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Changes in the Distribution of European Mistletoe (*Viscum album*) in Hungary During the Last Hundred Years

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Abstract The hemiparasitic European mistletoe (*Viscum album*) from the family Viscaceae (Santalaceae s.l.) is able to infest more than 380 woody taxa in Europe. At the beginning of the 20th century, less than 10 % of Hungary was infested. The distribution area was centralized in the Transdanubian Mountains, and no mass occurrence was noticed elsewhere. Since then, the infested area has almost tripled, and heavily infested forests can be observed in numerous parts of Hungary, especially in the northeast area of the Hungarian Great Plain. However, the central region of the Hungarian Great Plain is still uninfested. In the North Hungarian Mountains, where the presence of potential hosts is very frequent,

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mistletoe is still quite rare. The most infested macroregion of Hungary is Western Transdanubia, the only region where all three different subspecies can be found. No significant changes have been observed in the proportions of the most common hosts in the last 90 years, with poplars (*Populus* spp.) and black locust (*Robinia pseudoacacia*) still being the most frequently infested species. Silver maple (*Acer saccharinum*) is now a heavily infested host in city parks, while the abundance of infested apple (*Malus* spp.) and pear (*Pyrus* spp.) trees has decreased with the transformation of cultivation techniques. In infested areas, nine to twelve of the most common 18 host species can be found, while only five to eight species can be observed in uninfested areas. The increased mistletoe occurrence can be attributed to several factors, including human impact, larger forest area and a growing number of breeding pairs of the mistle thrush (*Turdus viscivorus*).

Keywords distribution map · habitats · hemiparasite · Hungarian macroregions · *Viscum album*

Plant nomenclature follows Flora Europaea (Tutin et al., 1964–80); zoological nomenclature follows Fauna Europaea (de Jong 2013).

Introduction

European or white berry mistletoe (*Viscum album* L.) of the family Viscaceae (Santalaceae s.l.; Nickrent et al. 2010) is a perennial hemiparasitic shrub growing on branches, and rarely also on trunks, of woody species (Grundmann et al. 2010). At present it is widely distributed throughout Europe, Asia and America (Watson 2001). Barney et al. (1998) listed 452 species, subspecies, varieties and hybrids in 96 genera of 44 families as potential hosts. Spontaneous mistletoe infestations of hardwood species in Europe were reported for 384 taxa, including 190 alien, introduced trees and shrubs. Hardwood trees are resistant to mistletoe infestation (e.g. *Fagus sylvatica* L.), although other species (e.g. *Quercus* spp. and *Ulmus* spp.) are rarely infested (Becker 2000). The mistletoe or mistle thrush (*Turdus viscivorus*) is one of the most important dispersal agents of mistletoe seeds (Hawskworth 1983).

European mistletoe is divided into several commonly accepted subspecies, which are most easily differentiated according to their hosts, as they are morphologically very similar. In Europe, four subspecies are recognized, including *Viscum album* subsp. *album* that lives on eudicots, *V. album* subsp. *abietis* that occurs solely on *Abies* spp. (Plagnat 1950) and *V. album* subsp. *austriacum* that is found only on *Pinus* spp. and *Picea* spp. (Zuber 2004). The fourth subspecies, *Viscum album* subsp. *creticum*, which grows on *Pinus brutia*, is exclusive to Crete (Böhling et al. 2003).

European mistletoe is one of the most common branch parasites in the Old World, but its distribution in Europe is rather uneven. The natural southern and western limits of its range are the Mediterranean Sea and the Atlantic Ocean, respectively (Zuber 2004). It also occurs in the British Isles, but is absent from Ireland (Briggs 2011). In the east it occurs in the Ukrainian Carpathians, and also to some extent in the other parts of western Ukraine and the Crimean Peninsula (Kubát 1997). It is not native to the Netherlands (Briggs 2011) and is not particularly common in north-western parts of

Germany, but it has a major presence in the other regions of Germany (Kuhbier 1997; FloraWeb 2013). Furthermore, it occurs sporadically in Denmark and in southern parts of Sweden, with its northern limit at Lake Mälaren (Fig. **1**; Tubeuf 1923; Zuber 2004). Mistletoe does not reach the northern and altitudinal limits of its hosts, because it is temperature-sensitive (Tubeuf 1923). According to Iversen (1944), both summer and winter temperatures restrict the geographic distribution of mistletoe. The mean monthly temperatures of the coldest and warmest months of the year correlate with the limits of occurrence of *V. album* (Skre 1979). Consequently, mistletoes will probably benefit from the warming climate and expand their ranges. This has already been shown to be the case for mistletoes growing on pines, whose altitudinal range has shifted 200 m higher in the Alps during the past century (Dobbertin et al. 2005).

The most common taxon in Hungary is *Viscum album* subsp. *album*, both *V. album* subsp. *austriacum* and *V. album* subsp. *abietis* being rare (Hirka and Janik 2009), but its distribution area seems to vary continuously.

In this study, we aim to (1) summarize the current occurrence of *V. album* in Hungary and provide distribution maps based on all records, (2) estimate the distribution changes during the last 90 years, and (3) provide information on the most common hosts in different parts of Hungary based on field surveys and published literature records.

Material and Methods

Published Records

The data initially included published studies of the Hungarian distribution of mistletoes and field surveys encompassing the last 100 years, most significantly the monograph by Tubeuf (1923), the study of Roth (1926), and the report of Bartha and Mátyás

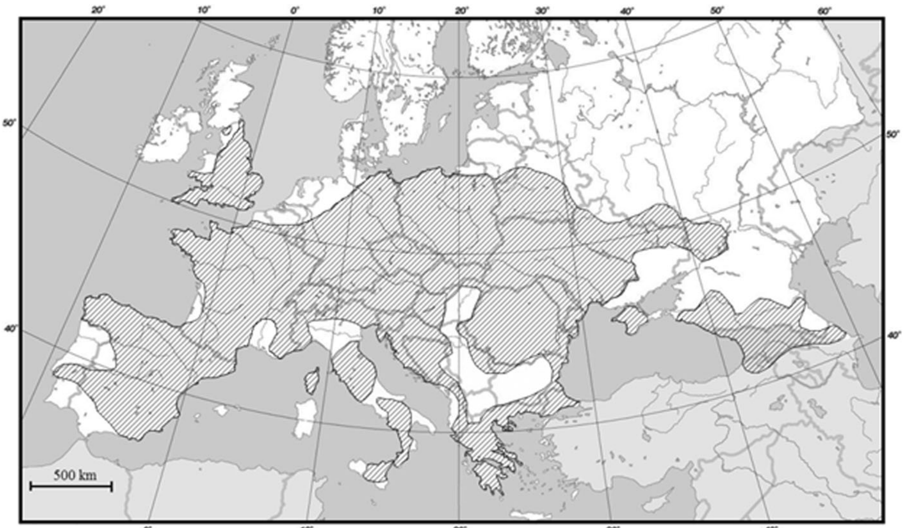

Fig. 1 Distribution of *Viscum album* in Europe without sporadic occurrences in Denmark and Sweden (based on data of Zuber 2004, Briggs 2011 and Tubeuf 1923)

(1995). Unfortunately, the literature is relatively incomplete between 1930 and 1990, and no critical review was made during this period. In addition to historical records, we used data provided by the Hungarian Forest Research Institute (HFRI) collected since 1990 from all 22 forest management corporations in Hungary, which include sizes of infested areas and intensities (percentages) of infestation. We distinguished three categories of infestation: (1) low-level infestation, if less than 10 % of host stands were infested, (2) medium-level, if the ratio of infested trees was 10–20 %, and (3) high-level, if more than 20 % of stands were infested. We listed all the data according to the geographic macroregions of Hungary.

Field Survey

In the summer of 2010, the distribution of the European mistletoe was assessed by a field survey that encompassed more than 4,000 km^2. This included all macroregions as well as specific areas where the occurrence of *Viscum album* was uncertain. This was supplemented by data collected during shorter surveys and field studies from 2008 to 2012 throughout Hungary. During these assessments, the most common hosts of mistletoe were recorded and compared with historical records. To further clarify the current distribution of mistletoe, the obtained data were also matched with distribution records deposited as part of the Hungarian Flora Mapping Programme.

Distribution Maps

The Central European Mapping System (Niklfeld 1971), based on geographic latitude and longitude, was used to construct distribution maps of *Viscum album*. The distribution patterns were defined in grid units of five longitude minutes and three latitude minutes. Furthermore, the Geographical Macroregion Map of Hungary (Fig. 2I.), provided by the Landscape Ecological Vegetation Database Map of Hungary (MÉTA; Marosi and Somogyi 1990), and the Hungarian Flora Mapping Programme, which has been collecting data for more than 10 years, were also used to create the distribution maps. We used quadrat data sheets, which contain data from 2002 to 2013 (Király et al. 2003).

The current distributions of all subspecies of *Viscum album* found in Hungary were depicted separately (Fig. 2IV; Fig. 4AB). In addition, a summarizing figure (Fig. 7) was drawn, representing the infestation intensity of mistletoe. This map shows the distribution of mistletoe from 2000 to 2013. Blank (white) squares indicate that mistletoe shrubs have not yet been observed, while uncertain data are indicated in grey. The latter are observations from the Hungarian Flora Mapping Programme before 2005 which we were unable to confirm during our field survey. The categories of infested areas are based on those used by the Hungarian Forest Research Institute. For the categories used, see above. We analysed the distribution patterns from the two previous surveys conducted in the 1920s (Roth 1926) and 1990s (Bartha and Mátyás 1995), and combined them with our own data. We them compared them with the aid of the geo-informatics programme Digiterra v.3.0. For the comparison, the distribution patterns were plotted in basic grid-cells of ten geographic longitude minutes and six geographic latitude minutes. This corresponds approximately to 12.5 × 11.1 km. Subspecies were not separated in this comparison. The abundance of mistletoe was compared with

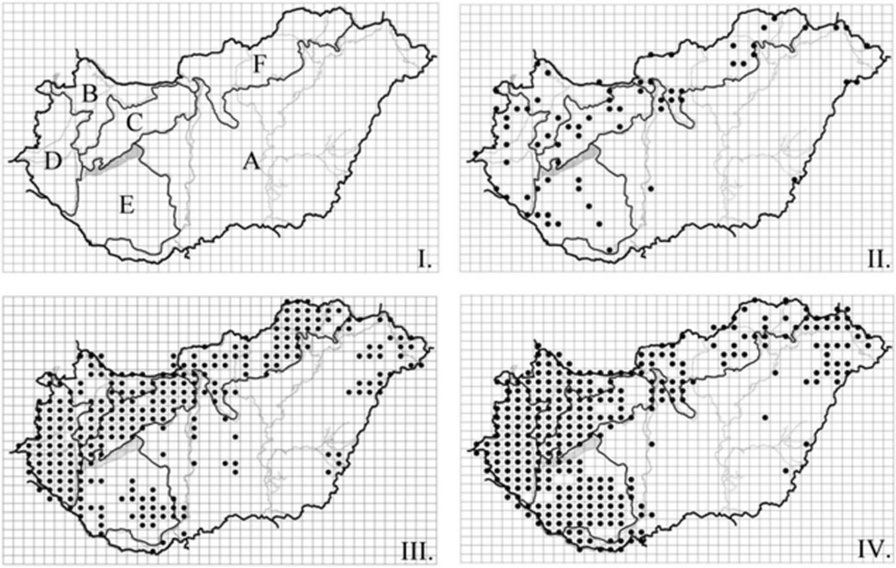

Fig. 2 **I.** Macroregions of Hungary (**A**: Hungarian Great Plain, **B**: Hungarian Small Plain, **C**: Transdanubian Mountains, **D**: Western Transdanubia, **E**: Southern Transdanubia, **F**: North Hungarian Mountains); **II.** Distribution of *Viscum album* in the 1920s (based on data of Roth 1926 and Boros 1926); **III.** Distribution of *V. album* in the 1990s (based on data of Bartha and Mátyás 1996); **IV.** Current distribution of *V. album* in the 2010s (based on data from the Hungarian Flora Mapping Programme and our personal observations)

changes in forest cover since the 1920s (Halász 1994; Kottek 2008), with the distribution of the mistle thrush (Hagemeijer and Blair 1997; Hungarian Bird Monitoring Centre 2013) and with the distributions of the 18 most common host species using data from the Hungarian Flora Mapping Programme.

Results

First Records of European Mistletoe in Hungary

The first comprehensive study of mistletoe in Hungary was done by Tubeuf (1923). This was partially based on the report of Roth, who started to collect data in 1913, but was unable to publish his study until 1926 because of World War I. Tubeuf's (1923) reported occurrence of *Viscum album* in Hungary was similar to Roth's (1926), who later published not only a distribution map, but also details of infestation for the whole area of the Hungarian Kingdom. Mistletoe infestation was reported from 258 locations, 41 times on *Populus* spp., 60 on *Malus* spp. (30 on cultivated *M. domestica* and 30 on wild *M. sylvestris* trees) and *Robinia pseudoacacia*, 21 times on *Pyrus* spp. (*P. communis* and *P. pyraster*) and *Salix* spp., 19 times on *Tilia* spp., 16 on *Acer* spp., and 14 times on conifers. Tubeuf's and Roth's original cartographic data are shown on a basic grid-cell map in Fig. 2II. The presence of mistletoe was reported from 67 quadrats, indicating that 9 % of the country was infested. At that time, the forest area was 1.1 × 10^6 ha, only 12 % of the total area of Hungary. The largest forests were concentrated in Transdanubia and in the North Hungarian Mountains (Halász 1994), although this region was not significantly infested at that time.

Mistletoes were also sparse in the Hungarian Great Plain due to a lack of host trees. Neither Tubeuf (1923) nor Roth (1926) found any contiguous infested area there. Only 2.3 % of this area, the largest macroregion, was infested, and mistletoe was reported from only nine quadrats. Its occurrence was observed only in riverine poplar forests (*Populus* spp.) of the Tisza floodplains (Roth 1926). Boros (1926) also reported some mistletoe bushes on poplar species in the north-eastern part of the Great Plain, for example in the Upper Hungarian Tisza Region. Tubeuf (1923) reported strong infestation on poplars and willows (*Salix* spp.) in the Danube valley and along its tributary streams, which was confirmed by Boros (1926) and Horváth (1917).

While Roth (1926) did not report the presence of mistletoe in the Hungarian Small Plain, Tubeuf (1923) described it from this area on poplars and black locust based on the observations of György Linhardt. As recalculated for our quadrat map, mistletoe was found in eight quadrats of this macroregion, representing an infested area of 14 %. In the Western Transdanubian region, Tubeuf (1923) identified a park where heavy mistletoe infestation was observed on many species (Table **3** in Electronic Supplementary Material). The yellow-berried mistletoe (*Loranthus europaeus*) on oaks was mentioned as heavily infesting host species and showing also hyperparasitism on *Viscum album*. Roth (1926) reported mistletoe from 12 localities in this macroregion; however, the occurrence of mistletoe was fairly sporadic, and only 18 % of Western Transdanubia was infested. This was the only area of the country where all three mistletoe subspecies were found, with Roth (1926) observing mistletoe on silver fir (*Abies alba*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) in addition to eudicot host species.

The presence of mistletoe was reported from the Transdanubian Mountains, where mistletoe distribution was substantial and the level of infestation was also the highest in the country, with 23 % of the area infested. Many species, such as poplar, maple (*Acer* spp.), apple (*Malus* spp., cultivated and wild) and lime (*Tilia* spp.) were observed as hosts (Roth 1926). Furthermore, Boros (1926) noticed mistletoe on red buckeye (*Aesculus pavia*).

Tubeuf (1923) reported some additional host species from Southern Transdanubia during that time in the Somogy county (Table **3** in Electronic Supplementary Material), but the occurrence of mistletoe was sporadic (Roth 1926). Boros (1926) reported higher infestation in the south-western part of the macroregion (Inner Somogy). In summary, 13 % of this macroregion was infested, and mistletoe was recorded in 12 quadrats.

Changes in the Distribution Area of European Mistletoe from the 1990s

After the thorough reports of Roth (1926) and Tubeuf (1923), no further study was published for more than 60 years, while at the same time there was a significant growth in forest coverage. In the 1920s only 12 % of Hungary was covered with forest (Kottek 2008), this increasing to 18 % in 1990 (1.7×10^6 ha), and to up to nearly 20 % by the end of 2006 (1.8×10^6 ha). This clearly represents a major change since the 1920s.

At the beginning of the 1990s, mistletoe was reported as a common species in Transdanubia and as sporadically occurring in the North Hungarian Mountains and the Danube-Tisza Interfluve in the Hungarian Great Plain (Gencsi and Vancsura 1992). At that time, the Hungarian Forest Research Institute started to collect data on mistletoe distribution throughout the country. While the size of the infested area was reported as being between 300 and 1,300 ha in 1990–1995, it varied from 1,800 to 3,000 ha between 2007 and 2011, as described in Fig. 3A and Table 1 in Electronic Supplementary Material. Besides the significant growth of the infested area, the infestation level also changed. At the beginning of the 1990s, the vast majority of Hungary was infested at low or medium levels. By 2010, based on the data of the Forest Research Institute, the proportion of heavily infested areas had become dominant (Fig. 3B).

The presence of mistletoe was reported from 275 quadrats by Bartha and Mátyás (1995; Fig. 2III.). The most heavily infested macroregions were Western Transdanubia and the Transdanubian Mountains, where the percentage of infested quadrats was almost 90 %. In the North Hungarian Mountains, mistletoe was found in 60 quadrats, with more than 60 % of the area already infested. While the presence of mistletoe was detected in only 12 % of the Hungarian Great Plain, 60 % of the Hungarian Small Plain was infested by the 1990s (Table 1).

In 2010 the number of infested quadrats was 313, representing a more than 5 % increase in less than 15 years (Fig. 2IV.). The largest growth can be seen in Southern Transdanubia, where 34 quadrats were infested in the 1990s, this now having risen to 64, representing almost a doubling in size of the infested area. In the Hungarian Great Plain, the presence of mistletoe was reported in 48 quadrats in the 1990s and in 66 quadrats after 2010 (Fig. 2IV.). Although the largest increase in the number of infested quadrats in the last 20 years was reported from the Hungarian Great Plain, this region is still the area where mistletoe is rarest, with only 17 % of the macroregion infested (Table 1).

Host Species of Mistletoe in the Last Twenty Years

Compared with the results of Roth (1926), no change was noticed in the most commonly infested trees; these are still poplars (*Populus* spp.), apples (*Malus* spp.; cultivated and wild), maples (*Acer* spp.), limes (*Tilia* spp.), black locust (*Robinia pseudoacacia*), willows (*Salix* spp.) and birch (*Betula* spp.). Similarly to Kołodziejek et al. (2013), strong mistletoe infestation was also noticed on silver maple (*Acer saccharinum*) in orchards and in populated areas.

Mistletoe infestation of *A. saccharinum* is affected by individual tree characteristics, such as height. A commonly proposed explanation is that larger and older trees may be more attractive to frugivorous birds for perching, which could deposit more mistletoe seeds onto perches (Reid and Lange 1988; Overton 1994; Kołodziejek et al. 2013). The other significantly parasitized woody host in urban areas (especially in city parks) was mountain ash (*Sorbus aucuparia*), confirming the observation of Kołodziejek et al. (2013) (Fig. 4).

Besides the most common species, Bartha (2012) listed rare hosts of mistletoe in Hungary (Table 3 in Electronic Supplementary Material). The current occurrence of the 18 most common hosts (Table 3 in Electronic Supplementary Material) is quite variable in the different quadrats of the Hungarian macroregions (Fig. 5). There are no quadrats in Hungary where all potential hosts are found, as the highest number observed is 17. The number of potential hosts is between 5 and 8 in most of the quadrats, which represents 36 % of the country (Fig. 6A). Nine to twelve potential host species can be

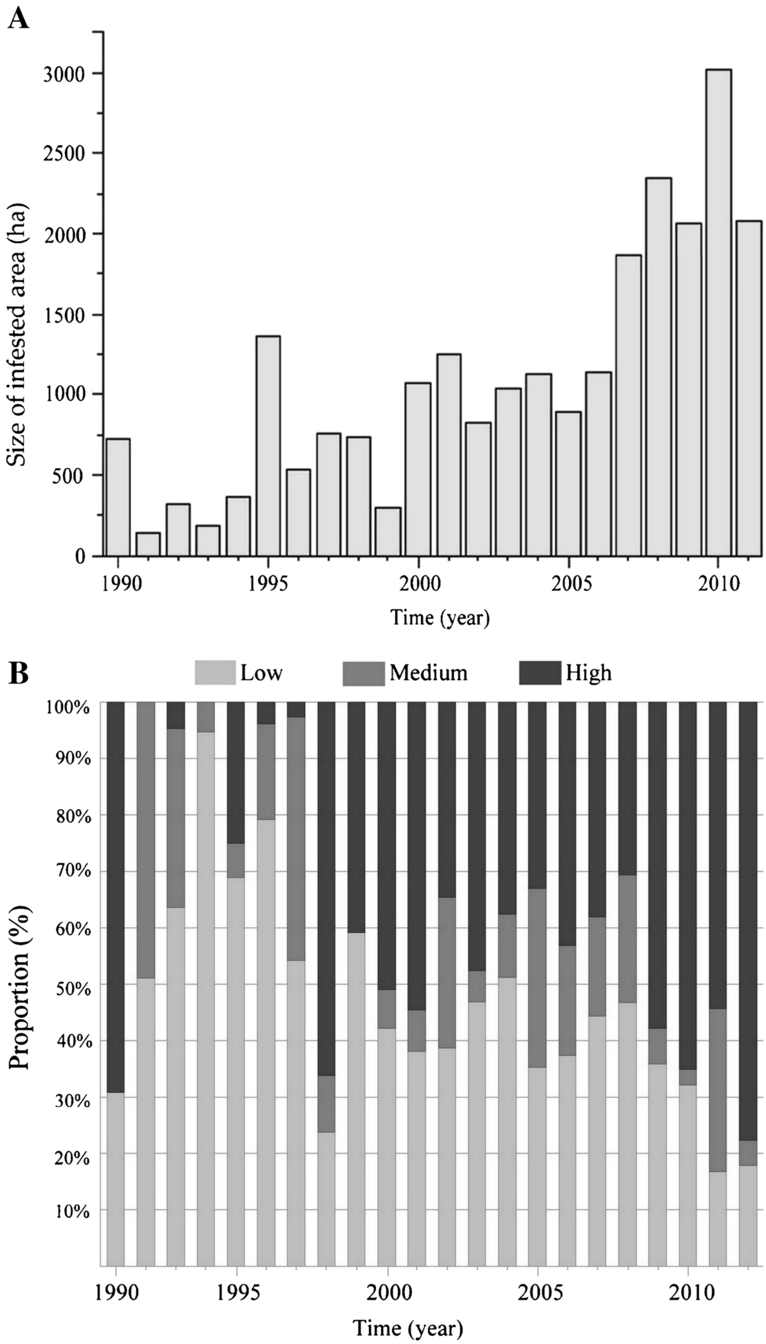

Fig. 3 **A** Size of infested area in Hungary since 1990; **B** Proportion of infested area (Hungarian Forest Research Institute 1990–2011).

found in 29 % of the country, while one to four potential hosts can be found in the additional 22 % (Table 2 in Electronic Supplementary Material).

Table 1 Number and percentage of infested quadrats in Hungary since the 1920s

Macroregion	Number and percentage of infested quadrats						Total number of macroregion quadrats
	1920s		1990s		2010s		
	Quadrats	%	Quadrats	%	Quadrats	%	
Hungarian Great Plain	9	2.09	48	12.37	66	17.01	388
Hungarian Small Plain	8	14.04	34	59.65	48	84.21	57
North Hungarian Mountains	16	16.84	60	63.16	41	43.16	95
Transdanubian Mountains	11	23.40	42	89.36	35	74.47	47
Southern Transdanubia	12	13.04	34	36.96	64	69.57	92
Western Transdanubia	12	18.18	57	86.36	59	89.39	66
Total number of quadrats	67	8.99	275	36.91	313	42.01	745

Mistletoe infested areas reach 54 % of the quadrats with nine to twelve potential hosts (Fig. 6C). Five to nine potential hosts are found in 38 % of the uninfested areas, while one to four potential hosts are found in the other 22 % of the uninfested areas. Two-thirds of those quadrats where the number of potential hosts reaches or exceeds 12 are infested, while areas with 9 to 12 potential hosts show a 50 % infestation rate. The rate of infestation drops significantly (~20 %) in those areas where 5 to 8 potential hosts are found (Table 2 in Electronic Supplementary Material). However, there are more than 200 quadrats where the number of potential hosts has not been studied yet. Most of these areas are concentrated in the Danube-Tisza Interfluvial region, where mistletoe has not been reported.

Level of Current Mistletoe Infestation

Based on the 2011 data, approximately 72 % of Hungary is still uninfested, and major areas have only a low infestation level (11 %). The total area with medium infestation reaches 10 %, while heavy infestation is found only in about 5 % of the country (Fig. 7 and Table 2). In the Hungarian Great Plain, mistletoe is rarely found, occurring only near the borders and in some limited areas in the middle of this region. Although mistletoe is completely absent from 90 % of this macroregion, we also observed the largest continuous mistletoe population here. This is found in the north-eastern part of the Hungarian Great Plain (Upper Hungarian Tisza Region), where mistletoe is found in gallery forests. Besides the mass occurrence of mistletoe, the size of the shrubs was also substantially larger than elsewhere. For example, in 2010 we found a shrub with a diameter of 1.6–1.7 m in Sárospatak.

In the Hungarian Small Plain, mistletoe is very abundant, but the intensity of infestation is mostly low (32 %). The proportion of heavily infested areas reaches only 9 %, while medium infestation affects only 21 % of the macroregion.

The North Hungarian Mountains are the least infested region after the Hungarian Great Plain. There are many sporadically infested quadrats with low infestation intensity in the macroregion, altogether representing around 10 % of the total area. The largest diversity in the occurrence of mistletoe is found in the Transdanubian

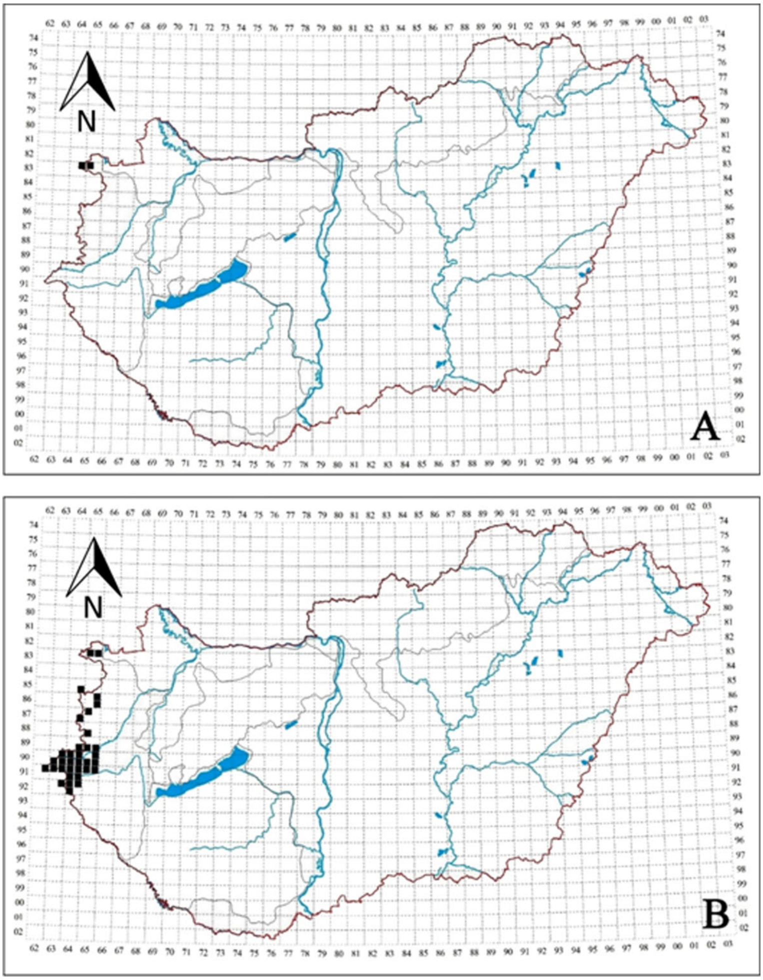

Fig. 4 **A** Current distribution of *Viscum album* subsp. *abietis* in Hungary; **B** Current distribution of *V. album* subsp. *austriacum* in Hungary

Mountains. A small, dense mistletoe population is found in the centre of the macroregion, altogether representing 7 % of the macroregion. The proportion of areas with medium infestation is approximately 22 %, with many sporadically infested quadrats occurring around a dense population in the centre. The largest proportion of distribution area in the macroregion, and the highest proportion of strongly and medium-infested areas, can be found in Western Transdanubia, where the largest forested area in Hungary is found (Kottek 2008). The proportion of the area with heavy infestation is 18 % of the macroregion, centred in the northern part and in the south-eastern area. Besides these areas, almost the whole macroregion is infested at medium intensity, with a proportion of around 36 %. The area of low infestation represents 18 % of the macroregion. This is the only macroregion where all three mistletoe subspecies can be found. *Viscum album* subsp. *abietis*, which parasites on firs (*Abies* spp.), is only found on *Abies alba* in the north-eastern part of Western

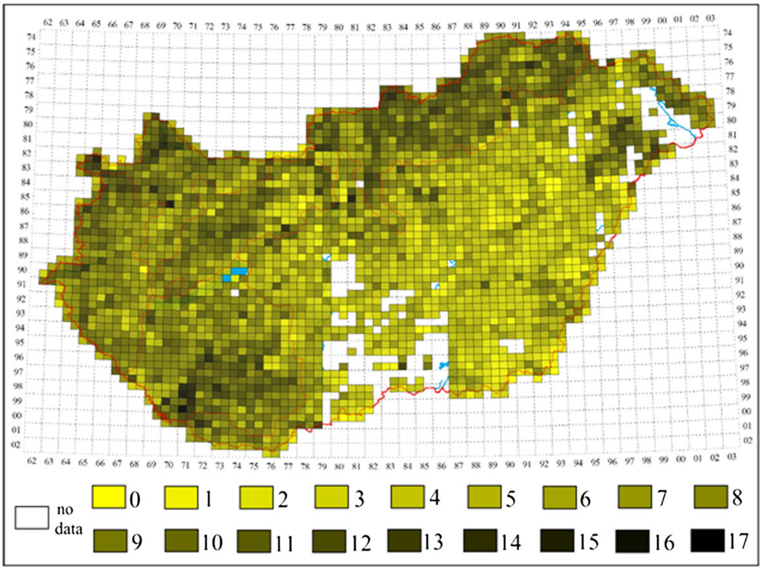

Fig. 5 Incidence of the 18 most common hosts (*Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *A. saccharinum*, *A. tataricum*, *Betula pendula*, *Malus domestica*, *M. sylvestris*, *Populus* ×*canescens*, *P. alba*, *P. nigra*, *P. tremula*, *Robinia pseudoacacia*, *Salix alba*, *S. fragilis*, *Tilia cordata*, *T. platyphyllos* and *T. tomentosa*) in Hungary in the 2010s (based on data from the Hungarian Flora Mapping Programme)

Transdanubia (Fig. 4A). Similarly, *V. album* subsp. *austriacum,* which parasites mostly on Scots pine (*Pinus sylvestris*), is also present here, with a larger distribution area due to its abundance throughout the entire western border area of the macroregion (Fig. 4B).

In the Southern Transdanubian macroregion, strong mistletoe infestations are centralized in the south-western area, while medium-infested zones generally occur around the heavily infested centres. The proportion of heavily infested areas is around 10 %, medium-infested areas 18 % and low-infestation areas 20 % of the total area.

Discussion

Changes of European Mistletoe Distribution in Hungary

The distribution area of European mistletoe has changed significantly in Hungary since Roth (1926) published his first summarizing study. While mistletoe occurrence was reported in less than 9 % of the country in the 1920s, the proportion of the infested area has grown more than threefold since then and now covers approximately 30 % of the country. In the last two decades, not only the size of the infested area, but also the proportion of heavily infested regions has increased.

In the early 1920s, European mistletoe was not regarded as a pathogen responsible for forest damage; it was used as fodder for cows, deer and fawns. Roth (1926) also mentioned mistletoe as a commonly collected plant for Christmas decoration, as verified also by Tubeuf (1923). Today it is of negligible significance as fodder and is rather mainly collected for decorative, herbal or medicinal purposes during winter.

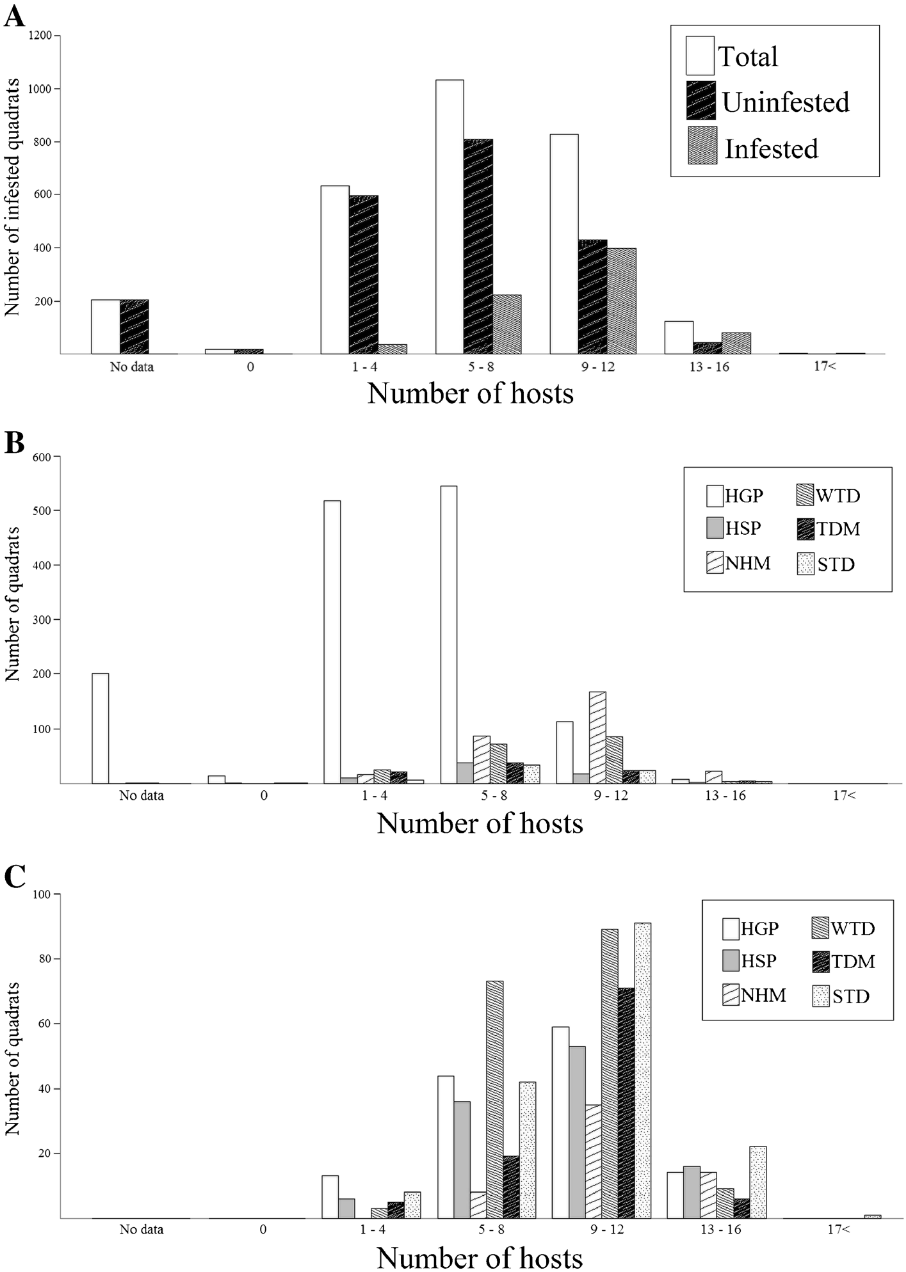

Fig. 6 **A** Distribution of the most common hosts in infested and uninfested areas of Hungary; **B** Distribution of the most common hosts in the uninfested area of Hungarian macroregions; **C**: Distribution of the most common hosts in the infested area of Hungarian macroregions (HGP: Hungarian Great Plain; HSP: Hungarian Small Plain; NHM: North Hungarian Mountains; WTD: Western Transdanubia; TDM: Transdanubian Mountains; STD: Southern Transdanubia)

Tubeuf (1923) described Hungary as very rich in mistletoe in his monograph, in which he based his distribution maps on reports of various Hungarian scientists and

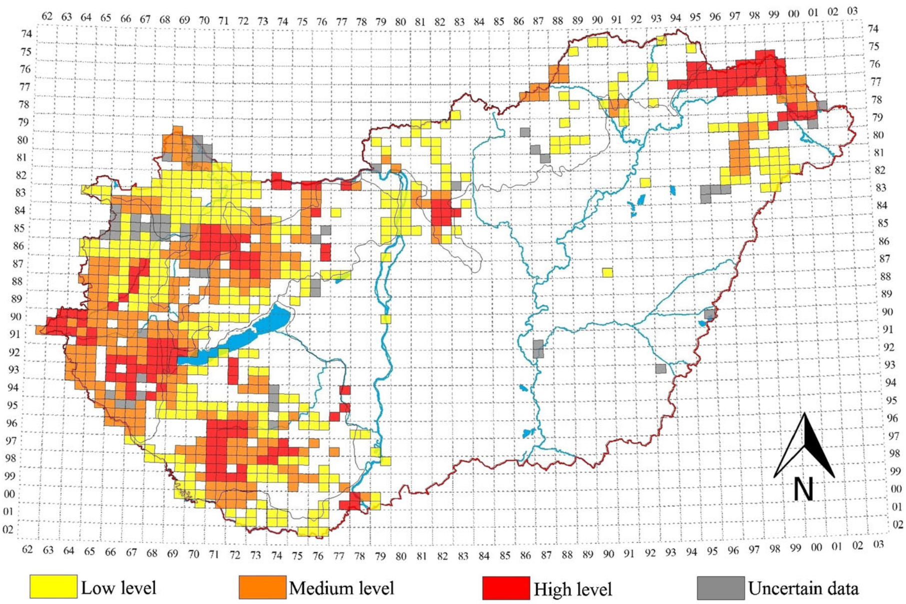

Fig. 7 Current distribution of *V. album* in Hungary (white grid-cells: uninfested, grey grid-cells: uncertain, yellow grid-cells: low level of infestation, orange grid-cells: medium level of infestation, red grid-cells: high level of infestation)

foresters. Roth (1926) reported no widespread mass occurrence and described the presence of mistletoe as mostly rare and sporadic, being common only in some parts of the countryside. In contrast, there are now numerous places in Hungary where heavily infested areas are dominant, such as the Transdanubian Mountains. Many of these are found in the same areas where Roth originally (1926) observed heavy infestation, and only few can be found in previously uninfested areas.

While in the 1920s the centre of the infested area was found in the Transdanubian Mountains in Northern Transdanubia, it shifted to the southern areas of the Hungarian Small Plain towards the end of the century. In the forests where the infestation was centred in 1920s, mistletoe occurrence is now significant lower, while the presence of mistletoe has become more intense west of its original centre.

The largest increase in the expansion of the infested area can be noted in Western Transdanubia, where more than 80 % of the quadrats are infested. Mistletoe was reported at only a few localities by Roth (1926) – now almost the whole macroregion is infested at a medium level, with many heavily infested areas.

The least infested macroregion in Transdanubia is Southern Transdanubia. The majority of the macroregion is still uninfested, although the number of infested quadrats has increased, this growth in occurrence being second only to that observed in the Hungarian Great Plain. The centre of the infestation is in the same area where Roth (1926) and Boros (1926) first mentioned the common presence of mistletoe. The centre of the mistletoe distribution area coincides with the region where the number of potential hosts is the highest.

European mistletoe is nowadays relatively rare in the North Hungarian Mountains, with only one heavily infested area found in the south-western tongue. We thoroughly

Table 2 Strength of mistletoe infestation in 2010s in the different macroregions

Macroregion	Number and percentage of infested quadrats										Total number of macroregion quadrats
	Non infected		Uncertain		Low level		Medium level		High level		
	Quadrats	%	Quadrats	%	Quadrats	%	Quadrats	%	Quadrats	%	
Hungarian Great Plain	1386	90.77	11	0.72	63	4.13	35	2.29	32	2.10	1527
Hungarian Small Plain	54	30.34	13	7.30	57	32.02	38	21.35	16	8.99	178
North Hungarian Mountains	280	79.77	4	1.14	38	10.83	17	4.84	12	3.42	351
Transdanubian Mountains	84	44.92	2	1.07	46	24.60	42	22.46	13	6.95	187
Southern Transdanubia	181	51.86	4	1.15	72	20.63	56	16.05	36	10.32	349
Western Transdanubia	51	21.07	17	7.02	44	18.18	86	35.54	44	18.18	242
Total number of infected quadrats	2036	71.84	51	1.80	320	11.29	274	9.67	153	5.40	2834

inspected this macroregion because Bartha and Mátyás (1995) reported the presence of mistletoe in many localities, especially in the east. Based on our field survey, mistletoe distribution is less significant than reported by Bartha and Mátyás (1995), and the rate of increase is the lowest in the country. This macroregion is the least infested area after the Hungarian Great Plain. While there are 1–8 potential hosts throughout two-thirds of the Great Plain, they are twice as numerous here, with 9–16 potential hosts found in more than 60 % of Western Transdanubia.

The sporadic presence of *Viscum album* in this macroregion contradicts the theory of Wangerin (1937), which states that the range of mistletoe is topographically and ecologically defined by host trees, because the number of potential hosts is significantly higher than the proportion of infested trees.

Factors Influencing the Distribution of Mistletoe

The occurrence and distribution of *Viscum album* is related to many factors, such as the vitality and extent of forests and orchards, changes in the proportions of forest tree species, increasing numbers of breeding pairs of mistle thrush (Aukema 2003; Hawksworth 1983), changes in many abiotic factors, e.g. changes in general climate, air pollution, droughts (Barbu 1991; 2007) and human impacts on the environment, e.g. cultivation techniques or planting of alien woody species (Wangerin 1937; Zuber 2004; Kołodziejek et al. 2013). Probably the most important factors influencing most of the distribution area are the host tree species and vectors for seed dispersal. Almost 100 years ago, Tubeuf (1923) had already noted that many bird species (e.g. *Turdus viscivorus, T. pilaris* and *T. iliacus*) have the potential to affect mistletoe distribution, but he was convinced that the seeds were dispersed in early spring, not during winter. The observations of Roth (1926) were contradictory, denying the role of birds in the distribution and instead identifying many mammal species as potential vectors (e.g. *Martes foina, Vulpes vulpes, Sciurus vulgaris*), based on observations of them eating the seeds.

It seems that the most common dispersal vector for mistletoe seeds in Hungary is the mistle thrush (*Turdus viscivorus*), which lives in the upland forests of Western and Northern Transdanubia and in the Transdanubian Mountains (Hagemeijer and Blair 1997; Zalai and Haracsi 2008; Hungarian Bird Monitoring Centre 2013; Fig. **1** in Electronic Supplementary Material). The species can also be seen occasionally in the residual oak forests of the Great Plain and in some areas of the Danube-Tisza Interfluve (Zalai and Haracsi 2008). Mistle thrush has also been observed in the Hungarian Small Plain (Balsay 1986), in Southern Transdanubia (Kasza 1983) and in the north-eastern area of the Hungarian Great Plain (Juhász 1995). Based on the observations of the Hungarian Bird Monitoring Centre, the number of breeding pairs in 1999–2002 was between 4,000 and 25,000, and the number of birds continues to grow, this being consistent with the findings of Hagemeijer and Blair (1997). Nowadays, mistle thrush inhabits almost all of the places where mistletoe is present, including city parks and populated areas during winter (Zalai and Haracsi 2008).

When the distribution of European mistletoe is compared with the habitats of the mistle thrush, a significant overlap can be observed. In the area of the Transdanubian macroregion, where the mistle thrush is found, the presence of mistletoe is more significant. In the Hungarian Small Plain, where fewer mistle thrushes nest, the number of mistletoe bushes is also lower. There were many observations of mistle thrushes in the north-eastern part of the Hungarian Great Plain, where the occurrence of mistletoe is the highest in the macroregion.

Although mistle thrushes are important dispersal agents of *Viscum album* seeds, potential hosts also play a significant role in the occurrence of European mistletoe (Wangerin 1937). The growing number of alien, planted woody species such as *Acer saccharinum* in city parks, the proportion of potential host species, which have a higher mistletoe infestation prevalence in orchards and urban areas, e.g. *Populus* spp., *Robinia pseudoacacia* (Kołodziejek et al. 2013) as well as intensive forestation all have positive effects on mistletoe distribution. In the last 100 years, the total area of Hungarian forest has increased by more than 60 %, while the area of poplar and other softwood forests has also grown significantly (Kottek 2008). In parallel with these developments, the occurrence of mistletoe has also increased.

Based on our personal observations, poplars are the most commonly infested species along roads in orchards, while silver maple (*Acer saccharinum*) is the most common host in towns. In populated areas, besides the dominant silver maple, rowan (*Sorbus aucuparia*) is very important because it was commonly planted as an ornamental tree in the 1980–1990s. The only difference is that silver maple can live with strong infestation for a fairly long time whereas rowan seems to be highly sensitive to mass infestations, causing huge losses in drought years, as we observed ourselves in 2011. During our field study, we also observed that black locust is highly sensitive to mass appearances of mistletoe, unlike apple trees, which have the same crown volume but can live longer with extremely heavy infestation, because the infested branches often break off and dry out fairly rapidly after infestation.

Human impact can also decrease the distribution of mistletoe. In the middle of the 1990s, apple cultivation techniques significantly changed in Hungary because the horticulture sector started to use intense orchard cultivation systems in place of the traditional apple cultivation method (Apáti 2007a). Easier canopy management and intense pruning can be used in these modern plantations, so mistletoe cannot colonize these orchards. Pruning of branches and crown thinning processes were not undertaken in traditional orchards (Szabó 2006), which were planted in the 1950s and 1960s (Apáti 2007b). These tall apple trees, which had bigger and less managed crowns, were probably more easily infested with mistletoe, as can be presumed based on Roth's (1926) observations. The adoption of newer cultivation techniques could be one reason why the importance of apple trees as a common host has decreased. Nowadays, apple infestations are found mostly on wild solitary trees and old ornamental trees in city parks and in abandoned old plantations. Jandrasits (2011) observed mistletoe to be common in non-cultivated old plantations in Western Transdanubia (Őrség).

Due to changes in agricultural and forest cultivation methods, the human impact on the presence of mistletoe is beyond doubt. In areas where negative abiotic factors are concentrated, such as greater erosion, higher pollination levels and frequent drought, the hosts become more sensitive to mistletoe infestation (Barbu 2007). In these forests, infested hosts have a higher mortality rate, thinner branches, lower height and trunk diameter, and a reduced quality and quantity of wood, fruit and seed production (Hawksworth 1983; Tsopelas et al. 2004). Furthermore, human-induced global warming is assumed to be an important factor affecting the spread of mistletoe (Dobbertin et al. 2005). The presence of this hemiparasite has also been observed to interact with infestation by other pathogens such as bark beetles (Tsopelas et al. 2004). All of these influences may contribute to the decline of the most common hosts, and thus to the decline of many European forests (Barbu 2007; Idžojtić et al. 2008). According to Koltay (2005), the 'forest decline spiral' is never the result of a single, well-defined factor. The visible symptoms of different types of damage or necrosis of woody species usually only appears as the final step in a long period of decline, which has many synergistic causes. Initial abiotic stress factors (e.g. drought, pollination) would not directly cause higher mortality of trees, but these effects contribute to the appearance of different pathogens, insects and parasites, including European mistletoe. All of these problems accumulate and together lead to an extremely sensitive state of health or to the maturation of latent diseases, which culminates in the serious forest decline spiral.

Nowadays, these symptoms appear in many European countries, where serious mistletoe infestation has also been detected (Tsopelas et al. 2004; Barbu 2007; Idžojtić et al. 2008). Although the most damaged hosts in the affected forests are still *Pinus* and *Abies* species, it cannot be assumed that the problem will not appear in forests in which broadleaved trees are in the majority, because mistletoe is also able to infest numerous angiosperm woody species. The most common species in Hungarian forests are broadleaved trees, while black pine and silver fir occur only in a few areas. In the last century, the total forested area in Hungary has grown to almost 20 %, but the occurrence of mistletoe has increased in parallel with this process. Accordingly, it is essential to constantly monitor the distribution of mistletoe and the damage it is causing as well as to find effective control methods that can be employed against it.

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