

Roadside invasion of *Dittrichia graveolens* in Slovakia and prediction of its potential future distribution

Hubert Žarnovičan^{1,+}, Róbert Šuvada^{2,+}, Božena Šerá¹, Marian Gábor³,
Pavol Eliáš Jr.⁴ & Iva Hodálová^{2,*}

¹Faculty of Natural Sciences, Comenius University Bratislava, Ilkovičova 6, SK-84215 Bratislava, Slovakia; ²Plant Science and Biodiversity Center, Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84523 Bratislava, Slovakia; ³National Forest Centre – Section of Forest management planning and Informatics, Zvolen, T. G. Masaryka 22, SK-96001 Zvolen, Slovakia; ⁴Institute of Plant and Environmental Sciences, Slovak University of Agriculture, A. Hlinku 2, SK-94976 Nitra, Slovakia

*corresponding author: iva.hodalova@savba.sk

+ these authors contributed equally to this publication

Abstract: The aim of this study was to determine the current distribution of *Dittrichia graveolens* along motorways in Slovakia, including adjacent sections in the Czech Republic, Austria, and Hungary, to assess to what extent the density of the species depends on the age of operation of the studied motorways, and to predict the potential distribution of the species in Slovakia for the period 2021–2040. In total, 1,440 occurrence points of the species were recorded along 419.9 km of surveyed motorways (out of 826.5 km of surveyed roads). Of the 1,157 occurrence points, the highest proportion (1,065 points) was recorded in the western part of the country, with occurrence decreasing towards the east. The generalized additive mixed model showed that the occurrence density of *D. graveolens* was highest on older motorway sections, specifically those constructed in the late 1970s and late 1990s, while the most recently built sections (post 2012) exhibited significantly lower invasion densities. The MaxEnt model for *D. graveolens* under the SSP370 scenario demonstrated robust predictive performance (AUC = 0.85, TSS = 0.61). Focusing on the primary study region, the model revealed that over 24,000 km² in Slovakia are climatically suitable for future invasion. However, given the species' strict concentration along immediate road edges, the actual potential area of occupancy represents 32.9 km² (0.07% of the total national area) localized within road verges. While current occurrences are heavily concentrated in the western lowlands, our predictions indicate a significant potential for continuous eastward expansion into the central and eastern regions along the road network. The primary climatic constraint is the minimum temperature of the coldest month (Bio06), which limits the species at higher altitudes. Our findings confirm that the *D. graveolens* invasion in Slovakia is driven by a combination of road operational age and climatic suitability. These road verges serve as critical corridors, facilitating the species' predicted eastward expansion into new regions.

Keywords: alien plant, highway, invasive species, MaxEnt, neophyte, road, species distribution modelling

Introduction

Plant invasions in recent decades have ecological, economic and social impacts worldwide (Gaertner et al. 2009, Stohlgren et al. 2011, Pyšek et al. 2012, Traveset & Richardson 2020). Trade, travel and climate change have accelerated the spread of alien species, with plant invasions occurring more frequently and being more severe (Hulme 2009, Lemke et al. 2019, Turbelin & Catford 2021). Invasive plants displace native species, reduce biodiversity, and alter the habitat structure, nutrient cycling, and water or light availability, which affects native biota (e.g. Funk & Richardson 2002, Pyšek et al. 2012, 2022, Skokanová et al. 2024).

Dittrichia graveolens (L.) Greuter (*Asteraceae*, stinkwort) has spread rapidly in several regions of introduction (Frajman & Kaligarič 2009, Brownsey et al. 2014, Kozłowska-Kozak et al. 2019). The natural range of this species extends from the Atlantic coast of North Africa and western Europe across the Mediterranean region, Asia Minor and the northern part of the Arabian Peninsula to the Iranian Plateau (Brullo & de Marco 2000, Qaiser & Abid 2005, POWO 2025). Its range has gradually expanded along roads to northern, central and eastern Europe (e.g. Lázaro-Lobo et al. 2024). Outside of Europe, it has been reported as an alien species in Central Asia, Australia, New Zealand, and the coasts of North and South America (POWO 2025). It is a nitrophilous species that tolerates dry and salty habitats (di Castri et al. 1990, Brullo & de Marco 2000, Kaplan et al. 2018, Pyšek et al. 2022). In native areas, it mainly occurs on sandy and rocky soils of fields, fallow land, uncultivated areas, gravel banks and gravel pits on riverbanks, roadside ditches and ruins (Rameau et al. 2008, Pignatti et al. 2018, Rico 2019).

Dittrichia graveolens significantly decreases the biodiversity in invaded areas (Ponticelli et al. 2022, Melen et al. 2024). It has an allelopathic effect on surrounding species, inhibiting their germination and seedling vitality and decreasing root and shoot growth (Almhemed et al. 2021). It also affects the composition of the soil microbiota (Ramirez et al. 2019), is toxic to farm animals, has a sedative effect on fish and can cause contact dermatitis in humans (Ponticelli et al. 2022).

In Europe, the first records of the species outside its original range were reported in 1876 in western Germany (Zimmermann 1907) and 1895 in Belgium (Verloove 2006), from where it gradually spread to northern and eastern Europe, especially through the mineral resources trade, the transportation of mined ores and the wool trade (Höppner & Preuss 1926, Verloove 2006, Buch 2020). In the past few decades, it has spread rapidly across a number of European countries (Fig. 1), mainly through viatic migration along major transportation corridors (Brownsey 2012). In addition to Germany and Belgium, this species is recorded in southern and northern England (Stace 2019), Sweden (Bauer 2024), Austria (Hohla 2001), the Czech Republic (Raabe 2009), Slovenia (Frajman & Kaligarič 2009), Slovakia (Király et al. 2014), Poland (Kocián 2015), Hungary (Takács et al. 2016), Romania (Szatmari & Hurdu 2020) and Lithuania (Gudžinskas 2024); these studies represent the first records in the respective countries.

Dittrichia graveolens has not received much attention in Slovakia and its expansion has gone unnoticed by both the scientific and lay botanical communities. The species was first reported from western Slovakia in 2014 (Király et al. 2014) at a petrol station car park near the state border with the Czech Republic (Fig. 2). Consequently, it was included in the list of alien species in Slovakia (Májeková et al. 2021). No new data from the

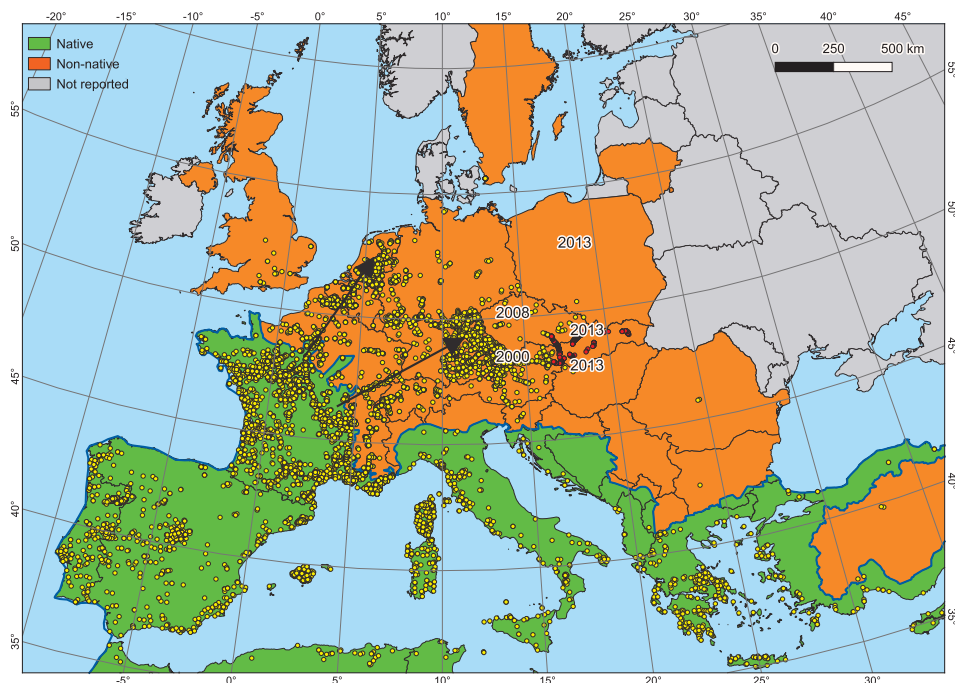


Fig. 1. Native and alien distribution areas of *Dittrichia graveolens* in Europe and years of the first findings of the species in the neighbouring countries of Slovakia. The boundary between the native and alien range (blue line) is shown according to Lustenhouwer & Parker (2022). Black arrows show the direction of the species' spread in Europe. Yellow dots show the occurrence records from GBIF (<https://www.gbif.org>, 9 November 2025), and red dots show our own occurrence points. The years of the first records in Slovakia and surrounding countries are shown: Slovakia (Király et al. 2014), Austria (Hohla 2001), Czech Republic (Raabe 2009), Poland (Kocián 2015) and Hungary (Takács et al. 2016).

Slovakian territory have been recorded or published since 2014. The species was not listed in any of the available databases, including the Slovak Vegetation Database (Šibík 2012, <https://www.pladias.sk>), <https://www.inaturalist.org>, <https://www.fotonet.sk>, and <https://www.nahuby.sk>, until 2024. In the countries neighbouring Slovakia, the most aggressive spread has been reported in the Czech Republic (Pyšek et al. 2022, Kalusová et al. 2024), it is reported as casual in Hungary (Csiky et al. 2023) and established in Austria (Glaser et al. 2025) and Poland (Wróbel & Nobis 2017).

Considering its spread in neighbouring countries (Hohla 2001, Raabe 2008, 2009, Király et al. 2014, Kocián 2015) occurring primarily along roads, we focused on mapping motorways in Slovakia, including selected motorway parts closely connected to the study area, namely in the Czech Republic, Austria and Hungary, to determine the route by which the species has spread to Slovakia.

This study aimed at (i) determining the current distribution of *D. graveolens* along road-sides (including road edges and dividing strips) of selected Slovakian motorways and connecting roads in neighbouring countries (Czech Republic, Austria and Hungary), (ii) identifying the degree of dependence of its occurrence density on the operational age of the studied motorways, and (iii) predicting the potential distribution in Slovakia in 2021–2040 using models fitted with global occurrence data across native and alien ranges.

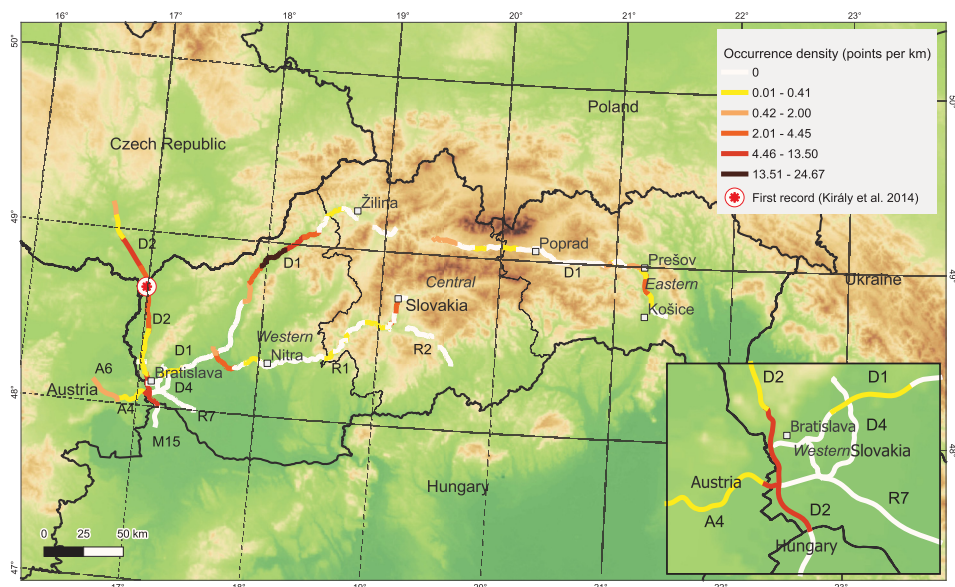


Fig. 2. Density of occurrences of *Dittrichia graveolens* per km along the motorways surveyed in Slovakia (D1, D2, D4, R1, R2, R7), the Czech Republic (D2), Austria (A4, A6) and Hungary (M15). The density of occurrences is colour-coded (density = number of occurrence points of *D. graveolens* per 1 km section). The background map used was TOPO-WMS (Mundialis 2025), which was derived from modified SRTM data (2014) from NASA.

Materials and methods

Study species

Dittrichia graveolens is an annual aromatic herb (smelling of camphor) from the *Asteraceae* family. The stem is 20–50 (–100) cm tall and branches from the base, with a glandular stem, leaves and bracts. The leaves are simple, linear to lanceolate, entire or remotely denticulate. The flowers are arranged in numerous small yellow heads composed of female, ligulate flowers on the outer edge and hermaphrodite, tubular flowers in the centre. It flowers from September to October in central Europe (Kocián 2015), and produces many seeds on a bristle pappus, which are easily dispersed, mainly by the wind, vehicles, with soil or loads (Parsons 1973, Brownsey 2012).

Study area

The construction of the motorway network in Slovakia began in 1969, and 775.9 km (1,551.8 km in both directions) of motorways were operational at the end of 2024 (<https://historiadialnic.sk>). These roads are distributed across the entire country, with the highest concentration in the western region (Supplementary Fig. S1). The monitored roads (Fig. 2, Supplementary Fig. S1) were mainly located in plains and basins (Mazúr & Lukniš 1986) at altitudes of 100–800 m a.s.l.

The potential vegetation of the lowlands in the southwestern and southern parts of the study area consists mainly of deciduous floodplain forests, willow and poplar floodplain

forests, and moist lowland forests in large river valleys. At relatively high elevations from the eastern part of the Czech Republic to the eastern part of Slovakia, mixed oak-hornbeam forests predominate, whereas at relatively high elevations in central and northern Slovakia, mixed beech and beech forests predominate (Bohn et al. 2000/2003).

Field data collection and survey design

The occurrence of *D. graveolens* was mapped in October and November 2023–2024, during the phenological optimum of this species in Slovakia. Given the species distribution pattern in central Europe (Hohla 2001, Raabe 2008, 2009, Király et al. 2014, Kocián 2015, Takács et al. 2016), we focused on mapping motorways. The surveys were carried out on the D1, D2, D4, R1, R2 and R7 motorways in Slovakia (Supplementary Fig. S1) and covered 746.73 km (1,493.46 km in both directions). In addition to Slovakia, selected motorways on the western and southern borders of Slovakia were also included in our study: (i) in the Czech Republic, D2 motorway from the Slovak–Czech border to the city of Brno in the southern part, covering 57.99 km (115.98 km in both directions); (ii) in Austria, the A4 and A6 motorways from the Slovak–Austrian border to the village of Fischamend, covering 42.30 km (84.60 km in both direction); and (iii) in Hungary, the M15 motorway from the Slovak–Hungarian border to the village of Hegyeshalom, covering 12.58 km (25.16 km in both direction). These roads were included in our map based on current knowledge of the species occurrence in the abovementioned countries and their connection to the largest road junction in Slovakia, the city of Bratislava.

Data were collected from the passenger seat using a car survey according to the methodology described in Žarnovičan et al. (2024). The car drove in the slowest lane at a speed of approximately 80–90 km/h, and the botanist sat in the passenger seat and used a Garmin GPSMAP 62st GPS device to record the data (Supplementary Fig. S2). The recorded occurrence points are listed in Supplementary Table S1. Each route was travelled in both directions without distinguishing occurrences on the roadside edge or dividing strip. The species was mapped from the distance visible (~1 m) from the mapping vehicle. Each occurrence point represents a presence-only record, in which the presence of the species was visually confirmed during a car journey, with no additional information on abundance or population vitality. As quantity was not recorded, all our occurrence points for *D. graveolens* are considered unit presence records, regardless of the number (i.e. abundance) of individuals at each site.

*Possible errors during *Dittrichia graveolens* recording*

Although *D. graveolens* is one of the most conspicuous fall herbs growing along road corridors, we considered several factors when mapping it. There were several potential sources of error: (i) similarities with the taxa *Atriplex tatarica* L., *Bassia scoparia* (L.) A. J. Scott, *Odontites vulgaris* Moench, *Ambrosia artemisiifolia* L. and *Symphotrichum lanceolatum* (Willd.) G. L. Nesom, which forms a morphotype similar to *D. graveolens* after mowing; (ii) overtaking slow-moving vehicles, which could have obscured the view of the monitored species (especially trucks); (iii) the technical limitations of the GPS device; and (iv) technical difficulties in verifying data collection. The most accurate method for verifying data from a vehicle survey is a direct comparison with data collected through field research (Žarnovičan et al. 2024). However, verifying the data on motorways in this

way is technically challenging. Therefore, we assessed the accuracy of the data by comparing the occurrence points obtained by two mappers. The D1 motorway section Bratislava, Senecká Road – Trnava (between kilometre posts 15.5 and 49.0 km, covering 67 km in both directions) was selected for the verification method. The kilometre posts are shown on the maps of the road network (Slovak Road Administration 2025). The route was covered by two cars (i.e. two drivers) with two botanists on two days in October 2024. The collected occurrence points were compared in 10-m segments (67 km = 6,700 segments), and we assessed either agreement (yes, yes; no, no) or disagreement (yes, no; no, yes) in the occurrence points from both mappers. The results showed 99.93% agreement (Table 1). While the high agreement indicates low observer bias, it does not allow assessment of detection completeness or account for potential false absences without independent ground-truthing.

Table 1. Verification of the data collection method, which was carried out on the D1 motorway section Bratislava, Senecká Road – Trnava (15.5–49.0 km). The occurrence points of *Dittrichia graveolens* were compared in 10-m segments (67 km = 6,700 segments), and either agreement (yes/yes; no/no) or disagreement (yes/no; no/yes) between the occurrence points from both mappers was used. Y – yes, N – no.

Verification road section in D1	No. of segments	YY	YN	NY	NN	Agreement (%)	Difference (%)
Bratislava, Senecká road – Trnava	3,350	0	0	0	3,350	100.00	0.000
Trnava – Bratislava, Senecká road	3,350	0	2	3	3,345	99.85	0.050
Total	6,700	0	2	3	6,695	–	–
Average	–	–	–	–	–	99.93	0.025

Software and analytical tools

Statistical analyses and the final visualization of analytical results were conducted in the R environment version 4.4.2 (R Core Team 2024). Specific R packages used for various analysis steps are cited within the respective methodology sections.

To predict the distribution and model the climatic suitability of *D. graveolens*, we used the Maximum Entropy algorithm implemented in MaxEnt version 4.3.3 (Phillips et al. 2006), one of the most popular tools for species distribution modelling (Lissovsky & Dudov 2021).

All map generation and visual data screening were performed in QGIS version 3.28 (QGIS Development Team 2025). The background was obtained from the topographic WMS service (Mundialis 2025), which was derived from modified SRTM data (2014) from NASA. The road types for Slovakia (motorways) were determined using the national database (Slovak Road Administration 2024). The motorways for Austria, Hungary and the Czech Republic were vectorized on the basis of the ArcGIS Imagery base map in ArcGIS Pro 3.4.0 software (ESRI 2024). Elevations were computed based on EU-DEM, which is available for each country (European Environment Agency 2016, modified 2024). The European country border dataset was obtained from the Technical University of Denmark dataset (Sevdari & Marmullaku 2023).

Table 2. Occurrence points of *Dittrichia graveolens* along motorways in Slovakia (SK), the Czech Republic (CZ) and Austria (AT), obtained from the car survey. Only road sections on which the species occurred are listed. No occurrences were found on Slovakian motorways R2 and R7 and the surveyed Hungarian section of the M15 motorway. The motorway sections are listed according to the year they were opened (for more details, see <https://historiadialnic.sk>). Density = number of occurrence points of *D. graveolens* per 1 km section. *The section length represents the length of a directionally divided road, forming a line (Žarnovičan et al. 2024).

Motorway	Motorway sections with the occurrence of <i>D. graveolens</i>	Year of open	Section length* (km)	No. of occurrence points	Density (per km)
D1-SK	Bratislava Senecká road – Senec	1975	16.80	5	0.30
	Ivachnová – Liptovský Mikuláš	1977	14.33	13	0.91
	Prešov south – Ličartovce	1982	8.64	28	3.24
	Ličartovce – Budimír	1988	10.50	1	0.10
	Liptovský Hrádok – Hybe	1990	7.87	1	0.13
	Chocholná – Skala	1996	11.20	246	21.96
	Skala – Nemšová	1996	7.50	185	24.67
	Široké bypass	1997	3.06	5	1.63
	Nové Mesto nad Váhom – Chocholná	2000	13.10	52	3.97
	Nemšová – Ladce	2000	16.63	199	11.97
	Horná Streda – Nové Mesto nad Váhom	2000	14.10	10	0.71
	Fričovce bypass	2003	3.17	1	0.32
	Važec – Mengusovce	2004	12.23	1	0.08
	Ladce – Sverepec	2005	8.04	45	5.60
	Vrtižer – Hričovské Podhradie	2007	12.90	1	0.08
	Svinia – Prešov west	2010	7.08	8	1.13
	Prešov west – Prešov south	2021	7.87	1	0.13
	Hričovské Podhradie – Lietavská Lúčka	2021	11.32	1	0.09
D2-SK	Bratislava, Lamačská road – Malacky	1973	29.34	9	0.31
	Malacky – Kúty	1978	24.18	84	3.47
	Kúty – Brodské/Břeclav	1979	4.49	14	3.12
	state border Slovakia/Czech Republic				
	Bratislava, Viedenská road – Čunovo/Rajka	2002	14.89	149	10.01
	state border Slovakia/Hungary				
D4-SK	Jarovce, Bratislava – Jarovce/Kittsee	1999	2.00	27	13.50
	state border Slovakia/Austria				
R1-SK	Kremnička – Banská Bystrica south	1975	4.50	19	4.22
	Báb – Nitra west	1980	10.37	1	0.10
	Stráž – Sliač	1980	1.42	6	4.23
	Trnava – Trnava D1	1981	3.50	4	1.14
	Šášovské Podhradie – Budča	1986	15.30	3	0.20
	Sereď – Šoporna	1998	6.80	17	2.50
	Trnava D1 – Sereď	2000	6.76	18	2.66
	Nová Baňa bypass	2003	5.30	2	0.38
	Žarnovica bypass	2006	4.47	1	0.22
D2-CZ	Brno south – Blučina	1978	9.02	18	2.00
	Blučina – Hustopeče	1979	13.05	5	0.38
	Hustopeče – Břeclav	1980	23.75	192	8.08
	Břeclav Czech Republic – Brodské/Břeclav	1980	12.17	33	2.71
	state border Slovakia/Czech Republic				
A4-AT	intersection A6/A4 – Fischamend	–	20.10	26	1.29
A6-AT	Jarovce/Kittsee state border	2007	22.20	9	0.41
	Slovakia/Austria – intersection A6/A4				
Total		–	419.93	1,440	–

Analysis of the current expansion in Slovakia

From the territorial survey and collection of occurrence data, a question arose as to whether there was a dependence between the presence of *D. graveolens* and the age of the motorways, or the period when the road was opened for use. For this analysis, we used only our own occurrence points (1,440), the layer of motorway sections (Table 2; division of motorways into sections is available at <https://historiadialnic.sk>), and the assigned year the section was first opened. For further data processing and evaluation, we standardized by calculating the occurrence density. The occurrence density per km was calculated as the ratio of the number of occurrence points to the length of the particular surveyed section.

Since the density was calculated for individual road sections and not for the entire motorway, we considered the sections to be nested data. This means that the observations were no longer independent, and it was highly probable that, for example two sections on the D1 motorway would be more similar to each other (e.g. due to the same maintenance management or similar surrounding conditions) than a randomly selected D1 section in Slovakia and an A4 section in Austria. Therefore, we used a generalized additive mixed model (GAMM) by adding the random effect ROAD.

A characteristic feature of the Slovak territory is that the motorways are more concentrated in the west of the country, which may have caused spatial bias during evaluation. In QGIS, the centre coordinate (X, Y) in WGS84 was calculated for each section and constrained to lie on the surface. Even if a section was highly curved, the centre always lied on the line, compared to calculating a standard centroid.

The centre coordinates of the sections were subsequently included in the GAMM. The calculation of the dependence of *D. graveolens* density on the age of motorways thus accounted for the addition of the random effect ROAD and coordinates X and Y to suppress the assumed spatial bias. Overdispersion in the response data was detected during model diagnostics; therefore, a negative binomial error distribution was used ($\theta = 0.61$). The final model structure was: Density $\sim$ s(Year) + s(X, Y) + s(Road, bs = "re"). By adding the spatial function s(X, Y) to the model, we ensured that the interpretation of the result was not affected by the geographical location of the individual road sections.

The GAMM was computed using the mgcv package (Wood 2017), which utilizes the nlme package (Pinheiro et al. 2024) internally for fitting the mixed-effects structure. The MASS package (Venables & Ripley 2002) was used to specify the negative binomial distribution. The graphical display of the resulting curve progression was performed using gratia (Simpson 2024) and ggplot2 packages (Wickham 2016). The motorway network, including the surveyed road sections and the spatial density of *D. graveolens* occurrences, was visualized in Fig. 2 and Supplementary Fig. S1.

MaxEnt model

Data collection. – For modelling, we utilized data from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>) spanning 1996–2025, in addition to our own occurrence points for species mapping from the territory of Slovakia and neighbouring countries (1,440 data points). In total, 24,068 occurrences for the target species (*D. graveolens*) were downloaded from GBIF (<https://doi.org/10.15468/dl.n4w3dw>, accessed 9 November 2025). Similarly, we downloaded all global occurrence data for the species from the same source and time period to be used for target-group background sampling, namely

Dittrichia viscosa (59,704 occurrences; <https://doi.org/10.15468/dl.pjt5xu>, accessed 9 November 2025), *Erigeron canadensis* (361,186 occurrences; <https://doi.org/10.15468/dl.yrj6f6>, accessed 6 November 2025) and *Ambrosia artemisiifolia* (159,298 occurrences; <https://doi.org/10.15468/dl.p7uv6s>, accessed 6 November 2025).

Data cleaning and thinning. – The occurrence records for the target species (*D. graveolens*) as well as the records used for target-group background sampling underwent the same cleaning and spatial thinning steps. After downloading the data from GBIF, the records underwent a data completeness check in QGIS to ensure the presence of valid coordinates and exact dates (only the 1996–2025 period) and were subsequently saved for further processing. Data cleaning was performed using the CoordinateCleaner package (Zizka et al. 2019), which was used to remove duplicate records, records with high uncertainty assigned to known centroids (e.g. capital cities and institutions), and records with identical latitude and longitude. Automated cleaning was followed by a manual check. During this stage, regularly arranged clusters of records were identified and deleted. The value in the ‘coordinateUncertaintyInMeters’ column was also consulted during the manual check, as frequent specific high values indicated coordinates derived from centroids of grids or large administrative units. To eliminate the influence of spatial sampling bias and minimize spurious correlation between species occurrence and environmental conditions, we spatially thinned the refined data using the spThin package (Aiello-Lammens et al. 2015). A minimum distance threshold of 2.5 arc minutes was chosen, corresponding to the resolution of the environmental predictor rasters (~4.63 km). Of 24,068 records downloaded from GBIF and 1,440 of our own records for *D. graveolens*, 5,159 data points remained after the cleaning and thinning process and were prepared for use in modelling the species distribution.

Environmental predictors. – After the downscaling and calibration (bias correction) of future climate projection with WorldClim v2.1 (Fick & Hijmans 2017) as the baseline climate, 19 bioclimatic variables with a spatial resolution of 2.5 arc minutes were downloaded from WorldClim – Future Climate Data (<https://www.worldclim.org/data/cmip6/cmip6climate.html>). To approximate present-day conditions, we used the EC-Earth 3 climate projection (SSP370-based for 2021–2040) in the EC-Earth3-Veg configuration (Döscher et al. 2022), as the original WorldClim v2.1 baseline (1970–2000) no longer reflects current climate conditions. When selecting predictors, we proceeded with selection based on ecological relevance (Petitpierre et al. 2017). For a Mediterranean invasive and ruderal species such as *D. graveolens*, it was crucial to select factors that represent critical limiting mechanisms (cold tolerance, summer drought, thermal stress and seasonality) while avoiding multicollinearity (Merow et al. 2013). To minimize this problem of collinearity between bioclimatic variables and to ensure the interpretability of the resulting model, we applied a two-step filtering process. Multicollinearity was tested using Pearson’s correlation coefficient threshold ($|r| \geq 0.7$) and the variance inflation factor (VIF) by employing the usdm package (Naimi et al. 2014). This involved a stepwise elimination of variables until all remaining predictors had a $VIF < 5$. Predictors that met this threshold were graphically displayed on a correlation plot (Supplementary Fig. S3) using the corplot package (Wei & Simko 2024). Table 3 summarizes the selected bioclimatic variables and their relevance to the occurrence of the target species, *D. graveolens*. In the final model, we used five variables (Bio02, Bio06, Bio10, Bio15, and Bio19) and a combination of linear, quadratic, and hinge features.

Table 3. List of selected environmental predictors and their ecological significance for the target species.

Code	Bioclimatic variable name	Ecological significance
Bio02	Mean diurnal range	This expresses the typical daily temperature fluctuations in a given locality. It helps distinguish between coastal and more continental parts of the territory.
Bio06	Minimum temperature of coldest month	Reflects the risk of frost and cold stress that plants are exposed to during winter. In the Northern Hemisphere, it limits the northern and continental range boundary of Mediterranean species.
Bio10	Mean temperature of warmest quarter	Reflects thermal stress during the period with the highest temperatures. In the Northern Hemisphere, it limits the southern range boundary of Mediterranean species into semi-arid and arid regions.
Bio15	Precipitation seasonality	Expresses the uneven distribution of precipitation throughout the year, which is typical for the species' native range.
Bio19	Precipitation of coldest quarter	Reflects the amount of available winter moisture critical for seed germination and the survival of juvenile plants following the typical dry period in the species' native range.

Background points. – To address the problem of spatial sampling bias, we adopted a strategy of weighting the background points (Bias File), which is the recommended procedure for bias correction in MaxEnt models (Phillips et al. 2006). The weight raster was derived from the occurrence records of a reference set of invasive species that share similar sampling effort patterns (Fourcade et al. 2014): a closely related invasive species (*Dittrichia viscosa*), an invasive species spreading through the same corridors (*Erigeron canadensis*) and an invasive species colonizing ruderal habitats (*Ambrosia artemisiifolia*). These data were obtained from GBIF (period 1996–2025), cleaned and spatially thinned in an identical manner to the occurrence data of the target species. Of 580,188 input records, 61,372 records remained after the cleaning and thinning process. Of these, a record density raster was generated in QGIS with the same resolution of 2.5 arc minutes as the selected environmental predictors. This raster was used to weight the background points in the MaxEnt model, ensuring a more realistic distribution of points in the area of the sampling effort.

Model evaluation and parameters. The parameters for the global model were set using the replicate run type with cross-validation and five replications, 30,000 background points, a convergence threshold of 0.00001 and a maximum of 2,000 iterations. The test and training data were separated in a 25:75 ratio. Following several rounds of testing, we selected the most suitable combination of features and a low regularization multiplier value, specifically considering the marginal areas of the species' occurrence, which have a high potential for shifting in the future due to the species' invasive behaviour. This testing also highlighted the low permutation importance of Bio15, indicating that the information this variable provides for the main prediction within the niche center is almost entirely captured by another variable or a combination. However, its exclusion led to a decrease in the model's accuracy in the marginal areas, particularly on the eastern edge of the species' European range, suggesting that under these marginal conditions, Bio15 provides unique complementary information that the other variables do not. Therefore, we retained Bio15 in the model. Maintaining high sensitivity at the margins was crucial

to avoid underestimating the spread risk of this invasive species. Based on initial model tuning, the regularization multiplier was set to 0.5 to accurately capture these specific marginal conditions. The model converged in every run, with an average number of iterations of 852. The performance was evaluated using the area under the curve (AUC) and True Skill Statistic (TSS). To visualize the potential distribution of *D. graveolens*, the global model outputs were classified using a single average threshold value (Maximum TSS) to create three binary suitability maps.

All information regarding model execution, such as predictor response curves and data point maps after cleaning and thinning, is provided in Supplementary Data S1. To calculate the area of potential spread around roads with a 1-m buffer zone in Slovakia, the road transport network layer provided by the Slovak Road Administration (2025) was used.

Results

Distribution pattern of Dittrichia graveolens in the study area

In total, 1,440 detected occurrence points of the species were recorded on surveyed roads (826.45 km; Fig. 2, Supplementary Fig. S1) in Slovakia, the Czech Republic and Austria, where they occupied 419.93 km (50.81%). In Hungary, no occurrences were found in the studied segment of the motorway (Fig. 2, Table 2). In Slovakia, 1,157 occurrence points were obtained over 319.66 km (44.8% of the Slovak motorway surveyed). The highest proportion of data was found in the western part of Slovakia (1,065 occurrence points, 92.05%), and the incidence decreased towards the east (Fig. 2, Table 4).

Table 4. Total number of occurrence points of *Dittrichia graveolens* on roads surveyed in the individual countries and the entire study area (Total).

Country	Region	No. of occurrence points
Slovakia	western Slovakia	1,065
	central Slovakia	47
	eastern Slovakia	45
Czech Republic	–	248
Austria	–	35
Hungary	–	0
Total	–	1,440

The highest occurrence density was observed in motorway sections D1 Chocholná – Skala (129.2–130.8 km), D1 Skala – Nemšová (131.2–136.1 km) and D2 Bratislava, Viedenská road – Čunovo, Rajka state border between Slovakia and Hungary (65.6–74.5 km) (Fig. 2, Table 2). The species appeared to prefer altitudes up to 300 m a.s.l. (94.0% of records), with occurrence at higher altitudes rarely recorded (Supplementary Table S2).

In the Czech Republic, 248 occurrence points were found over 57.99 km, with the highest density occurring at D2 Břeclav – Hustopeče motorway (Fig. 2, Table 2). In Austria, 35 occurrence points were found over 42.30 km, with the highest occurrence on motorway section A4 (intersection A6/A4 – Fischamend; Fig. 2, Table 2). In both countries, the species was found at elevations up to 300 m a.s.l. (Supplementary Table S2).

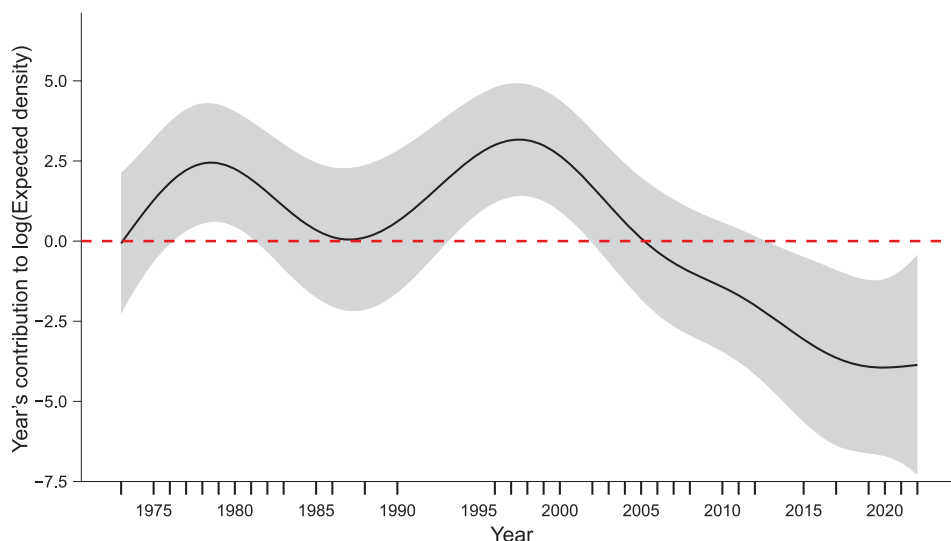


Fig. 3. Nonlinear relationship between the occurrence density of *Dittrichia graveolens* and the period of motorway section commissioning (YEAR). The partial effect of the smooth function $s(\text{YEAR})$ from the GAMM model (Negative Binomial distribution, random effect ROAD, controlling for coordinates X, Y) is displayed. The solid black line represents the estimated contribution to the logarithm of the expected density, the grey area represents the 95% confidence interval, and the horizontal dashed red line at 0.0 indicates a null contribution to the expected density.

GAMM showed that the relationship between the year of construction and the occurrence density of *D. graveolens* was highly statistically significant ($P < 0.001$) and strongly nonlinear ($\text{edf} = 6.62$). In the curve progression of the negative binomial model (Fig. 3), two periods of statistically significant positive contribution to density were clearly visible in older road sections, specifically in 1976–1981 and 1996–2002. Conversely, the newest sections after 2012 had a statistically significantly lower density compared to the overall average. The use of a mixed model for nested data was essential, as significant differences in occurrence density were observed between individual motorways ($\text{std. dev.}_{\text{Road}} = 1.982 > \text{residual std. dev.} = 0.413$). A key issue was also the uneven distribution of motorways, which are mainly concentrated in western Slovakia, a fact confirmed by the model showing a highly significant spatial effect ($P < 0.0001$).

Distribution prediction

The global distribution model of *D. graveolens* under the climatic conditions of the SSP370 scenario for 2021–2040, created using the MaxEnt algorithm, demonstrated a high predictive power with an AUC of 0.8447 ± 0.004 , signalling very good performance (Araújo et al. 2005) and an overall good to very good accuracy, as confirmed by a TSS of 0.6120 (Allouche et al. 2006). The resulting global model is shown on the map (Fig. 4). The sensitivity (0.9251) and specificity (0.6869) metrics reflected our intention that the model was optimized with an emphasis on minimizing the overlooking of true occurrences.

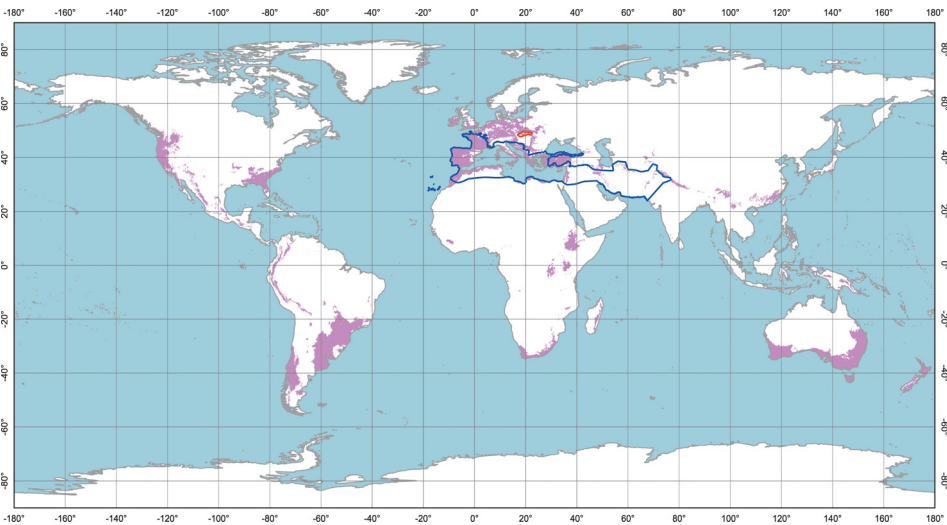


Fig. 4. Potential distribution of *Dittrichia graveolens* in the world based on the MaxEnt model. Areas with high climatic suitability (pink colour) are defined by the maximum TSS threshold and represent the predicted presence of the species for 2021–2040 (ssp3). The boundary of the native range (blue line) is shown according to Lustenhouwer & Parker (2022). The border of Slovakia is marked in red.

In terms of environmental factors, the species’ distribution was primarily constrained by winter temperatures. The variable minimum temperature of the coldest month (Bio06) was the dominant limiting factor (Table 5), with the highest contribution (35%) and an extremely high permutation importance (61.8). This confirmed that this variable had the most unique information about the ecological limits of the species, which were related to its frost sensitivity. Secondary constraints were represented by the mean temperature of the warmest quarter (Bio10) and precipitation of the coldest quarter (Bio19).

Table 5. Importance of environmental variables used in the final MaxEnt model.

Variable Description		Importance of variables in the final MaxEnt model	
		Percent contribution	Permutation importance
BIO02	Mean diurnal range (mean of monthly (max temp – min temp))	4.9	4.0
BIO06	Minimum temperature of the coldest month	35.0	61.8
BIO10	Mean temperature of the warmest quarter	15.0	18.3
BIO15	Precipitation seasonality	27.4	0.1
BIO19	Precipitation of the coldest quarter	17.7	15.8

The response curve for Bio06 (Supplementary Data S1) showed that the distribution of *D. graveolens* was strongly constrained at the cold end of the temperature gradient. The probability of occurrence was zero at temperatures below –15 to –10 °C. Maximum climatic suitability was achieved in a relatively narrow range, particularly at temperatures between 5 and 12 °C, while a flatter phase of the curve was observed in the range of –3 to 1 °C.

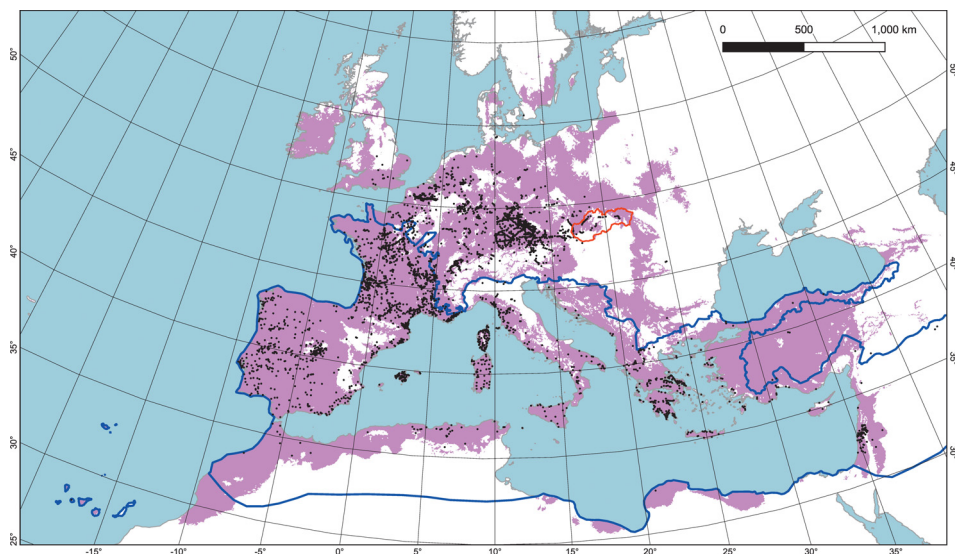


Fig. 5. Potential distribution of *Dittrichia graveolens* in Europe based on the global MaxEnt model. Areas with high climatic suitability (pink colour) are defined by the maximum TSS threshold and represent the predicted presence of the species for 2021–2040 (ssp3). The boundary of the native range (blue line) is shown according to Lustenhouwer & Parker (2022). Black dots show the occurrence records from GBIF and our own occurrence points used in the model. The border of Slovakia is marked in red.

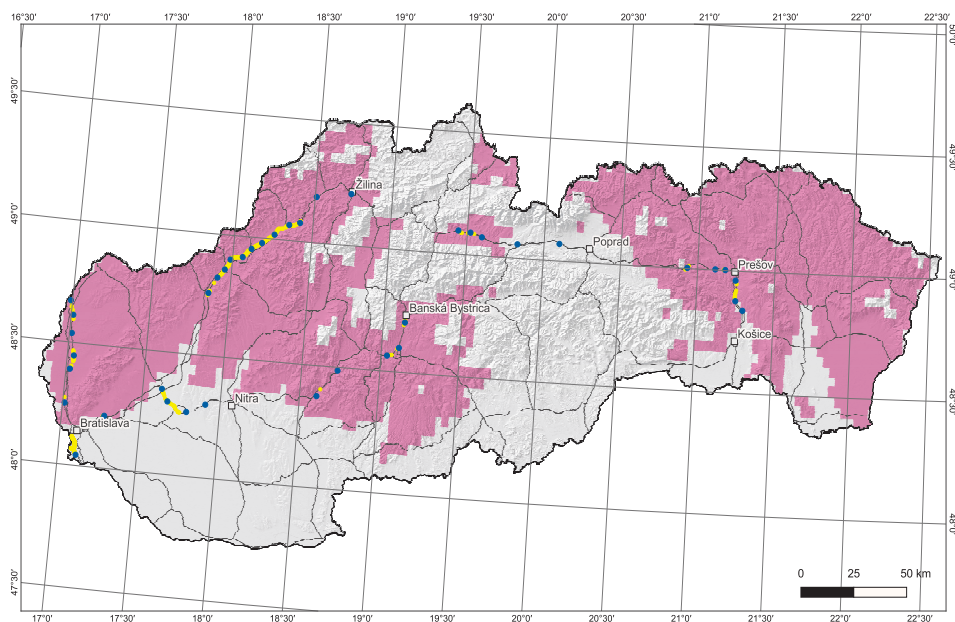


Fig. 6. Potential distribution of *Dittrichia graveolens* in Slovakia based on the global MaxEnt model. Areas with high climatic suitability (pink colour) are defined by the maximum TSS threshold and represent the predicted presence of the species for 2021–2040 (ssp3). Blue dots show our own occurrence points used in the model (after the thinning process), and the yellow dots show our other occurrence points not used in modelling.

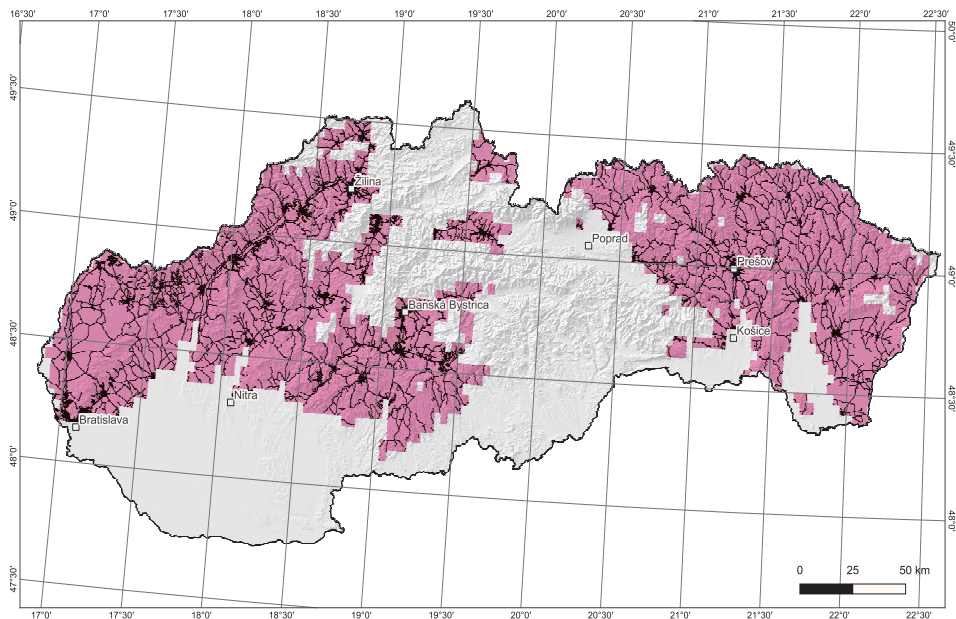


Fig. 7. Map of the road network of all categories (motorways and roads of I, II, III class – roads are classified according to Slovak Road Administration 2025) in suitable areas (pink colour) for the occurrence of the species *Dittrichia graveolens* in Slovakia in 2021–2040 (ssp3).

The response curve for Bio10 (Supplementary Data S1) showed that optimal conditions occurred in areas with a mean temperature of the warmest quarter of 25–28 °C, with the curve exhibiting a slightly flatter part at 19–23 °C. Regarding Bio19, the third bioclimatic variable with the highest permutation importance, the response curve (Supplementary Data S1) showed that sufficient precipitation in the coldest quarter was important for high climatic suitability, whereas suitability was almost zero at values below 50 mm.

The first map represented the worldwide distribution (Fig. 4), reflecting the potential niche of the species and identifying the main global areas at risk of invasion. Narrowing our focus to Europe (Fig. 5), the projection provided a detailed assessment of the invasive potential across the continent. Most importantly, the third map, specifically focusing on the territory of Slovakia (Fig. 6), provided the finest resolution essential for future detailed monitoring. The areas within the territory of Slovakia designated as climatically suitable by the Maximum TSS threshold for 2021–2040 covered more than 24,000 km². However, considering that the species' spread has thus far been concentrated only on the immediate edges of existing roads and using a 1-m bilateral marginal zone to calculate the area of potential spread, the species had the potential to occupy 33.0 km² in these climatically suitable areas along the road verges. This area represents 0.07% of the total area of Slovakia (Fig. 7). Based on these results, its expansion was predicted in many new localities, such as the Turčianska kotlina Basin between the towns of Vrútky – Martin – Turčianske Teplice and the road verges in Trenčín – Prievidza – Žiar nad Hronom – Zvolen – Brezno – Detva. In the eastern part, this includes Levoča – Prešov – Humenné – Michalovce and Kežmarok – Stará Ľubovňa – Bardejov – Svidník – Vranov and Topľou.

Discussion

*Current distribution of *Dittrichia graveolens* along motorways*

Our results revealed the massive spread of *D. graveolens* in Slovakia compared to 2014 (Király et al. 2014). It has been recorded exclusively along motorways and has not yet penetrated into natural habitats. Our findings indicate a significant association between the operational age of the motorway and species density. Rather than a continuous linear increase, the highest densities occurred on specific older road sections (Fig. 2, Table 2), while significantly lower densities were observed on the newest sections built after 2012 (Fig. 3), which may be related to a shorter colonization period.

In Austria, it was first recorded in 2001 in the western part of the country (Hohla 2001). By 2007, it had also spread to the eastern part (Raabe 2008), where our study confirmed a substantial spread within less than 20 years since the first record (Fig. 2, Table 2). In the Czech Republic, the species was already widespread in 2008 (Raabe 2009); therefore, detection of dense occurrence of this species along the motorway bordering Slovakia was expected (D2 motorway; Fig. 2, Table 2). Currently, most occurrences in the Czech Republic are documented along the D1, D2, D5, D11, D46, D48 and D55 motorways (Chytrý et al. 2021). We did not record any *D. graveolens* individuals in Hungary (motorway M15), probably due to the short length of the monitored section (Supplementary Fig. S1). The first records in Hungary, near the cities of Győr (Takács et al. 2016) and Szombathely (Schmidt 2019), involved only single individuals. Despite the initial assumption that a rapid invasion along Hungarian motorways did not occur (Schmidt 2019), a large population (several thousand individuals) was discovered in 2020 near Hegykő (Király & Takács 2020), and the occurrence was observed near the Csorna bypass (Schmidt & Haszonits 2021).

Drivers of potential distribution and of spread

In view of our results, which are consistent with the work of Raabe (2008), Frajman & Kaligarič (2009) and others, we consider intensive traffic, together with the species' morphological and reproductive characteristics (Wróbel & Nobis 2017, Kozłowska-Kozak et al. 2019), as the key factors in the spread of the species. In studied areas, the populations of *D. graveolens* successfully survive in dividing strips and along the edges of roads up to ~1 m from the edge, a phenomenon reported also from Germany, Austria and the Czech Republic (Raabe 2008, 2009, Šajna et al. 2017, Kaplan et al. 2018). These habitats are strongly affected by salting (chemical de-icing), with soil salinization decreasing with the distance from the road. Simultaneously, they provide the species with sufficient light, which confirms its heliophilous nature (Brownsey et al. 2014). The tolerance of *D. graveolens* to soil salinity is one of its main competitive advantages, enabling it to survive and spread along road corridors (Grašič et al. 2016).

The species prefers gravelly to sandy habitats (Kaplan et al. 2018, Pyšek et al. 2022), which are typical for road edges. In the study area, the species successfully establishes and persists on gravel substrates along roadsides and readily colonizes newly exposed gravel surfaces of road constructions and disturbed soils of reconstructed sections (e.g. during guardrail replacement).

Despite the current knowledge of the preferential spread of *D. graveolens* along roads, the risk of this species spreading into natural populations due to its reproductive characteristics and invasive potential must be considered (Brownsey et al. 2013, 2014, Melen et al. 2024). This phenomenon has been observed, for example, with *Geranium purpureum* Vill. in Belgium (Verloove 2000) and Slovakia. *Geranium purpureum* initially spread in synanthropic populations on railroad station grounds. Since 2024, it has been recorded in natural habitats in Slovakia (P. Meredfa, personal communication; P. Eliáš Jr., personal observation). The legitimate concern about the spread of *D. graveolens* to native habitats was confirmed by findings in California, where the species massively invaded grazed pastures, wetlands and riparian floodplains (Brownsey et al. 2013). It has also been recorded on sandy-gravelly substrates on natural riverbanks in Chile (Santilli et al. 2021), which corresponds to its natural habitat in the native distribution area (Rameau et al. 2008). Its potential invasion into natural communities would pose a threat to biodiversity and health risk to humans and livestock – *D. graveolens* seeds cause dermatitis in humans and enteritis in sheep and cattle (Philbey & Morton 2000, Thong et al. 2008).

In our modelling approach, we intentionally prioritized high sensitivity to minimize the risk of overlooking true occurrences. This optimization is crucial for assessing invasive plants at the expanding margins of their ranges (Jiménez-Valverde et al. 2011). While this approach inevitably results in a compromise regarding lower specificity, we do not consider this a model error. Rather, it reflects the prediction of a wider potential niche, capturing areas that are climatically suitable but have not yet been colonized (Peterson 2003). Consequently, the model effectively highlights regions at the greatest risk for future spread. At the continental scale, our European projection (Fig. 5) provides a detailed assessment of this invasive potential, confirming the presumed migration corridors extending outward from the boundary of the species' native range (Lustenhouwer & Parker 2022).

The modelled response curves clearly reflect the ecological limitations and invasive potential of *D. graveolens*. The zero probability of occurrence at extreme negative temperatures (Bio06) suggests that the species is highly sensitive to prolonged or extreme frost. This, similar to many other species of Mediterranean origin (García-Plazaola et al. 2003, Walther et al. 2005), effectively defines the northern and mountainous limits of its range.

While maximum climatic suitability aligns with conditions typical for coastal and Mediterranean areas (mild winters of 5–12 °C and hot summers of 25–28 °C), the species exhibits a broader tolerance that facilitates its spread into central Europe. Specifically, the observed tolerance to mild frost (–3 to 1 °C) and warmer central-European summers (19–23 °C) corresponds directly to the conditions found in regions of Slovakia, particularly in the southern lowland and hilly tiers, where the species is currently present. The ability to survive under these conditions, coupled with climate change, gradually opens the door for the species to move deeper into moderately continental areas. This trend strongly aligns with the well-documented phenomenon where climate warming relaxes historical cold-temperature constraints, explicitly facilitating the poleward and inland expansion of thermophilic alien species into temperate Europe (Walther et al. 2009).

Furthermore, its strict requirement for sufficient winter precipitation (Bio19) confirms that *D. graveolens* does not tolerate extremely dry winters, effectively limiting its spread into desert or dry subtropical regions. However, in temperate and moderately continental regions with sufficient moisture, the species has demonstrated a rapid expansion of its climatic niche during its invasion (Lustenhouwer & Parker 2022).

Management implications

Although the rapid-spreading ability of *D. graveolens* (e.g. by wind, human activities, and its capacity to thrive in competitively disturbed habitats; Parsons 1973, Brownsey et al. 2013, Grašič et al. 2016) makes it difficult to control, its early detection and continuous management are crucial to prevent further spread and to minimize its ecological impact. According to Brownsey et al. (2014), to determine effective management measures for the species, it is necessary to rely on its reproductive biology. This would determine the appropriate timing for mowing grass and herbaceous vegetation on roadsides and embankments. Because the flowering period of this species extends from summer to fall, mowing in the fall could accelerate its spread (Seybold 1994).

Supplementary materials

Data S1. Additional data on MaxEnt modelling setup and results.

Fig. S1. Map of the motorway network in Slovakia and adjacent areas.

Fig. S2. *Dittrichia graveolens* population along the D2 motorway between the city of Bratislava and the town of Malacky.

Fig. S3. Matrix displaying the Pearson correlation coefficient between pairs of selected bioclimatic variables.

Table S1. List of occurrence points of *Dittrichia graveolens* along motorways in Slovakia, the Czech Republic and Austria, obtained from the car survey.

Table S2. Distribution of occurrence points of *Dittrichia graveolens* based on altitude.

Supplementary materials are available at <https://www.preslia.cz>

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Invaze *Dittrichia graveolens* podél dálnic na Slovensku a predikce dalšího šíření

Tato studie mapuje rozšíření, ekologické faktory a invazní potenciál druhu *Dittrichia graveolens* podél slovenských dálnic a v přilehlých regionech. Druh je zatím omezen především na dálniční krajnice (1440 výskytů), s nejvyšší koncentrací na západě země, obdobná je situace v Česku a Rakousku. Klíčovým zjištěním je nelineární vztah mezi stářím dálnice a hustotou invaze. Nejstarší úseky (postavené v 70.–90. letech 20. století) vykazují největší výskyt, zatímco nové úseky (postavené po roce 2012) jsou výrazně méně zasaženy. Modelování pomocí programu MaxEnt (scénář SSP370) identifikovalo potenciální výskyt na 33,0 km² v blízkosti dálnic. Primárním limitujícím klimatickým faktorem je minimální teplota nejchladnějšího měsíce (Bio06), která omezuje rozšíření do vyšších nadmořských výšek a v severním směru. Projekce naznačují výrazný potenciál pro další expanzi na východ podél dopravních koridorů, kterou podporuje probíhající oteplování klimatu. Dálniční krajnice fungují jako kritické koridory pro šíření. Jejich správa, zejména včasná detekce a cílené ošetřování s ohledem na fenologii druhu, je klíčová pro zamezení další expanze druhu *D. graveolens*.

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