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Bioclimatic constraints of European mistletoe *Viscum album* at its southern distribution limit at past and present temporal scales, Pannonian Basin, Hungary

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ABSTRACT: The present study investigates climatic factors limiting a significant section of the southern boundary of the distribution of the European mistletoe *Viscum album*. Our study area was located in Hungary, within the Pannonian Basin biogeographical region in Central Europe, where forest and forest-steppe climates meet. We collected data from literature on the local distribution of *V. album* L. subsp. *album* (Wiesb.) Vollm., complemented by our own observations, in order to identify the boundary of the local range. We investigated the importance of climatic predictors in identifying the range, using discriminant analysis. July aridity was the best predictor of the limit of the occurrence of the study species, followed by mean July temperature and the sum of air temperature during the growing season. Results based on data from meteorological stations for 1901–1950 and on data from E-OBS grids for 1950–2010 identified similar bioclimatic preferences of *V. album* subsp. *album*.

KEY WORDS: *Viscum album* · Bioclimatic analysis · Aridity · Distribution boundary · Discriminant analysis

1. INTRODUCTION

Bioclimatology is an interdisciplinary field of science located between meteorology and ecology, aiming at disentangling climate–plant relationships within the larger context of climate–soil–vegetation interrelationships. The objectives of studies motivated by bioclimatology include the reduction of an entire set of meteorological parameters (holoclimate) to a smaller set of relevant predictors (ecoclimate) in the context of the investigated plant species or vegetation type. Bioclimatological investigations into plant distributions are frequently applied at macroecological scales (Brown 1995).

Mistletoe *Viscum album* is an optimal candidate for bioclimatic studies, as the basic climate–soil–vegetation interrelationship is reduced further to a climate–vegetation relationship because of its epiphytic and hemiparasitic life-form, which lacks any remarkable host specificity. Factors difficult to deal with on a large scale, such as large variations in soil types and the existence of competitors (Farber & Kadmon 2003), are not present across its large distribution area, which ranges between latitudes 10° W and 80° E and longitudes 60° N and 35° N (Jalas & Suominen 1976). *Viscum album* subsp. *album* often prefers agricultural (Briggs 2011) and urban habitats (Zachwatowicz et al. 2008), and thus its sensitivity to human disturbance is low. However, *V. a. album* also occupies a broad spectrum of natural habitats. Therefore, the original distribution is expected to be modified to a lesser degree.

Climatic factors governing the distribution of *V. album* have long been the subject of investigation.

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Iversen (1944), for example, showed that earlier expansions of this species can be associated with the former Holocene climate optimum. Studies on the climate–area relationships of *V. album* using species distribution models (SDMs) (Skre 1979, Jeffree & Jeffree 1994, 1996, Dobbertin et al. 2005) detected the importance of mean temperatures in January and July. Specifically, these bioclimatic analyses indicated a minimum of 15°C (Atlantic climate-area end) and a maximum of 25°C (continental climate-area end) annual fluctuation in mean monthly temperatures (AFMMT) within *V. album*'s area (Zuber 2004, Kahle-Zuber 2008). Its thermosphere ranges between 15 and 22°C for July and between −7 and +6°C for January mean temperatures. Most of the occurrences fall into ranges between 15 and 20°C for July and −4 and +4°C for January mean temperatures, indicating the species' temperature optimum (Skre 1979). The upper limit of the thermosphere provided by Jeffree & Jeffree (1996) ranges between 25 and 26°C, which seems to be too high. This discrepancy is probably attributable to the lack of knowledge regarding vertical altitude differences between southern mountain occurrences and the nearby meteorological stations, which provided the data used to characterize these mountain occurrences. In our study area, which covers the topographically homogeneous Hungary, this type of discrepancy does not occur. The thermal tolerance spectrum of *V. album* seems to be narrow, not occurring in continental regions with an AFMMT above 25–27°C (Skre 1979, Jeffree & Jeffree 1996).

Furthermore, both the sum of the air temperature in the vegetation period (hereafter TSUM) and the average annual extreme minimum temperature (hardiness of winter) can drive the distribution of *V. album*, as shown by a previous study by Woodward (1988) on perennial plants. The above-mentioned studies illustrate that the most frequently used parameters in the SDMs of *V. album* are related to temperature, mainly monthly averages or mean temperature (Hocker 1956). Mean monthly temperature data are also generally widespread in recent SDMs (Guisan & Zimmermann 2000, Rasztovics et al. 2012).

Previous SDM studies focusing on *V. album* were conducted on the northern limit of the species range, or at the highest altitudinal limits (Iversen 1944, Waldén 1961, Skre 1979, Jeffree & Jeffree 1996, Dobbertin et al. 2005, Walther et al. 2005, Briggs 2011), and were then extrapolated to the northeastern boundary of distribution (Zuber 2004). Thus, it is still unclear which climatic parameters limit the occurrence of *V. a. album* at the southern limit of its area. Our study is motivated by questions related to understanding (1) what climatic parameters predict the southern boundary of distribution of *V. a. album* in the Pannonian Basin, more precisely in Hungary, and (2) what relative importance plausible weather predictors have for the studied species.

First, we suppose there has been a stable area edge (distribution limits of the species) on the studied area while climatic factors are predicted to have changed significantly in the investigated time interval. We suggest that this stability is based on the overlap between the area map produced by Jalas & Suominen (1976) and our local area-edge map, which is based on cumulative data from relevant local literature and our 30 yr survey. Because there are no significant differences between the 2 sides of the area edge in terms of host availability, distribution of bird species functioning as vectors, and topography (Hungary is basically flat), the only limiting factors are expected to be of climatic origin. If we focus on temperature-related parameters, the question arises as to why the significant warming of the last decades has not resulted in a change in the area. What emerges here is the possible role of parameters related to water supply, such as aridity. This is supported by the fact that the degree of aridity has not changed remarkably at the area edge.

Our assumption of a stable area edge contrasts with the study of Varga et al. (2014), who reported a notable expansion of *V. a. album* in the Pannonian Basin. According to their study, the infected area has almost tripled in size since the beginning of the 20th century. In our opinion, the suggested expansion is not supported by the data, nor by the methods used. The earliest dataset used by the authors was that of Roth (1926), who was able to use only the undeveloped transport of that time; Varga et al. (2014) did not take into account other data reported (Boros 1926, Soó 1937a,b, Tubeuf 1923). The next source used by Varga et al. (2014) was a questionnaire study (Bartha & Mátyás 1995) in which countryside foresters were asked in the 1990s about all species of trees and shrubs in Hungary. However, *V. album* is not a forest-dwelling plant that would automatically attract the attention of forest managers, which is why memories could have faded, and, for example, confusion between *V. album* and *Loranthus europaeus* might be common in the dataset. The third source was a detailed floristic field survey of Hungary, carried out in 2002–2003, largely by botanists (Bartha & Király 2015). Of the 3 sources selected, only this latter dataset can be considered as relevant to the study. Our fieldwork in NE Hungary does not confirm any remarkable expansion of *V. album* over the past 30 yr. Additionally, no investigations have reported on similar large expansions in any other part of the continent; these studies with expansions were all small-scale phenomena (Zachwatowicz et al. 2008).

To answer our study questions, we formulated the following hypotheses: (1) because *V. a. album* does not occur in regions of continental and Mediterranean climate characterized by hot summer temperatures (mean summer monthly temperatures above 22–23°C) and continental climate characterized by AFMMT values above 25–27°C, factors describing summer heat are expected to be related to its distribution in our study area, Hungary; and (2) as Hungary is not only relatively hot, but also a western outpost of the Eastern European semi-wet forest-steppe zone, constituting the southern limit of the distribution of *V. a. album*, we suggest that drought stress is important in driving the distribution. Thus, we expect factors describing water supply to be important proxies in predicting the southern limit of distribution around the forest-steppe boundary.

2. MATERIALS AND METHODS

2.1. Study area

The study area covers the Hungarian part (93 000 km^2) of the Pannonian Basin, also referred to as the Carpathian Basin (ca. 200 000 km^2; Figs. 1 & 2). Because our investigation focuses on a 50-km-wide zone extending beyond the boundary of the distribution of *Viscum album* subsp. *album*, the western and southwestern parts of Hungary are excluded from the study area. Hungary is more or less flat, with less than 2% of its area higher than 300 m above sea level, hence orographic influences are insignificant, facilitating the interpretation of climatologic data.

Hungary constitutes a part of the southern limit of the area of the subspecies, although this limit is not a line running parallel with the Equator (Fig. 2). However, this subspecies is found closer to the Equator on the Balkan, Iberian and Italian peninsulas. Further, it is absent or mostly absent from the lowlands and hills of regions with a real Mediterranean climate and is

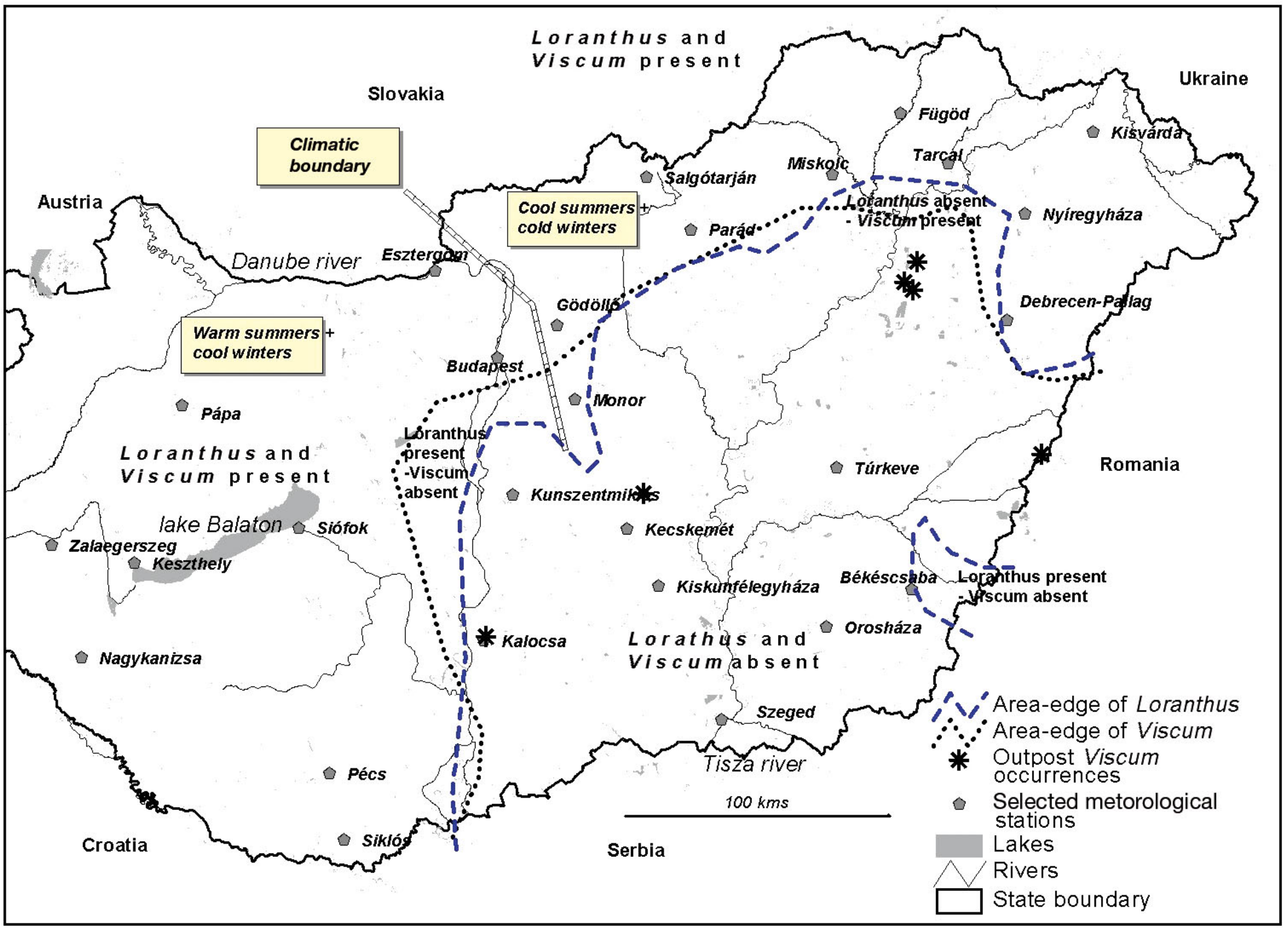

Fig. 1. The area boundaries of *Viscum album album* and *Loranthus europaeus* in Hungary

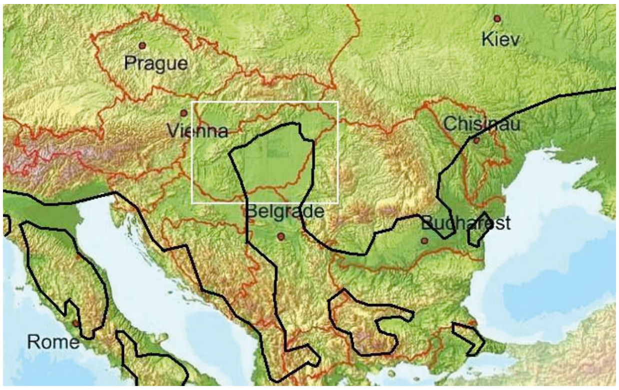

Fig. 2. The SE European section of the distribution of *Viscum album album*. After Jalas & Suominen (1976) and Kahle-Zuber (2008), modified after Săvulescu (1952), Flora Croatica Database (http://hirc.botanic.hr/fcd/) and our own data. The white square indicates the area of the local map shown in Fig. 1; the bold black line marks the simplified (southern and isolated) boundary of the subspecies

restricted to the mountains (Jalas & Suominen 1976, Kahle-Zuber 2008). The 'empty peninsula' — where *V. a. album* is absent — between the central part of the Balkans and western Hungary (Jalas & Suominen 1976, Kahle-Zuber 2008) receives special focus in this study.

Hungary is also close to the continental, eastern area edge, as a result of the increasing AFMMT. Because it is located in the centre of the distributions of most of the host plant species of *V. a. album*, the probability of host availability being a limiting factor in the distribution is very low, as most of these species are widespread. Additionally, large plantations of host trees are found in the area, mainly consisting of poplar and *Robinia* plantations. Although the proportion of orchards harboring a couple of host species is high in Hungary, orchards have less importance than they do in the UK (Briggs 2011). *Viscum a. album* also occurs on planted trees and in country lanes. Its seminatural and natural habitats include mainly riverbanks, areas around streams and wetlands, where native *Fraxinus*, *Populus*, *Salix* and *Betula* species — acting as host plants — are frequent.

All subspecies of *V. album* are missing from most of the lowland part of Hungary, as well as from the southern part of the Pannonian Basin further south, which is mainly characterized by a forest-steppe climate with a mean temperature of −1.0 to −3.0°C in January and 21.0 to 22.5°C in July, while the AFMMT stands at 22.5–24.5°C. Annual precipitation ranges between 480 and 590 mm, with a peak in June. This climate has a semi-wet period in late summer lasting for 2–4 mo, defined by Bagnouls & Gaussen (1957). The lowest amounts of precipitation are measured in January, February, March and April. Fig. 3a illustrates such a climate in the case of Orosháza, a town in SE Hungary where *V. a. album* does not occur.

The distribution of *V. a. album* falls within 2 subtypes of forest climate: (1) the western part of the region, with warmer summers and winters, with 2 precipitation peaks during late spring and in autumn (Fig. 3b illustrates such a climate for the town of Pécs in southern Hungary, where meteorological data show a weak and short semi-humid period lasting for 2 mo, preceded and followed by humid months, creating an overall forest climate); and (2) the northern part of the region, with slightly cooler summers and colder winters, with one precipitation peak in June (see Fig. 3c for the town of Salgótarján). Both of these climate types are classified as forest climates. Thus, the climate of the *V. a. album*-occupied subregion is more diverse than the forest-steppe zone as a whole, which is characterized by temperatures ranging from −1.0 to −4.0°C in January and 17.0 to 22.0°C in July, with an AFMMT of 21.0–24.0°C. Annual precipitation ranges

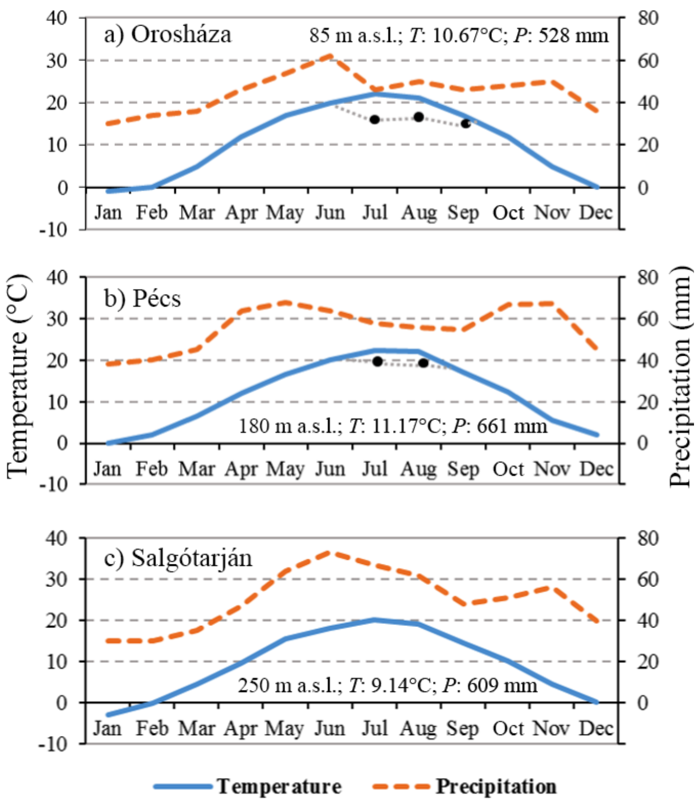

Fig. 3. Walter–Lieth climate diagrams of (A) Orosháza (46° 34′ N, 20° 41′ E), (B) Pécs (46° 00′ N, 18° 14′ E) and Salgótarján (48° 06′ N, 19° 38′ E) meteorological stations (see Fig. 1). Points below the temperature diagram are the cut-off points of the semiaridity curve (2/3 × precipitation line). a.s.l.: above sea level; *T*: mean temperature; *P*: mean precipitation

between 570 and 900 mm, with precipitation values above 650 mm only occurring in small patches in the mountains and in the westernmost part of Hungary.

Generally speaking, the central and western part of the Pannonian Basin falls into USDA winter hardiness zone 7, with annual extreme minimum temperatures ranging between −17 and −12°C, while the northeastern part is classified as USDA zone 8 (annual extreme minimum temperature between −23 and −17°C).) The forest-steppe zone is characterized by warmer summers than N Hungary and colder winters than W and SW Hungary.

2.2. Study species

Considering autecology, the seeds of *V. a. album* are dispersed within Hungary by the mistle thrush *Turdus viscivorus* and by other thrushes, especially the fieldfare *Turdus pilaris*, but not by the blackcap *Sylvia atricapilla*, as dispersion by blackcap occurs on the Atlantic coasts of W Europe (Briggs 2011) and in S Europe. As in most parts of continental Europe (Mokwa 2009), the blackcap is migratory in Hungary, breeding and dispersing in the region between late March and mid-October. Since the ripening of *V. a. album* berries starts in November in Hungary and seed dispersal continues until early May (Kahle-Zuber 2008), the blackcap is absent during most of this period. Although other bird species reported to be occasionally important in S Europe (Mellado & Zamora 2014) do not have any importance in this region, the Bohemian waxwing *Bombycilla garrulus*, which feeds on berries, appears in huge flocks (up to tens of thousands of individuals) irregularly and can be important locally. In contrast, thrush migration is more regular and evenly distributed through Hungary.

In the study area, the other widespread European hemiparasitic *Santalales* species, *L. europaeus*, also occurs, occupying approximately the same parts of Hungary (Fig. 1). Because of their different host plants, interspecific competition between these species is low.

On a regional scale, the core area of *V. a. album* is more or less evenly occupied, showing a fuzzy edge and satellite outposts including single specimens or smaller groups occurring around the edge on scales of kilometers. Since *V. a. album* is evergreen and the host trees are deciduous, mistletoe can induce a strong visual stimulus for winter dispersers (mistle thrush and other *Turdus* spp.), resulting in effective dispersal of single specimens and small groups of individuals. Presumably, this is the main reason why *V. a. album* has an indistinct area boundary.

Mistletoe species are usually aggregated on various scales. The aggregation pattern on a scale larger than 4–5 km corresponds to changes in vegetation structure or abiotic factors. An aggregation scale below 1 km, however, is the result of seed-dispersing birds (Aukema & Martínez del Rio 2002, Rist et al. 2011), corresponding to the disperser's predation effect (Mellado & Zamora 2016). This implies that outposts in distances further than 5 km from the continuous occurrence can be attributed to the magnitude of vegetation changes or abiotic proxies — if the aggregation is significant in size. However, these occurrences are too sporadic and occasional in the case of the present study.

2.3. *Viscum a. album* data

The mapping of the area boundary of *V. a. album* was based on published floristic records (Tubeuf 1923, Boros 1926, Roth 1926, Soó 1937a,b, 1938, Kovács & Molnár 1981, Szujkó-Lacza & Kováts 1993, Bartha & Mátyás 1995, Vojtkó 2001, Nagy 2007, Tuba et al. 2008, Baltazár et al. 2013, Varga 2013, Varga et al. 2014, Bartha & Király 2015) and on our own field observations. Assuming a stable area edge in Hungary, we summarized the data on a map (Fig. 1). Distribution data were mapped in ArcView (version 3.3) using geographical coordinates. Our distribution results are similar to those found through countryside floristic data collections in the last decade (Hungarian FLORA database; Varga et al. 2014, Bartha & Király 2015).

Viscum a. album individuals occurring at a distance of 5–10 km or more from each other were excluded from the mapped species area. According to our personal observations, the local occurrences of these outposts are not stable and permanent, and individuals can often survive for only a few years, and thus these settlements cannot become a starting point for future expansion. This process is indicated in the more or less stable density of such outposts around the area edge in NE Hungary that we have observed over the last 30 yr. Fig. 1 shows the most important satellite outposts and the area edge of *V. a. album*

2.4. Climatic data

We chose 2 main sources of meteorological data for our analysis. First, we used the relatively old, but fairly comprehensive, database prepared by Kakas

(1967), which contains meteorological parameters on a monthly basis, derived from the data collected at meteorological stations in the period between 1901 and 1950. This dataset includes hundreds of meteorological parameters, from which we selected 7 variables, as detailed below. Second, we used the database of the European Climate Assessment & Dataset (ECAD) to characterize recent climatic patterns (Haylock et al. 2008; www.ecad.eu/). This dataset provides gridded E-OBS (observational dataset for Europe) records in a 0.25° resolution regular grid for 1950–2010, and contains mean, minimum and maximum temperature, average precipitation and average air pressure data. As the ECAD E-OBS dataset provides daily records, we transformed the required data to monthly scales (www.ecad.eu/download/ensembles/download.php#datafiles).

As the first step, we identified 21 suitably located meteorological stations providing relevant climatic parameters for the period 1901–1950 (Kakas 1967) (Fig. 4) in order to identify factors distinguishing areas occupied (12 stations) and not occupied (9 stations) by *V. a. album*. Following this, we repeated the same calculations using E-OBS gridded data for 1950–2010, in order to compare the results obtained by the 2 approaches. Finally, we included all available E-OBS gridded data (53 grids) closer than 10–20 km to the edge of the distribution in the study area with the exception of those grids split by the edge of the area of *V. a. album* (Fig. 4). As a result, 22 grids were located outside the distribution, while 31 were included within the area of *V. a. album*. Here we aimed to test the robustness of the selected distinguishing climatic parameters in an extreme condition where the 2 groups of selected grids are as close as possible to each other (20–30 km, on average 0.25°; Fig. 4).

We applied 7 meteorological variables in our first analyses: (1) July mean temperature, (2) AFMMT, (3) cumulative daily mean temperature during the vegetation period (March–November), (4) average annual extreme minimum temperature, (5) average annual extreme maximum temperature, (6) Gaussen–Bagnouls aridity index, calculated for July, and (7) average relative humidity at 14:00 h, July.

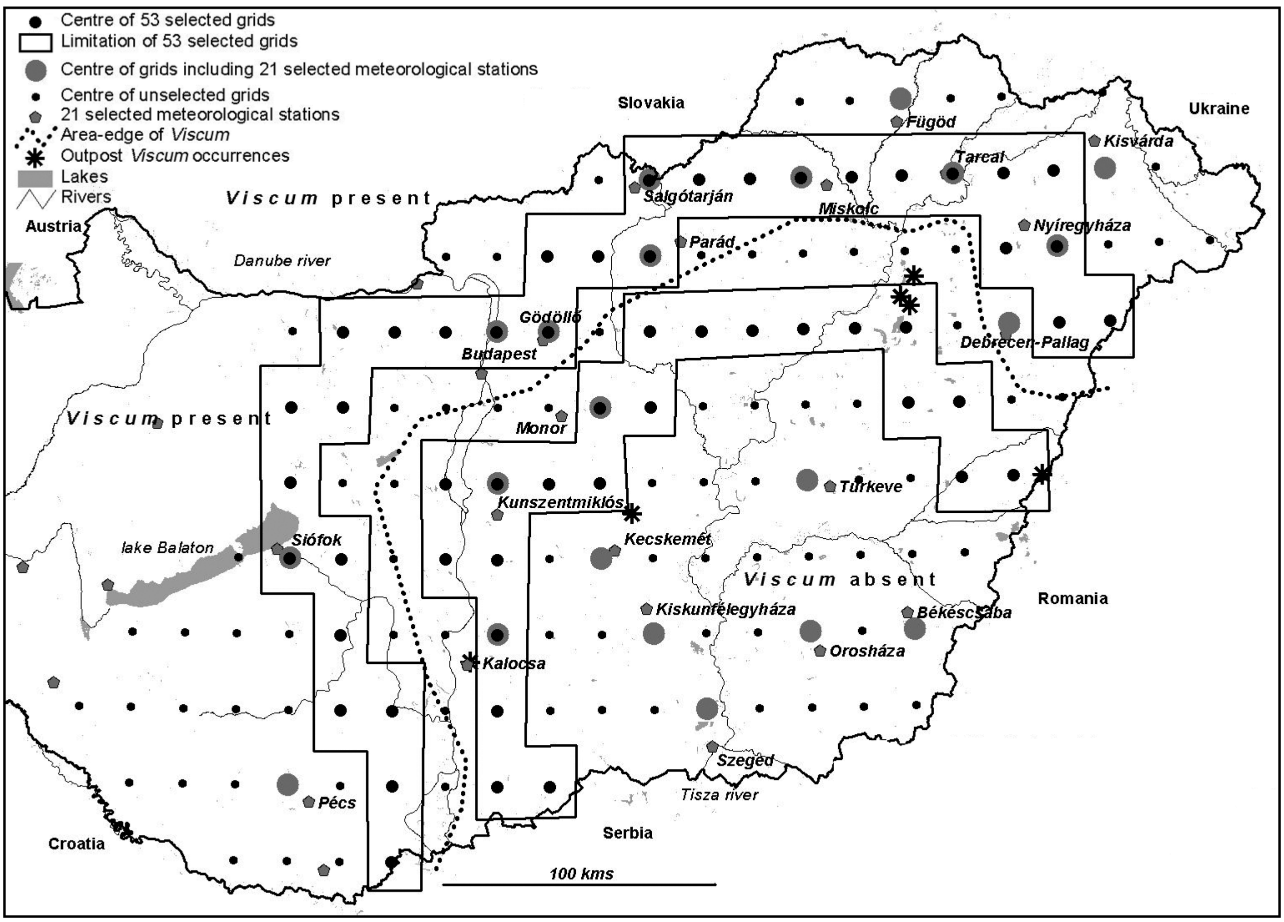

Fig. 4. Sources of meteorological data (meteorological stations and E-OBS grids)

(1) July mean temperature. The mean temperature of the warmest month (henceforth T_7) can be strongly connected to the occurrence of *V. a. album* on the southern area edge (Skre 1979, Jeffree & Jeffree 1996).

(2) Annual fluctuation of mean monthly temperature (AFMMT). Based on literature on the distribution and thermosphere of *V. a. album*, we predict that *V. a. album* does not occur in regions with an AFMMT above 25–27°C (Iversen 1944, Skre 1979, Jeffree & Jeffree 1996). Given that T_7 is a fixed parameter in the calculations, this fluctuation index also includes information on mean January temperature.

(3) Cumulative daily mean temperature in the vegetation period (TSUM). The general importance of TSUM in the thermosphere characterization of plants was shown by Woodward (1988), and was also suggested by agrometeorological investigations. In our study it is a metric of daily cumulative temperature obtained by summing daily mean temperatures across March to November. We considered this interval as an approximation of the vegetation period, characterized by a daily mean temperature above 5°C.

(4) Average annual extreme minimum temperature. Perennial herbs are more sensitive to this parameter (Woodward 1988) than to mean temperature data. Winter harshness can be important for *V. a. album*, because of the continental character of the Pannonian Basin climate. Its significance is also supported by the United States Department of Agriculture (USDA) Plant Hardiness Zone Map.

(5) Average annual extreme maximum temperature. We considered this parameter to be of key importance, possibly acting directly on the individuals physiologically. Average annual extremes are strongly correlated with the mean monthly temperatures of the warmest and coldest months, but their influence can be physiologically different.

(6) Gaussen–Bagnouls aridity index (I_A), calculated for July. In the second year of *V. album*, the primer haustorum (parasitic root) reaches the secondary xylem of the host (Kahle-Zuber 2008). Although *V. album* is dependent on the water supply from the host, and not from the environment, from this event onwards the attached embryo is highly susceptible to dehydration while striving to penetrate the host's vascular system (Mellado & Zamora 2014). Adult *V. album* individuals are constantly supplied by water from the host plant through their haustoria (Kahle-Zuber 2008), they are thus sensitive to the state of the host, as they have to tolerate negative water potential to a greater degree than the host tree (Glatzel & Geils 2009).

Water-supply factors can be especially important in Hungary, as the central part of the Pannonian Basin has a semi-wet forest-steppe climate (rather than a forest climate). Precipitation data themselves do not reflect the exact extent of the water supply, as evaporation is temperature dependent. Since aridity indices are more appropriate proxies for water supply, we chose the Gaussen–Bagnouls aridity index (henceforth I_A), which is equivalent to $P/2T$ (where P is mean precipitation in mm [most frequently, monthly] and T is mean temperature in °C). The advantage of this index is the opportunity to measure the water balance in various periods of the year. This index is used to classify periods into wet (when $I_A > 1.5$), semi-wet (when $1.5 > I_A > 1.0$) and arid categories (when $I_A < 1.0$) (Bagnouls & Gaussen 1957). An area is classified as having a forest climate if all months in a year are grouped into the wet type, and as having a forest-steppe climate when at least a significant period during the year is not wet but semi-wet. The widely known application of this index is the Walter–Lieth climate diagram (Walter & Lieth 1960) (see Fig. 3). We selected the July period because this is the driest month, referred to as I_{A7}.

7. Average relative humidity at 14:00 h, July. Transpiration can be related to the physiological conditions of the plant, influenced not only by temperature, but also by water balance, wind and relative humidity. We selected July values at around 14:00 h (the hottest part of the day) for the same reasons which support the use of I_{A7}.

2.5. Statistical analyses

We conducted linear discriminant analysis to find a linear combination of meteorological parameters that separates the areas with and without *V. a. album*. Our methodology follows the canonical approach, where the classes are pre-selected in advance and variables constitute a uniform set without any grouping. Discriminant analysis is a widely accepted statistical analysis in ecological studies, and is used to explore factors affecting actual distributions (Hocker 1956, Williams 1983). All analyses were carried out using SPSS 21 statistical software.

3. RESULTS

Four out of the 7 investigated parameters describing the climate of 21 meteorological stations (Fig. 1) were significantly different at stations outside and inside *Viscum album* subsp. *album*'s distribution area (all $t > 3.34$, all $p < 0.01$). Stations where *V. a. album* is present are characterized by a higher I_{A7} value (mean ± SD = 1.48 ± 0.17, compared with 1.15 ± 0.06); lower T_7 values (20.57 ± 0.76°C, compared with 21.81 ± 0.35°C); lower TSUM values (3564.00 ± 205.92°C, compared with 3846.67 ± 91.55°C); and lower annual extreme maximum temperature (34.54 ± 0.69°C, compared with 35.41 ± 0.42°C). However, annual extreme minimum temperature, AFMMT and relative humidity values at 14:00 h in July did not differ significantly.

The discriminant function analysis resulted in a significant relatedness between group identity (stations where *V. a. album* was present or absent) and the climatic variables ($\lambda = 0.12$, $p < 0.01$), explaining 88% of the variance. The structure matrix reveals 3 variables with significant predictive power: I_{A7} ($r = 0.495$), T_7 ($r = -0.381$) and TSUM ($r = -0.326$) (Table 1). The classification resulted in a perfect (100%) coincidence between the actual and predicted status of meteorological stations of different group identity (with or without *V. a. album*). Fig. 5 provides an overview of the results of the 4 discriminant analyses applied, where the first part of the figure on the left illustrates the results from this first analysis.

Although the classification of the stations proved to be very effective using the 7 parameters, a number of probable biases arose. First, the sample size was relatively low, as we had a limited number of stations that had documentation for the entire set of the studied 7 variables. Second, this documentation was collected a long time ago (Kakas 1967), with data covering the period 1901–1950. Therefore, we needed to enhance the sample size and to turn to more recent meteorological data to minimize the possibility that an earlier set of meteorological parameters is connected only accidentally to the recent distribution of *V. a. album*.

Table 1. Correlations between independent variables and the discriminant functions, based on the structure matrix. The function included 7 parameters and classified 21 meteorological stations concerning their *Viscum album* subsp. *album*-related status. I_{A7}: Gaussen–Bagnouls aridity index in the driest month (i.e. July); T_7: mean temperature of the warmest month (i.e. July); TSUM: cumulative daily mean temperature

Variable	Correlation with the discriminant function
I_{A7}	0.495
T_7	−0.381
TSUM of the vegetation period	−0.326
Average annual extreme maximum	−0.285
Annual fluctuation of mean monthly temperature	−0.109
Relative humidity at 14:00 h in July	0.085
Average annual extreme minimum	−0.052

To do so, we first repeated the classification by restricting the variables to those with absolute correlation values reaching at least the moderate value of 0.3, as obtained from the structure matrix (I_{A7}, T_7 and TSUM). As a result, the sample size increased, with an additional 7 stations providing satisfactory data from the period 1901–1950. The discriminant function described a significant relationship between the groups (stations with or without *V. a. album*) and climatic variables ($\lambda = 0.35$, $p < 0.01$), explaining 65% of the variance. The structure matrix revealed that all 3 variables exhibited significant predictive power. Stations where *V. a. album* is present showed a larger I_{A7} value (less aridity) with a cooler July and lower TSUM values. The classification of the stations resulted in an almost perfect match between the actual and predicted status of the meteorological stations in relation to the occurrence of *V. a. album*. The classification predicted the status of 25 stations correctly, and incorrectly assigned only 3 stations.

Second, we derived data for these 3 parameters (I_{A7}, T_7 and TSUM) from the E-OBS dataset of 0.25° regular grid resolution for the period from 1950 to 2010. Following this we were able to compare the classification resulting from the analysis related to the 28 meteorological stations with that resulting from the analysis using the 28 E-OBS grids that overlapped with these stations. The classification of the data again resulted in significant relationships between group identity (grids with or without *V. a. album*) and climatic variables ($\lambda = 0.35$, $p < 0.01$), explaining 65% of the variance. Based on the structure matrix, all 3 variables exhibited significant predictive power in the same direction as they did in the first and second analyses. Twenty-five grids out of 28 (88%) were correctly classified by the discriminant function. Table 2 shows the function correlation values of variables in the structure matrix, comparing the results of the analysis using station data from the time interval of 1901–1950 and grids from the period 1950–2010. Clearly, based on all 3 of the above analyses, I_{A7} proved to be the most influential factor in predicting the presence of *V. a. album*, while the second most important was T_7 and the third was TSUM.

Finally, we tested the classification under the extreme condition where the 2 groups of 53 grids on both sides of the boundary of the distribution were as close to each other as possible, on average at a distance of 0.25°

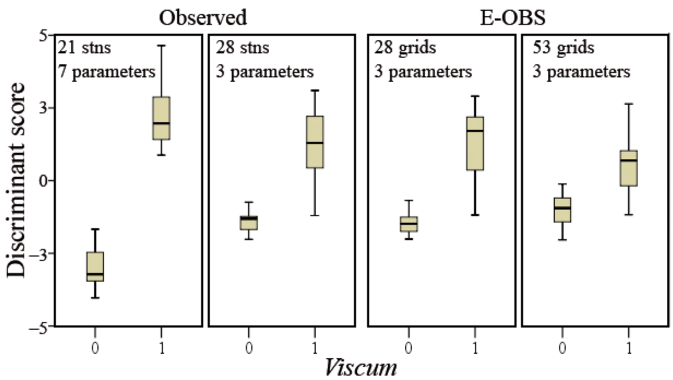

Fig. 5. Summary of the results from the 4 discriminant analyses on climatic factors that are related to the presence (1) or absence (0) of *Viscum album album*. The first 2 diagrams are based on meteorological data from meteorological stations from the period 1900–1950. The second 2 diagrams are based on recent E-OBS grids data from the period 1950–2010. The scores on the leftmost diagram are based on the discriminant function involving 7 independent variables (mean July temperature, air temperature sum of the vegetation period, average annual extreme minimum temperature, average annual extreme maximum temperature, the Gaussen–Bagnouls aridity index calculated for July, annual fluctuation of mean temperature and relative humidity at 14:00 h in July). In the other 3 cases, the discriminant function involves 3 variables (mean July temperature, air temperature sum of the vegetation period and Gaussen–Bagnouls aridity index calculated for July)

(Fig. 4). In this analysis we again applied the 3 studied parameters. This function also provided significant relationships between the groups and the climatic variables ($\lambda = 0.57$, $p < 0.01$), explaining 43% of the variance. The structure matrix revealed that the 3 variables exhibited significant predictive power in the classification, with stations having a greater I_{A7} value (0.943), a cooler July (–0.923) and a lower TSUM (–0.713) where *V. a. album* occurs. The classification categorized 44 grids (83%) correctly and 9 grids were misclassified. Thus, the categorization still worked effectively using this strict condition (Fig. 5).

Table 2. Correlations between the independent variables and the discriminant functions, based on the structure matrix from 2 functions. The functions involved 3 parameters and classified 28 meteorological stations regarding their *Viscum album album*-related status, relying on data either from the 28 meteorological stations or the 28 corresponding E-OBS grids. See Table 1 for abbreviations

	Meteorological stations	Corresponding E-OBS grids
I_{A7}	0.927	0.924
T_7	–0.826	–0.767
TSUM of the vegetation period	–0.332	–0.715

The relative homogeneity of the area without *V. a. album* compared with the heterogeneity of the *V. a. album*-occupied region is remarkable in all cases (Fig. 5). This can be explained by the fact that 2 subtypes of climate can be characterized within the distribution area of *V. a. album*: one with warm summers and cool winters, and the other with cool summers and cold winters.

5. DISCUSSION

Our results support the hypothesis that although the southern edge of the distribution of *Viscum album album* within Hungary is climatically limited, it is limited not only by temperature factors — as along the northern edge of the distribution — but also by aridity. The area boundary of *V. a. album* almost completely overlaps with the local boundary between the forest and forest-steppe climates.

Besides the importance of aridity, our results indicate the significance of heat. The mean July temperature and cumulative air temperature of the vegetation period proved to be of key importance. For the southern limit of occurrence in Hungary, our findings did not support Woodward's statement that perennial plants are very sensitive to low (or high) temperature extremes (Woodward 1988), as *V. album* itself is a perennial, hemiparasitic shrub.

These 3 climatic parameters exhibited significant relationships with the occurrence of *V. a. album*, even when choosing grids of finer resolution. To date, the majority of bioclimatic studies on *V. a. album* have focused on the cold, northern edge or upper altitudinal limits of the species, including studies from Scandinavia (e.g. Skre 1979), or orographic studies (e.g. Dobbertin et al. 2005). Although investigations conducted in colder regions show that *V. a. album* is limited by winter harshness, our study showed that summer aridity is a limiting factor in Hungary, an area that makes up a section of the southern boundary of the species.

The novelty of our method is the selection of sample sites as close as possible to the boundary of a distribution: if sample sites are extremely close to the dividing line and the discriminant function still describes a significant relationship between group identity and climatic parameters, the discriminant function appears to have high predictive power.

According to the results of our study, the present boundary of *V. a. album* within Hungary can be explained using both 50-yr-old and current climatic data. The analysis based on data from meteorological stations from the period 1901–1950 and the analysis based on grid data from 1950–2010 did not reveal differences in classifying climatic parameters. Therefore, we conclude that bioclimatic constraints on *V. a. album* have not significantly changed over the past few decades, at least around the ca. 50-km-wide zone of its boundary that we investigated. Importantly, temperature has changed over the past few decades along with precipitation, resulting in a more or less stable water balance. The dataset of the Hungarian Meteorological Service indicates a 1.3–1.8°C increase in mean annual temperature between 1980 and 2010 and a 0–25% increase in annual precipitation around the area edge between 1960 and 2010. Notably, summers have become rainier, which balances the increasing temperature and increasing year-round aridity (www.met.hu/eghajlat/eghajlatvaltozas/megfigyelt_valtozasok/Magyarorszag/).

Regions occupied by *V. a. album* appeared to be more heterogeneous in relation to climatic parameters than areas without *V. a. album*. This pattern is probably explained by the fact that the *V. a. album*-occupied area can be divided into 2 subclasses — a humid area with a hot summer (W Hungary) and a cooler and humid area (N Hungary) — within the Pannonian Basin.

A probable bias in our study may be that we studied correlational and not causal relationships between climatic factors and occurrences of *V. a. album*. Furthermore, identifying the edge line was, to some extent, discretional. In practical terms, the excluded outposts did not influence the localization of the investigated meteorological stations except for the Kecskemét station, which would fall into the area of *V. a. album* instead of the area without *V. a. album*. However, when tested, we found that this difference did not change the result of the climatic data analyses.

Our results support the relevance of including specific factors in SDMs (Davis et al. 1998). In our case, the important climatic factors appeared to be different from those on the opposite northern side of the distribution. Hocker (1956) obtained similar results for *Pinus taeda* in North America, as limiting factors were not the same around the western and northern edges of this plant's distribution. In line with the importance of including regional characteristics in SDMs, we also argue for data collection on a regional scale. Studies dealing with the ecological impacts of possible climate change often take a micro-ecological approach (Brown 1995) by collecting local data and attempting to generalize on a global scale (Walther et al. 2005). In most cases, historical biogeographical data are absent.

One way of avoiding this bias is to properly map units of the whole area of the investigated species that are considered to be homogeneous regarding interactions between species (competition, predation and parasitism), the types and historical background of distribution, and edaphic factors.

In the case of *V. a. album*, the lack of competitors and edaphic relationships, and the unlimited availability of hosts, allow relatively straightforward bioclimatic investigations. However, dispersers are different in different regions. *Viscum a. album* is dispersed by the blackcap *Sylvia atricapilla* around the Atlantic coast and the Mediterranean part of Europe (Mokwa 2009), while this role is taken by the mistle thrush *Turdus viscivorus* further to the east in continental Europe. Dividing the *V. a. album* area into these 2 regions and taking into account the localization of the adjacent area edge (the southern continental in our case) can be expected to result in an adequately homogeneous division of *V a. album*'s area for conclusively interpretable autecological–climatologicinvestigations. In our study, we applied this regional perspective, limiting our study to: (1) the mistle thrush disperser (continental European) area; (2) the southern boundary of the distribution; (3) the continental (forest-steppe) edge of the area; and (4) the Pannonian Basin.

Comparison of these subregions should only be made with caution as, for example, sporadic *V. a. album* occurrences far from Hungary, in and around the Danube delta or in the lowlands of the Mediterranean region, where semi-humid and even semiarid summer periods exist, can be explained in several different ways.

6. CONCLUSIONS

On the southern limit of the distribution of *Viscum album*, in Hungary, it is not only heat limitation that is present, but also the negative effect of water deficit. Furthermore, in the Pannonian Basin, where forest and forest-steppe climates meet, aridity proved to be a dominant factor in the distribution of the species.

The distribution of *V. album* has not changed remarkably over the last 50 yr in the study area, probably because of the simultaneous rise in temperature and precipitation, resulting in a stable climatic water balance (aridity).

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