only one tree (*Pinus sylvestris* L.), although there are 11 species of the genus *Pinus* (9787 trees) present in the database, and many more in parks and surrounding forests. A similar situation was noted for *V. album* ssp. *abietis*: 6 species of the genus *Picea* (1648 trees) and 7 species of the genus *Abies* (238 trees) were recorded in the cadastre. However, mistletoe was found on only one tree of *Abies alba* Mill.

L. europaeus accounted for 3 % and was only found on the genus *Quercus* on the following species: *Q. cerris*, *Q. petraea*, *Q. robur* and *Q. rubra*. At the same time, a total of 15 species of the genus *Quercus* were recorded in the database (*Q. cerris, Q. coccinea* Muenchh., *Q. dentata* Thunb., *Q. frainetto, Q.* x *hispanica* Lam., *Q. ilex* L., *Q. libani* G. Olivier, *Q. macranthera* Fisch. & C.A. Mey. ex Hohen. *Q. petraea, Q. pubescens, Q. robur, Q. rubra, Q. suber* L., *Q.* x *kewensis* Osborn, *Q.* x *turneri* Willdenow).

At least 20 genera have been identified as hosts for *V. album* (Fig. 1). About 58 % of all infected trees in Vienna belong to the genus *Acer*. Among other genera, *Tilia* (17 %), *Populus* (12 %) and *Robinia* (5 %) were most common. *Fraxinus, Juglans* and *Malus* were presented with 1–2 %. *Aesculus, Alnus, Amelanchier, Betula, Carpinus, Celtis, Crataegus, Maclura, Prunus, Pyrus, Salix, Sorbus, Tetradium* and *Ulmus* infected plants were found on fewer occasions. Among conifers only *Pinus sylvestris* and *Abies alba* (only one tree of each of these species) were infected.

As a result of this research, nine new host trees of *V. album*, previously undescribed in the scientific literature, were identified in Vienna. They comprise *Acer hyrcanum* Fisch. & C.A.Mey., *A. griseum* (Franch.) Pax, *Aesculus flava* Sol., *Corylopsis platypetala* Rehder & E.H. Wilson, *Fontanesia phillyreoides* Labill., *Styrax obassia* Siebold & Zucc., *Tetradium daniellii* (Benn.) T.G.Hartley, *Tetradium ruticarpum* (A.Juss.) T.G. Hartley and *Tilia x euchlora* K.Koh. None of these tree species are native to Austria.

We inspected 216 trees of the *Quercus* genus (13 % of the total number of infected trees of the *Quercus* genus). Only one tree was infected with *V. album*, all other trees were infected with *L. europaeus*. Thus, the infection of the *Quercus* genus by *V. album* is a rare phenomenon in Vienna.

Infections have different intensities for different woody species. It is important to identify mistletoe-resistant species and to differentiate between mistletoe host species that are heavily, moderately and lightly infected.

Having studied the literature and considered the features of infection of trees belonging to different taxa, we identified five groups of plants in Table 1. Infected trees in the city of Vienna were also ranked by these groups. Plants presented in groups I and II are noted as hosts for the entire distribution area and constitute the majority of infected species in Europe (Barney et al., 1998; Krasylenko et al., 2020; Thomas et al., 2022). There are 170 non-infected woody species in Vienna (group V). Some are represented by only a few trees in the city while others have about 3000 trees (for example *Corylus colurna* L.).

Mistletoe settles on both native and introduced woody species, which were introduced in Vienna, primarily from Asia, North America, and the Balkan countries. The total number of infected species is 114. Thereof, 47 species are native and 67 are introduced. That means the majority of infected species are introduced (Fig. 2). Regarding the total number of trees, 6537 are recorded as infected in Vienna. Thereof 5425 trees are native and 1112 introduced. Native species prevail in terms of the number of trees in Vienna (Fig. 2).

Comparing the species affected by mistletoe within a genus showed a pronounced adaptation to mistletoe of native species and significant infections in introduced, related species. For example, *Fraxinus excelsior* L. is less infected than the introduced species *F. ornus* L. and *F. pennsilvanica* Marshall, or *Acer campestre*, *A. platanoides* L. and *A. pseudoplatanus* L. are less infected than *A. saccharinum* L.

Within the same family or genus, there are species that are highly susceptible, weakly susceptible, or not susceptible at all. In the *Fagaceae* family, *Quercus robur* in Vienna can be severely affected by mistletoe, while *Fagus sylvatica* is not affected at all. Species of the *Fabaceae* family are intensively infected by mistletoe (*Robinia pseudoacacia* L.) or not infected (*Sophora japonica* (L.) Schott). In the family *Juglandaceae*, the intensity of *Juglans nigra* L. mistletoe infection reaches 35 %, but *Juglans regia* L. is quite resistant to mistletoe infection (0.05 %), and *Pterocarya faxinifolia* (Lam.) Spach is not infected at all. Some species of the *Betulaceae* family are susceptible (*Betula pendula*), slightly susceptible (*Alnus glutinosa* Medik.) or not susceptible (*Corylus colurna*). In the genus *Acer*, *A. campestre* gets more likely infected with mistletoe than *A. negundo* L., and *A. buergerianum* Miq. is not infected at all.

In some species, the question of susceptibility comes down to the cultivar level – specific cultivars can be resistant to mistletoe in an otherwise susceptible species. Weakly infected by mistletoe are e.g.: *Acer platanoides* 'Cleveland', *Fraxinus excelsior* 'Diversifolia', *F. excelsior* 'Westhofs Glorie', *F. ornus* 'Obelisk', *Prunus cerasifera* 'Nigra', *Prunus serrulata* 'Kanzan', *Pyrus calleryana* 'Chanticleer' and *Tilia cordata* 'Greenspire'. Some culitvars are not infected at all: *Acer campestre* 'Elsrijk', *Fraxinus angustifolia* 'Raywood', *F. excelsior* 'Altena', *F. excelsior* 'Globosa', *F. ornus* 'Meczek', *Pyrus calleryana* 'Aristocrat' *and Tilia tomentosa* 'Brabant'.

3.2. Density of host trees and site-related factors

In the various districts of the city, the number of mistletoe and the dynamics of its population differ significantly. This usually depends on the area of the district, the number of trees present, their growth density, the tree species composition, and the location of the district. The vast majority of infected plants in Vienna grow in groups (54 %), rows or in alleys. Single plants were infected only in 5 % of cases.

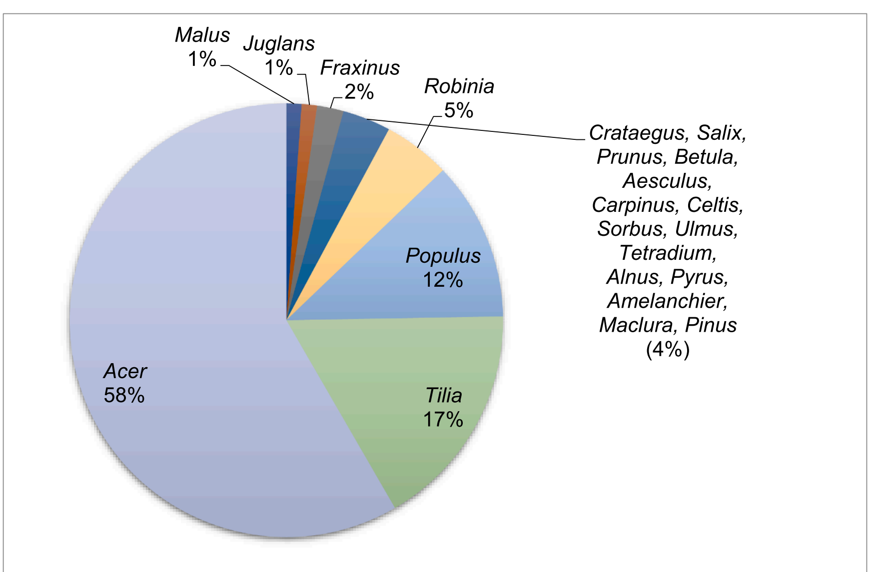

Fig. 1. The spectrum of host plant genera of *Viscum album* in Vienna. Percentage ratio of plant genera out of the total number affected by mistletoe.

Table 1
Groups of host plants of *Viscum album* (only species, but no cultivars are given).

Group Characteristic	Species in the literature	in Vienna*(%)	
I. **Main hosts** Species that are most often infected throughout the growth area	*Acer platanoides* L. *Acer saccharinum* L. *Populus nigra* Mill. *Robinia pseudoacacia* L. *Salix alba* L. *Tilia cordata* Mill.	*Acer saccharinum* L. (16.2) *Acer platanoides* L. (9.7) *Celtis occidentalis* L (21.5) *Juglans nigra* L. (35.2)	*Malus purpurea* Rehder (18.7) *Populus canadensis* Moench (16.4) *Populus balsamifera* L. (26.3)
I. **Secondary hosts** Species that are infected often, but with a lower intensity	*Betula pendula* Roth. *Crataegus monogyna* Jack *Prunus mahaleb* L. *Sorbus aucuparia* Poir.	*Acer campestre* L. (6.9) *Acer opalus* Mill. (5.1) *Acer pseudoplatanus* L. (4.7) *Acer tataricum* L. (6.5) *Aesculus flava* Sol. (6.3) *Crataegus laevigata* (Poir.)DC. (6.8) *Crataegus monogyna* Jack (5.6) *Fraxinus pennsylvanica* Marshal. (5.2)	*Populus nigra* Mill. (7.6) *Populus simonii* Carriere (8.8) *Robinia pseudoacacia* L. (5.1) *Salix alba* L. (5.9) *Tilia americana* L. (7.8) *Tilia cordata* Mill. (4.9) *Tilia platyphyllos* Scop. (5.3)
I. **Irregular hosts** Species that are infected only when a complex of ecological and biotic conditions is combined	*Aesculus hipocastanum* L. *Alnus glutinosa* Medik. *Maclura pomifera* (Raf.) *Syringa spp.* Mill. **	*Acer monspessulanum* L. (2.1) *Alnus glutinosa* Medik (1.5) *Betula pendula* Roth. (1.2) *Crataegus lavallei* Sarg. (1.3) *Fraxinus americana* L. (1.6) *Fraxinus angustifolia* Vahl. (1.3) *Fraxinus ornus* L. (1.1) *Malus sylvestris* (L.) Mill. (3.1) *Populus alba* L. (2.3) *Populus canescens* (Aiton) Sm. (2.2)	*Prunus domestica* L. (0.7) *Prunus mahaleb* L. (2.5) *Prunus padus* L. (2.3) *Sorbus aria* (L.) Crantz (3.3) *Sorbus aucuparia* Poir. (2.1) *S. intermedia* (Ehrh.) Pers. (0.7) *Tilia euchlora* K. Koch (2.0) *Tilia tomentosa* Moench (0.9) *Tilia vulgaris* Hayne (3.1) *Ulmus laevis* Pall. (1.6)
IV. Rare hosts Species that are noted as a host for *V. album* only in single reports	*Juglans regia* L. *Quercus robur* L. *Ulmus pumila* L. **	*Acer negundo* L. (0.1) *Aesculus carnea* Hayne. (0.1) *Aesculus hippocastanum* L. (0.1) *Carpinus betulus* L. (0.2) *Celtis australis* L. (<0.1) *Fraxinus excelsior* L. (0.3) *Juglans regia* L. (<0.1)	*Pinus sylvestris* L. (0.2) *Prunus avium* L. (<0.1) *Prunus cerasifera* Ehrh. (0.4) *Quercus robur* L. (<0.1) *Ulmus glabra* Huds. (0.4) *Ulmus minor* Mill. (0.1)
V. Species that are not infected Species that have not been noted as a host for *V. album*	*Albizia julibrissin* Durazz *Catalpa ovata* G.Don *Fagus sylvatica* L. *Gingo biloba* L. *Magnolia kobus* DC: **	*Castanea sativa* Mall. *Catalpa bignonioides* Walter *Cercis siliquastrum* L. *Chamaecyparis lawsoniana* A.Murr. *Cornus mas* L. *Corylus colurna* L. *Cupressocyparis leylandii* Dallim *Elaeagnus angustifolia* L. *Fagus sylvatica* L. *Gleditsia triacantho* L. *Gymnocladus dioicus* (L.) K.Koch *Larix decidua* Mill. *Liquidambar styraciflua* L. *Liriodendron tulipifera* L. *Magnolia kobus* DC. *Metasequoia glyptostroboides* Hu Cheng, *Morus nigra* L. *Ostrya carpinifolia* Scop. *Parrotia persica* (DC.) C.A.Mey *Paulownia tomentosa* (Thunb.) Steud. **	*Picea abies* (L.) Karst *Picea omorika* (Pančić) Purk. *Picea pungens* Engelm. *Pinus leucodermis* Antoine. *Pinus nigra* Arnold *Platanus orientalis* L. *Platycladus orientalis* (L.) Franco *Populus tremula* L. *Prunus armeniaca* Thunb. *Prunus cerasus* L. *Pseudotsuga menziesii* (Mirb.) Franco *Pterocarya fraxinifolia* (Poir.) K.Koch *Pyrus communis* L. *Quercus frainetto* Ten. *Quercus pubescens* Willd. *Sambucus nigra* L. *Taxus baccata* L. *Thuja occidentalis* L. *Zelkova serrata* (Thunb.) Makino **

*the percentage of infection among trees of the same species is given in the brackets
**not a complete list of species is given

The spatial analysis of tree positions suggests a significant trend towards aggregation of mistletoe-bearing trees, expressed by a positive value of the Moran's I statistic (0.1102, p-value < 0.001) (Supplementary Information, Section B). Comparing the nearest neighbor distances of mistletoe-bearing trees with the overall nearest neighbor distances, we found that mistletoe-bearing trees had a slightly lower mean nearest neighbor distance (6.32 ± 0.06 m) compared to the overall mean (7.46 ± 0.01 m).

After analysing the location of individual plants infected with mistletoe, we were able to identify places with the highest degree of infection within the city. As shown in Fig. 3, these are the territories of large green park areas, the Prater, Türkenschanzpark and Pötzleinsdorfer Schlosspark.

A number of favourable factors for the spread of white mistletoe are combined in these places. Many trees of different species are growing in a limited area; among them many introduced species. There are also ponds that attract birds affiliated with mistletoes. Repeating the nearest neighbor analysis for park trees only, we found that the distances between park trees are actually smaller than the total distances (6.12 ± 0.06 m), though again by a small margin. That definitely seems to affect the level of infection.

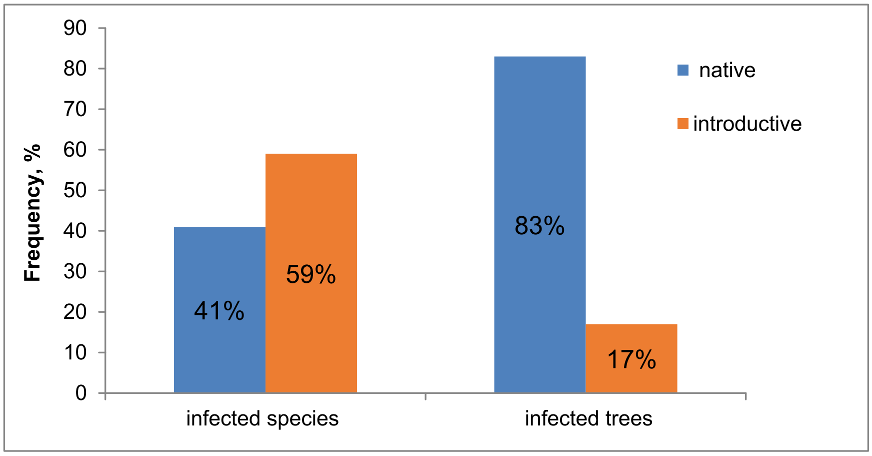

Fig. 2. Ratio introduced and native infected species and trees.

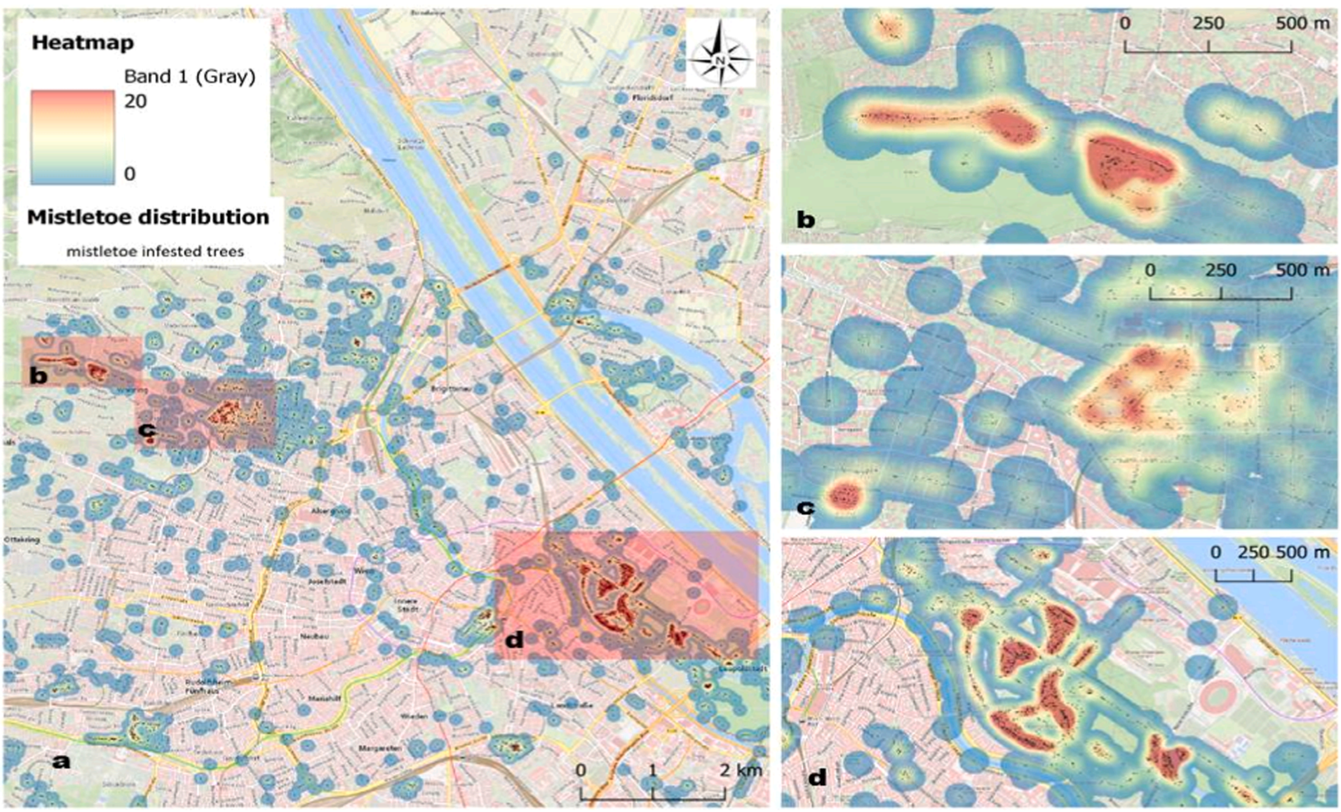

Fig. 3. Location scheme of the most infected places in Vienna (a – overview, and zoom-ins: b – Pötzleinsdorfer Schlosspark, c – Türkenschanzpark, d – Prater). The change in color on the map indicates different numbers of infected plants in the area, with the intensity increasing from blue to red. In the base map, rose colors indicate built-up areas, light blue are water bodies, and light green are vegetation; lines are main traffic routes.

3.3. Mistletoe in the botanical garden

The Botanical Garden of the University of Vienna is home to numerous species of woody plants, most of which are introduced or rare. The trees are planted quite densely there. We found a significant number of affected trees, including *Acer griseum*, *A. monspessulanum* L., *Aesculus carnea* Hayne., *Celtis occidentalis* L., *Corylopsis platypetala*, *Davidia involucrate* Baill., *Fontanesia phillyreoides*, *Malus baccata* (L.) Borch., *Pseudocydonia sinensis* (Thouin) C.K.Schneid., *Quercus macrocarpa, Styrax obassia*, *Syringa persica* L., *S. reticulate* (Blume) H.Hara, *S. josikaea* J.Jacq. ex Rchb., *Tetradium ruticarpum* and *Tilia americana* L.

More common native species are also affected by mistletoe: *Acer campestre*, *Betula pendula*, *Crataegus laevigata* (Poir.) DC, *C. monogyna*, *Laburnum anagyroides*, *Populus nigra* Mill., *Quercus robur*, *Q. pubescens* and *Tilia platyphyllos* Scop. Most trees are severely affected, with more than five bushes per plant.

3.4. Tree age

As a result of the analysis of the age structure of tree plantatings in Vienna, we have seen that the majority of plants growing here are plants up to 40 years old. Almost 35 % of all trees in the city are under 20 years old, 25.5 % between 20 and 40 years old. Infected individuals are observed among all age groups, but the vast majority belong to the group of 41 – 60 years (Fig. 4).

Considering each age group separately, we can note that the frequency of infection among young trees is very low (0.2 %). In the age group 21–40 years old, 2.8 % of the trees were infected. In the groups of plants over 40 years old, 5 % were infected, over 80 years up to 9 %, and over 120 – up to 10.8 %.

Using the χ2-test, we found a statistically significant relationship between plant age and *V. album* infection. The same result was confirmed separately within all genera except for *Prunus, Sorbus* and *Aesculus*.

Among the trees over 100 years old infected by mistletoe (456 in total), there were 131 trees of the genus *Acer* (*A. campestre* L., *A. platanoides*, *A. pseudoplatanus*, *A. saccharinum*, *A. tataricum* L.), 130 trees of the genus *Populus* (*P. alba* L., *P. balsamifera, P. nigra*, *P. simonii* Carriere., *P. canadensis, P. canescens* (Aiton.) Sm.), 68 trees of the genus *Quercus* (*Q. cerris, Q. robur, Q. rubra*), 96 trees of the genus *Tilia* (*T. americana, T. cordata* Mill., *T. platyphyllos*, *T. tomentosa* Moench., *T. euchlora*, *T. vulgaris* Hayne.) and to a small extent *Aesculus hippocastanum* L:, *Celtis occidentalis*, *Robinia pseudoacacia* (in total 31 trees). These species are not only the most common hosts of mistletoe, but also those that can coexist with mistletoe for the longest period of time.

3.5. Tree size and height

We analysed several tree size characteristics including stem circumference, crown volume and height. By using the Pearson's chi-squared test for statistical analysis, we demonstrated the association between mistletoe infection and all three parameters. The FAMD-analysis (Supplementary Information, Section A) showed no particular association between tree size/age variables and mistletoe infection for the whole dataset. By repeating this analysis for the three most infected genera using balanced subsets of infected and uninfected trees, we found an association between tree hight and mistletoe infection for *Acer* and *Tilia*, but not for *Populus.* Therefore, using different statistical approaches, we obtained partly overlapping results, emphasising the relevance of tree height over other variables related to tree size for mistletoe infection.

As shown in Fig. 5, trees with a circumference of 101–150 cm are most often infected (30.5 %), although the vast majority of plants have a circumference ranging from 1 to 100 cm. In trees with a circumference of more than 350 cm, nearly 13.2 % were infected with mistletoe (111 trees out of 841).

A similar situation was found with the size of the crown diameter. The majority of trees in Vienna can be attributed to two groups with sizes of 0–3 m (29.7 %) and 4–6 m (31.3 %). However, trees in these groups have a fairly low level of infection. Only 0.4 % of trees with a crown size of up to 3 m were infected. Among plants with mistletoe, 34.5 % have a crown diameter between 7 and 9 m (Fig. 6). The percentage of infected plants increases among trees with a larger crown, up to 9.5 % at the size of 19–21 m and up to 10.2 % at the size of more than 21 m.

Of trees with a height of 11–15 m mistletoe was observed in 43.5 % (Fig. 7). Trees up to 5 m and trees taller than 20 m are less likely infected (below 5 %). In Vienna, there are only 19 trees that are taller than 30 m. The level of infection with 11,3 % among these trees is higher than in all other groups (0,4 % for group 0–5 m, 2,1 % for 6 – 10, 4,8 % for 11 – 15, 7,2 % for 16 – 20, 7,0 % for 21 – 25, 8,2 % for 26 – 30).

3.6. Host vitality

Vitality is an important parameter to fully assess the tree. About 12 % of trees with mistletoe in Vienna are in the exploration stage. Nearly 55 % of trees are in the degeneration stage and 27 % in the stagnation stage.

More than 60 % of trees with *V. album* had dry branches measuring 30 – 50 mm in diameter. Nearly 29 % of trees have small dry branches 50 – 100 mm in size and drying of large axial branches more than 100 mm was noted in 8 % (Fig. 8). In oaks, the host for *L. europaeus*, this ratio is similar. However, it should be noted that the amount of large dry branches increases to 18 %.

We analysed the morbidity and damage of trees inhabited by mistletoe. Looking at the indicators for the crown, stem and root separately, only damage to the bark and wood was standing out. About 20 % of the analysed trees with mistletoe were affected. For such genera as *Fraxinus, Betula* and *Crataegus,* this indicator reached 32 –34.9 %.

If we compare mistletoe-infected and non-infected tree species, the results in the distribution of bark texture are very similar (Fig. 9). We grouped all trees by bark type as follows: fissured, smooth, scaly, smooth-fissured, smooth-scaly. The difference between the bark texture of infected and non-infected species is 1–5 %. Mistletoe infections occurred regardless of whether the bark is smooth (*Carpinus betulus*, *Tetradium daniellii* (Benn.) T.G.Hartley, *Styrax obassia*) or fissured (*Acer campestre*, *Populus nigra*, *Robinia pseudoacacia*, *Tilia americana*). On the other hand, there were trees with fissured bark (*Sophora japonica*, *Catalpa ovata* G.Don, *Liquidambar styraciflua* L., *Pterocarya fraxinifolia*, *Corylus colurna*) where no mistletoe was found.

4. Discussion

Mistletoe exhibits peculiarities in establishing relationships with

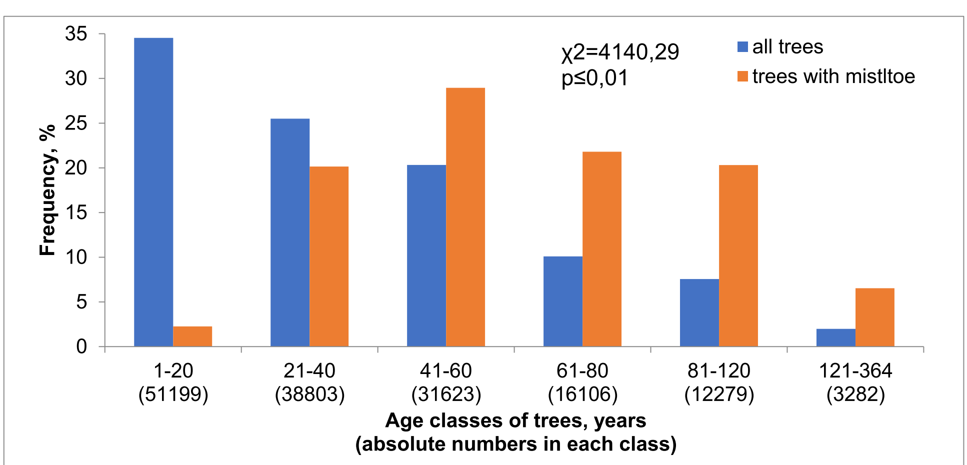

Fig. 4. Frequency distributions across age classes (years) of all trees, and those infected with mistletoe; (χ^2=4140.29), level of statistical significance (p-value) $p < 0.01$; absolute numbers in each class in brackets.

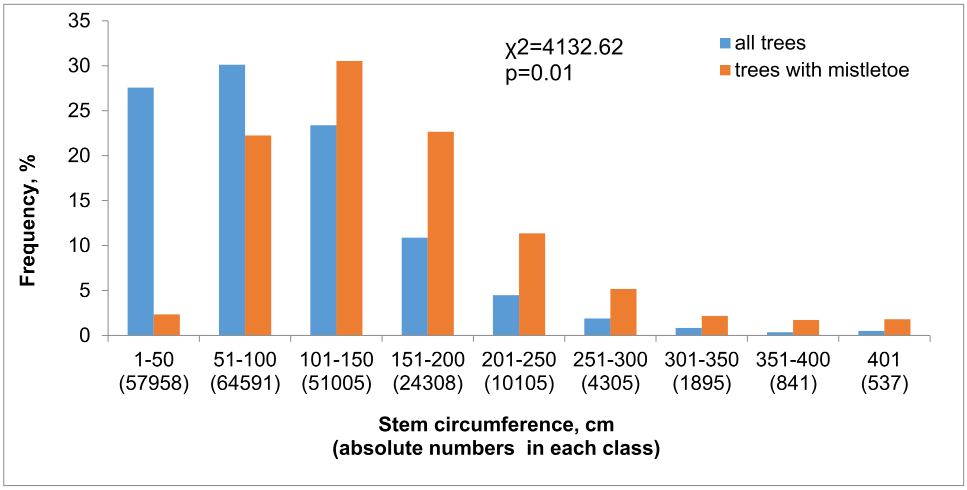

Fig. 5. Frequency distributions across stem circumference (cm) of all trees, and those infected with mistletoe; ($\chi 2$ =4132.62, level of statistical significance (p-value) $p = 0.01$); absolute numbers in each class in brackets.

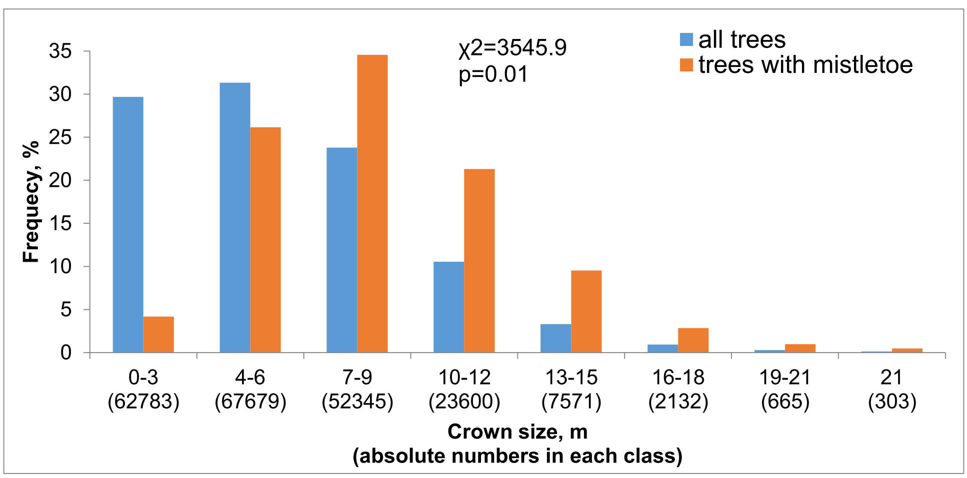

Fig. 6. Frequency distributions across crown size classes (years) of all trees, and those infected with mistletoe; ($\chi 2$ =3545.9, level of statistical significance (p-value) $p = 0.01$); absolute numbers in each class in brackets.

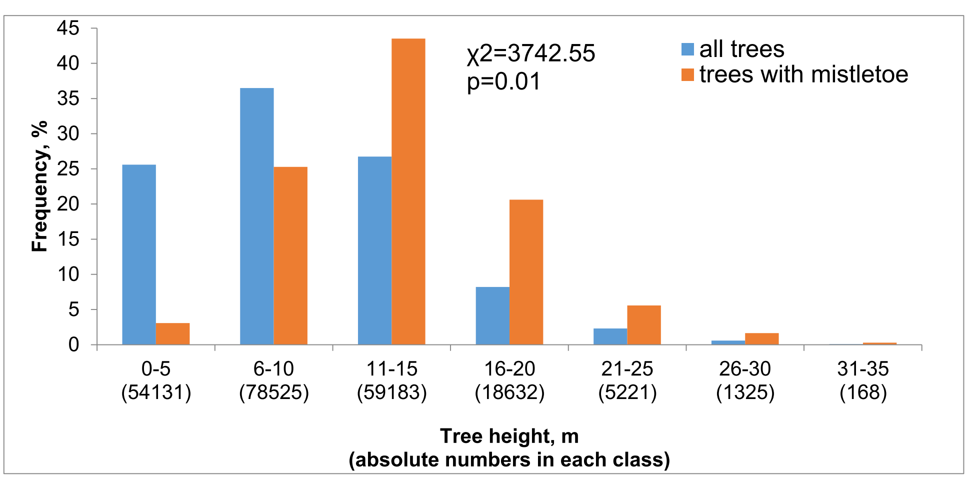

Fig. 7. Frequency distributions across trees height classes (years) of all trees, and those infected with mistletoe; ($\chi 2$ =3742.55, level of statistical significance (p-value) $p = 0.01$); absolute numbers in each class in brackets.

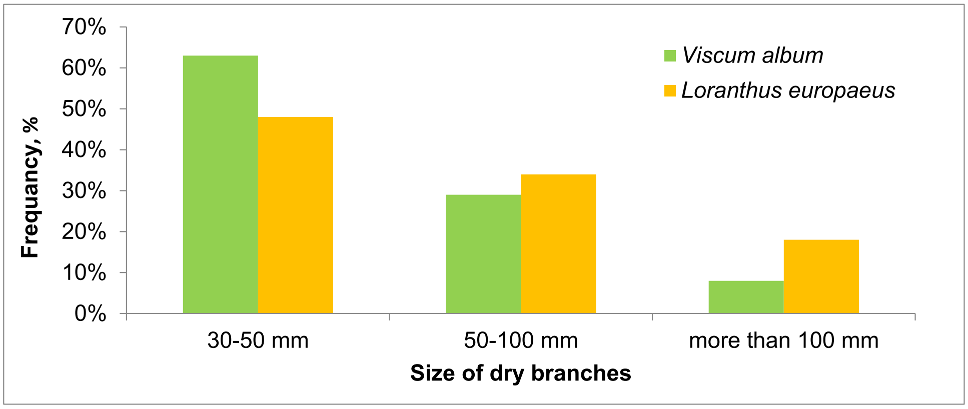

Fig. 8. Frequency of dry branches on trees infected with *Viscum album* and *Loranthus europaeus*.

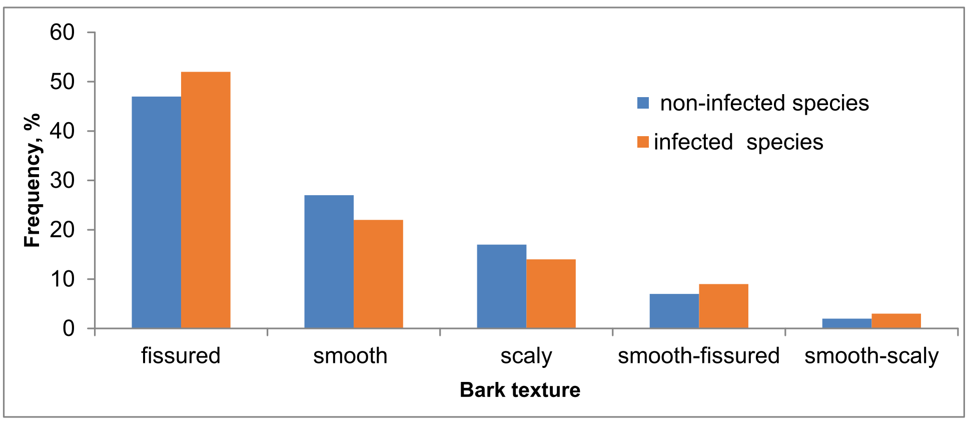

Fig. 9. Distribution of infected and non-infected species by tree bark texture.

host species. The selectivity of mistletoe's actions has not yet been fully explained or validated. Consequently, within the same family, mistletoe can severely infect, moderately infect, or not infect certain species. The results highlight the necessity of identifying mistletoe hosts by species or even cultivars, rather than relying on family categorizations. It is advisable in scientific literature to avoid generalizations when naming host genera or families, as is often the case.

According to literature, the plants on which *V. album* can settle include about 500 species of trees and shrubs (Barney et al., 1998; Szmidla et al., 2019; Krasylenko et al., 2020; Thomas et al., 2022). Cases of *V. album* settling on *Quercus* spp. are very rare within the entire European part of the range of this species (Briggs, 2021; Rutkowski et al., 2023). The infection of new host plant species by mistletoe and its appearance on previously resistant species of woody plants were noted in Vienna. A secondary check of *V. album* hosts in California in 2019 revealed 7 new species that were classified as uninfected in 1991 (Shaw and Lee, 2020). Such observation suggests a growing adaptation potential of *V. album* in urban conditions. This may also be explained by inoculum load. An increase in the number of mistletoe plants leads to an increase in the number of seeds dispersed.

The author of a study on the genetic characteristics of *P. nigra* in Vienna in the 1990s noted that the trees studied were not infected with mistletoe (Heinze, 1998). Currently, 7 % of all trees of the genus *Populus* in the city are infected (63.4 % thereof are *P. nigra*). The increase in the infection of these plants could be due to changes in climatic conditions and stress factors that may have a cumulative effect. Because of these changes, it is necessary to periodically check the emergence of new host trees, mistletoe species, the appearance of mistletoe on previously uninfected plants, and monitor the degree of mistletoe infection. Compared to other tree pests or parasites, mistletoe has a relatively slow rate of development and spread (Hawksworth et al., 1991). While there is a lack of research in Europe indicating the rate of mistletoe spread, an increase is evident. In Brandenburg, the infection level of pine trees rose from 1 % in 2009 to 11 % in 2015 (Kollas et al., 2018). Regarding Vienna, data on mistletoe infection cannot be compared with historical data, as past data collection did not focus on mistletoes.

In recent years, climate change has become increasingly evident. Indicators such as temperature and precipitation significantly affect the condition of woody plants. This is especially evident within large cities where there are a large number of buildings, roads, industrial enterprises, and automobiles. It is likely that plants weakened by stress factors may be more susceptible to various diseases and parasites. Mistletoe, as a hemiparasite, also adapts to changes in climate and the condition of host plants. Over the past 100 years, its range has gradually expanded to new territories, and the number of host species has increased (Varga et al., 2014; Thomas et al., 2022). The study by Walas et al. (2022), provides a projection of future changes in *V. album* ranges in Europe based on climate data. The key is temperature change. It demonstrates that the potential mistletoe range will shift in a north-easterly direction and towards higher altitudes in mountainous areas. Conversely, *V. album* populations from southern Europe may face disappearance.

While mistletoe is highly selective in choosing its host, the primary method of preventing the spread of mistletoe in an urban setting (mainly for aesthetic reasons) is to select an assortment of trees with either no or low susceptibility to mistletoes. In Vienna, a significant number of mistletoe-resistant species are conifers and could thus be considered potential candidates for urban greening. However, conifers do not play a big role in Vienna and make up only 6,7 % of the city's trees. This could also indicate that environmental conditions in the city are not very suitable for many conifers, and also that their 'host quality' there is low for mistletoes. Generally, under the premise of the avoidance of heavy mistletoe infections by the city's parks and gardens administration, it is worth considering species that are weakly affected or not affected under local conditions, even if, according to the literature, they are classified as host trees. It is also crucial not to plant tree species with a high risk of mistletoe infection to prevent its rapid spread.

Vienna's urban trees play a crucial role in delivering essential ecosystem services in densely populated areas, including evaporation, providing shade, binding dust, fixing carbon dioxide, and releasing oxygen. Plans are underway to plant 25,000 trees in Vienna by 2025 (https://www.wien.gv.at/umwelt/parks/baumsortiment.html). However, these trees themselves face challenges under stress conditions, such as mechanical damage, soil compaction, heat radiating from glass and concrete facades, and the increasing temperatures and drought associated with urban environments.

The municipal department Parks and Gardens (MA 42) has compiled a list of tree species capable of thriving in Vienna's urban conditions (https://www.wien.gv.at/umwelt/parks/baumsortiment.html). This list comprises 25 tree species, with 19 specifically identified as heat-resistant. Importantly, the majority of the species on this list also demonstrate resistance to mistletoe infection.

Species such as *Koelreuteria paniculata* Laxm., *Platanus orientalis* "Minaret", *Pyrus calleryana* «Chanticleer» not only improve the microclimate in the city but are also resistant to the spread of mistletoe, while species such as *Acer campestre* 'Elsrijk', *Acer campestre* 'Korinthosz', *Tilia tomentosa* 'Brabant' should be used with caution. They easily become hosts for mistletoe, which can shorten their life expectancy and change their perceived aesthetic value. Therefore, it is better to plant them in places where there are no mistletoe trees, or to plant them singly or in mixed plantings.

Mistletoe distribution in the city depends on trees used in landscaping or which are part of local forests, parks, and cemeteries. Botanical gardens and other natural protected areas deserve special attention. In such areas, there is usually a quite high level of mistletoe infection, and thus can be important sources for the spread of mistletoe to adjacent areas. Exotic plants in the collections of botanical gardens often experience more adaptation stress. Due to unfavourable conditions of introduction and direct contact with already infected plants, they are more easily infected with mistletoe. Trees with mistletoes can live and grow for a long period, which is more likely in the case of native plants. Introduced species, however, and mistletoe can lead to rapid die-off. Therefore, botanical gardens need to develop and implement special measures to prevent the further spread of mistletoe.

Within the scope of our research, we sought to identify factors that contribute to the infection of trees and the spread of mistletoe. We showed the dependence of the level of infection on the age of the plant. Infected cases are observed in all age groups. However, the vast majority of them belong to the 41–60 and 61–80 years age groups. The age of the tree affects the attractiveness of mistletoe-bearing birds (convenient branches, presence of other fruits). However, with age, the number of mistletoe bushes per tree increases, which, in turn, is the source of fruits. It can infect branches below when they fall. According to the literature, aged plants are infected more often than young plants (Barbu, 2012; Bilonozhko et al., 2022; Lorenc and Vele, 2022). This has also been shown for other species of parasitic plants (González-Elizondo et al., 2018; Ferrenberg, 2020). On the other hand, when studying the features of infections in *Pinus aristata* Engelm. by mistletoe *Arceuthobium microcarpum* (Engelm.) Hawksw. & Wiens (Santalaceae), a predominance was shown for young plants up to 30 years old (Scott and Mathiasen, 2012). Therefore, age is not always a decisive factor when trees are infected with mistletoe, although it has a significant effect.

In Vienna, 81 % of all trees are between 1 and 150 cm in circumference, and 75 % of mistletoe-infected trees are between 51 and 200 cm. A relationship between mistletoe infection and tree height was shown. Kołodziejek et al. (2013) found that tree height and diameter were significantly positively correlated with the number of *V. album* per host tree. Some other studies have also established the specifics of mistletoe attachment height (Zuber, 2004). This is due to the fact that birds prefer higher places for perching and nesting (Aukema and Rio, 2002; Kolodziejek et al., 2013). A similar effect was observed for other mistletoe species. Thus, a higher degree of infection was observed on trees with a larger diameter and height for *Erianthemum dregei* (Eckl. & Zeyh.) V. Tieghem, *Taxillus nigrans* (Hance) Danser, and *Scurrula parasitica* L. (Gairola et al., 2013; Ma et al., 2020). According to the literature, such a connection is not always confirmed. For example, in a study by Kartoolinejad et al. (2007), it was shown that the degree of *V. album* infection did not depend on the height of the tree.

We found a statistically significant difference between tree crown size and mistletoe infection. The largest of the infected trees had a crown reaching 7–9 m. With further increases in size (up to 10–12 and 13–15 m), the number of such trees in the city decreased. However, the level of infection of such trees is still higher than that of trees with crowns up to 4 m in size. Lech (2020) reported that a larger crown is more convenient for birds. However, among heavily infected trees, there are also species that have a columnar shape (e.g., *Populus nigra* 'Italica'). While their crowns are quite narrow, they are still very long. Maybe the most likely determining value is the "crown surface" or "crown volume".

Birds are not the only way mistletoe seeds are spread. Autochory plays a certain role in the spread of mistletoe. It is also possible that mistletoe bushes are mechanically hit by branches of nearby trees. It is obvious that the probability of infection of plants in groups is higher. Even with direct overlapping of branches, the seeds of *V. album* ssp *album* do not seem to settle on *P. sylvestris*. This can be explained by the fact that in the process of specialization for settling on coniferous plants, *V. album* ssp. *abietis* and *V. album* ssp. *austriacum* had to adapt to the action of oleaginous resin. This substance can be a protective factor, both chemically and mechanically.

Sargent (1995) found that the size of the branches had a strong effect on the growth of mistletoe. Small host branches (< 100 mm diameter) dried up frequently after mistletoe parasitism, leading to the death of the mistletoe seedlings on them. We also found more intensive drying of small branches on trees infected by *V. album* and *L. europaeus*.

When analysing the damage, we could not find a correlation between mistletoe infection and the presence of other diseases or damage to the tree. The database also did not allow to determine which came first, mistletoe infection, or tree damage. However, the most frequently observed damage on infected trees was bark damage. In our opinion, this may be rather a consequence of the weakening of the tree as a result of its infection. Mistletoes use the host tree as a source of mineral substances; mistletoe also mechanically changes the structure of the wood by growing inside the tissues of the host.

The spread of mistletoe is a rather complex ecological and physiological process (Guerra et al., 2018; Ma et al., 2020), which can be influenced by quite different factors. In some studies it was shown that branches with smoother bark are more difficult to be infected by mistletoe (Arruda et al., 2006). However, Thomas et al. (2022) state that host bark morphology seems unimportant. This is probably due to the fact that mistletoe establishes most effectively on thin, smooth bark of young branches, even on hosts with fissured bark. The present research did not reveal a dependence of the effectiveness of tree infection on the type of bark.

Seeds of many plant parasites germinate only in response to chemical signals from host plants (Musselman and Press, 1995). Some parasitic angiosperms (including mistletoes) may require chemicals (haustorium-inducing factors) such as strigolactones, favonoids, quinones (Muche et al., 2022). However, it is quite easy to germinate mistletoe seeds without any chemical signals from a compatible host plant (Zuber, 2004, Stanton et al., 2010). In the review by Thomas et al. (2022) an effect of bark pH and chemistry on establishment is not recorded. In addition, quite often the germination of mistletoe seeds is observed within the mature berry, without breaking it, as well as when the seeds are stored in the refrigerator at a temperature of $+5\ ^{0}$C (unpublished observations).

Host plants defend themselves against mistletoe infection mechanically by producing lignin and suberin, and chemically by killing or inhibiting the establishment of the haustorium using secondary metabolites (terpenes, phenolics, and N-containing compounds) (Muche et al., 2022). Perhaps stressful growing conditions affect these protective mechanisms, reducing their effectiveness. Moreover, differences in the production of chemicals can vary among different species within the same genus (El Hariri et al., 1991). Due to the complex interaction of different factors in mistletoe infection, the multivariate approach provided further insight into the relationship between these factors as well as their association with mistletoe infection (Supplementary Information, section A). This approach suggested that tree height and species/cultivar information were the most relevant factors among those considered in this analysis. Interestingly, the importance of tree height was not consistent across the three genera analysed, which is similar to the findings of other authors (Kartoolinejad et al. 2007; Kolodziejek et al., 2013). This illustrates the difficulty of identifying single explanatory variables for mistletoe infection and encourages the use of multivariate techniques in this context.

Among the many factors that are likely to influence the effectiveness of mistletoe spread in cities, we have identified that species composition and their density, homogeneity of species, age structure of plant groups and tree height play a very important role. Other factors are secondary or important only in certain combinations.

5. Conclusion

By assessing the complex of factors that can affect the occurrence and spread of mistletoe, it is possible to prevent or significantly slow down the rate of spread, thereby reducing the area affected. In our opinion, it is not possible to identify one main reason that contributes to the intensity of mistletoe infection of trees. The primary factors for mistletoe expansion are the species of the host, climatic factors, tree density, size, and age. The structure of the bark and the presence of damages or pests are not decisive factors in the occurrence of mistletoe. An important factor is also the location of the tree itself and the ecological conditions in this area.

CRediT authorship contribution statement

Bilonozhko Yuliia: Writing – original draft, Investigation, Conceptualization. **Feichter Jonathan:** Software. **Kodym Andrea:** Writing – review & editing, Project administration, Funding acquisition. **Tokarieva Olha:** Writing – original draft, Investigation. **Heinze Berthold:** Writing – review & editing, Conceptualization.

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.ufug.2025.128740.

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