Ambrosia artemisiifolia in the Czech Republic: history of invasion, current distribution and prediction of future spread

Ambrosia artemisiifolia v České republice – historie invaze, současné rozšíření a predikce dalšího šíření

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We analyse the dynamics of invasion of *Ambrosia artemisiifolia* (common ragweed), one of the most noxious invasive species in Europe with a great impact on human health. We investigate the habitats and factors that shape its current distribution and specify areas in the Czech Republic endangered by the further spread of this species. The analysis is based on a total of 281 records in 164 grid cells, recorded up to 2016, of which 37 harbour naturalized populations and 127 casual populations. The majority of records (49%) was from railway corridors, followed by human settlements (11%), and there was a recent increase in records from roadsides. A conditional inference tree revealed factors shaping the species distribution with the effect of the proportional area of industrial, commercial and transport units as the most important, highly significant variable, further fine-tuned by factors related to human-related dispersal and climate, such as density of railway network and temperature, respectively. The prediction model indicated that many suitable grid cells are unoccupied. Many of these grid cells are in the proximity of currently occupied ones but there are also some cells rather far from current populations. Further spread of *A. artemisiifolia* in the Czech Republic is thus highly probable.

Keywords: common ragweed, Czech Republic, environmental factors, plant invasion, predicted spread, species distribution modelling (SDM)

Introduction

Predicting the future distribution of alien plants and the role that specific pathways and drivers are likely to play in this process in the context of the ongoing global climate change are among the highest priorities of invasion biologists and managers (e.g. Thuiller et al. 2005, Gallien et al. 2010, Essl et al. 2015a, Uden et al. 2015). Understanding the drivers that influence the spatiotemporal patterns in plant invasions is a crucial step in limiting their spread and minimizing their negative impact (Ewel et al. 1999, Sakai et al. 2001, Pyšek & Hulme 2005). This is especially true for rapidly spreading species that have a great impact on native biodiversity and human health (Pyšek & Richardson 2010, Essl et al. 2015b, Pergl et al. 2016). However, the relative influence of individual drivers, such as human-mediated disturbance and changing climate, is unknown for most invasive

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plants and hence limits the effectiveness of risk assessments and adaptive management (Uden et al. 2015).

Ambrosia artemisiifolia L. (common ragweed) is an annual herbaceous plant that originates from North America and is one of the most noxious invasive species in Europe (Lambdon et al. 2008, DAISIE 2009) mainly because it produces large quantities of allergenic pollen (Kazinczi et al. 2008) and causes up to 80% loss in the yield of certain crops (Essl et al. 2015b). It is strongly self-incompatible with high outcrossing rates (see Essl et al. 2015b and the references herein). The species only reproduces by seed, with an average of 1213 seeds per plant reported for the Czech Republic (Moravcová et al. 2010), and between 18,000 and 48,000 (with an extreme value of 94,900) for Hungary (Essl et al. 2015b). Most seed falls within 1 m of the mother plant (Essl et al. 2015b). Seed dispersal by mammals and birds is reported in its native range (Rosas et al. 2008), but there is little evidence of seed dispersal by animals in Europe (Bullock et al. 2012). Dispersal of seeds by water is uncommon (Fumanal et al. 2007). The long-distance seed dispersal is primarily through human activities; either directly by the transport of contaminated litter or soil, or indirectly as a contaminant of agricultural products (e.g. crops and bird feed) or agricultural and construction machinery that is then inadvertently distributed along transport corridors (see Bullock et al. 2012 and the references herein). *Ambrosia artemisiifolia* forms a persistent seed bank in soil and is able to germinate after 40 years (Darlington 1922). Seed dormancy is broken by low (winter) temperatures under wet conditions (Willemsen 1975, Baskin & Baskin 1987, Fumanal et al. 2006).

Ambrosia artemisiifolia was originally introduced into Europe in the 18th century through botanical gardens (DAISIE 2009, Bullock et al. 2012), and then repeatedly as a contaminant of agricultural products from North America (Brandes & Nitzsche 2006, Chauvel et al. 2006). The species began to spread and naturalize within Europe from the 1930s, these processes accelerated from the 1960s and since the 1990s there has been a rapid spread and increase in abundance of local invasive populations (Essl et al. 2015b). The largest, recently-recorded European populations are on the Pannonian Plains of Hungary and in Croatia, Serbia and Ukraine (Essl et al. 2015b). In Russia, naturalized populations are recorded in 10 regions in the GloNAF global database of naturalized alien floras (van Kleunen et al. 2015), ranging from the western part of the country eastwards to Khabarovsk. A considerable increase in abundance is also recorded in southern and central France, in particular along the Rhône valley and on the plains of northern Italy (Chauvel et al. 2006, Essl et al. 2015b). It is predicted that it will spread further in Europe, favoured by ongoing global warming; the species is assumed to benefit from warmer summers and absence of late autumn frosts (Cunze et al. 2013, Richter et al. 2013a, Chapman et al. 2014, Storkey et al. 2014, Leiblein-Wild et al. 2016). In contrast, some regions, especially in the south, are predicted to become unsuitable due to the increase in the incidence of summer droughts and temperature (Jacob et al. 2013).

As local scale variation in soil characteristics and anthropogenic factors are thought to interact with the effect of climate change on the distributions of plant species (Stratonovitch et al. 2012, Guo et al. 2013), not only climate needs to be taken into account when predicting the future spread of *A. artemisiifolia*. However, factors other than climate are investigated only occasionally and over a limited area in analyses of *A. artemisiifolia* distribution. Besides climatic factors, landscape variables explain the current distribution of *A. artemisiifolia* in Austria (Essl et al. 2009) and soil characteristics, position within a field and crop type and cover in arable fields in Hungary (Pinke et al. 2011, 2013).

To extend the knowledge about the occurrence and distribution of *A. artemisiifolia* in Europe, and demonstrate that such information can be used to predict future trends, we analyse records from the Czech Republic. In this country the species was first reported in 1883 (see Pyšek et al. 2012a, b), with early records originating from agricultural fields in the southern and western part of the country where it was probably introduced with contaminated seeds. The first record from Moravia, the eastern part of the country, was reported in 1948. The species was sometimes cultivated in botanical gardens (Jehlík 1998). The number of records (see Pyšek et al. 2012a for a detailed account of the situation in the Czech Republic) has been rapidly increasing since the second half of the 20th century (Williamson et al. 2005). However, the factors that have facilitated its invasion in the Czech Republic are unknown and need to be understood if future risks are to be identified and effective management strategies developed to reduce the spread and impact of this species.

In this paper we address the following questions: (i) What were the pathways of invasion by *A. artemisiifolia* in the Czech Republic and do the invasion dynamics of this species differ in different habitats? (ii) What is the proportion of sites with casual versus naturalized populations, and under what conditions are the former likely to progress into the latter? (iii) Which climatic and landscape factors shape the current distribution of this species? (iv) Which parts of the Czech Republic are likely to be colonized by *A. artemisiifolia* in the future?

Materials and methods

Study area

The Czech Republic, a central-European country with an area of 78,864 km^2 and population of 10.6 million, is prone to invasions by plants due to its position on the crossroads of many natural and human-created migration routes, which provide dispersal opportunities and pathways. In addition, a heterogeneous landscape and long history of human influence provides a variety of disturbed sites that are suitable for establishment of alien plants (see Pyšek et al. 2012a for details). These features, together with a strong botanical tradition, make the country a suitable model for studying and predicting regional patterns in plant invasions (Pyšek et al. 2002, 2012a, b, Chytrý et al. 2005, 2009).

Data collection

Botanical records of *A. artemisiifolia* in the Czech Republic up to July 2016 were collected from various sources: Czech National Phytosociological Database (Chytrý & Rafajová 2003); Species Occurrence Database held by the Nature Conservation Agency of the Czech Republic (http://www.ochranaprirody.cz); a database of the distribution of vascular plants in the Czech Republic (FLDOK, Štepánek unpubl.); public and private herbaria; other literature sources and unpublished records (e.g. Williamson et al. 2005). The records (281 in total) were, based on their location, assigned to nine types of habitat: arable fields; countryside (unmanaged sites in open landscape where the species occurs, such as ponds and river banks, pedestrian paths, seminatural grasslands); industrial areas; other agricultural areas; railways; river harbours; roads; settlements; and others) and to 5' × 3' grid cells (longitude × latitude, ~32 km^2 at 50° northern latitude) of KFME (Kartierung der Flora Mitteleuropas of 2551 cells for the Czech Republic; Schönfelder 1999). Cells were further categorized according to the stage in the invasion process that best represented the *A. artemisiifolia* record(s) (Richardson et al. 2000, Blackburn et al. 2011): (i) naturalized, for grid cells with a population of more than 50 individuals or records for at least 5 years or at least 5 sites, or records for 3–4 years and 3–4 sites, (ii) casual, for grid cells that did not meet the above criteria, or the population size and other details are unknown, (iii) absence. Each cell was characterized by climatic data and anthropogenic variables such as density of transport corridors and land use (Electronic Appendix 1).

Data analysis

Analysis of covariance (ANCOVA) was used to test the difference in the cumulative number of *A. artemisiifolia* records for particular habitats, with year as a covariate. The data was log-transformed to meet the assumptions of the analysis and the models were further checked and confirmed by diagnostic plots.

Decision tree models, which are also known as classification and regression trees (Breiman et al. 1984, De'ath & Fabricius 2000), were used to identify the most important predictors for the presence of *A. artemisiifolia* in individual 5' × 3' grid cells within the Czech Republic. As a non-parametric statistical method, decision tree models can handle data with a non-normal distribution, mixed types of data and non-linear relationships, and the results from the models are easy to interpret (Breiman et al. 1984, De'ath & Fabricius 2000, Pinke et al. 2011). To compensate for the overfitting of traditional decision tree models, the conditional inference tree implements a permutation test at each split to statistically determine when the model should stop (Hothorn et al. 2006, Strobl et al. 2009). The conditional inference tree was constructed with the ctree function in the party package (Strobl et al. 2009) in R (version 3. 2. 5, R Core Team 2016).

Species distribution modelling (SDM) was used to assess the likelihood of *A. artemisiifolia* occurring in the Czech Republic under current conditions. SDMs develop statistical connections between known presence of the species and environmental variables, and they can then map the connections to geographical space (Elith & Leathwick 2009). SDMs are frequently used in predicting hotspots of rare and endangered species and the potential spread of invasive species (Thuiller et al. 2005). Grid cells harbouring populations classified as casual and/or naturalized were counted as presence. We used pseudo-absence data randomly selected from all absence grid cells. Two pseudo-absence datasets with 200 absences for each dataset were generated. We used an ensemble method to overcome the variability in SDM models and maximize the usefulness of the multiple models (Araújo & New 2007). Seven modelling algorithms were used in the ensemble procedure: artificial neutral network (ANN), classification tree analysis (CTA), generalized boosting model (GBM), generalized linear model (GLM), maximum entropy (Maxent), multiple adaptive regression splines (MARS) and random forest (RF). All models were calibrated via 10-fold cross-validation by randomly splitting the data into two subsets: training data (70%) and test data (30%). The default settings of each model were used.

Two evaluate measures, TSS (Allouche et al. 2006) and AUC (Fielding & Bell 1997, Phillips & Dudík 2008), were calculated. Models with TSS greater than 0.5 and ROC larger than 0.8 were included in the ensemble models (Allouche et al. 2006, Phillips & Dudík 2008, Thuiller et al. 2009). All SDMs and ensemble models were constructed using the BIOMOD2 package (Thuiller et al. 2009, 2012) in R (R Core Team 2016). The suitable habitat maps were presented in ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, CA).

Results

Total number of records and frequency in different habitats

The first two records of *A. artemisiifolia* in the Czech Republic (both in 1883) were followed by a lag phase. It was not until the 1950s that a rather sharp increase in the number of records and occupied grid cells occurred (Fig. 1). The first grid cell with a naturalized population was recorded in 1962, and the number of such grids increased dramatically after 2005. Up to 2016 there were a total of 281 records in 164 grid cells. Of these grid cells, 37 harboured naturalized populations and 127 harboured casual populations.

Despite the first records coming from arable fields, the number of records in this type of habitat increased rather slowly (Fig. 2). About half of the records are from railway corridors, both historically and currently (49% of all records). Human settlements are the second most frequently colonized habitat (11% of all records). Another trend is the very recent increase in the cumulative number of records from roadsides (Fig. 2). However, the regression slopes of the cumulative records by year for railway corridors, settlements and roadsides do not differ significantly (Electronic Appendix 2), indicating that the rate of spread of *A. artemisiifolia* over time in these habitats was similar.

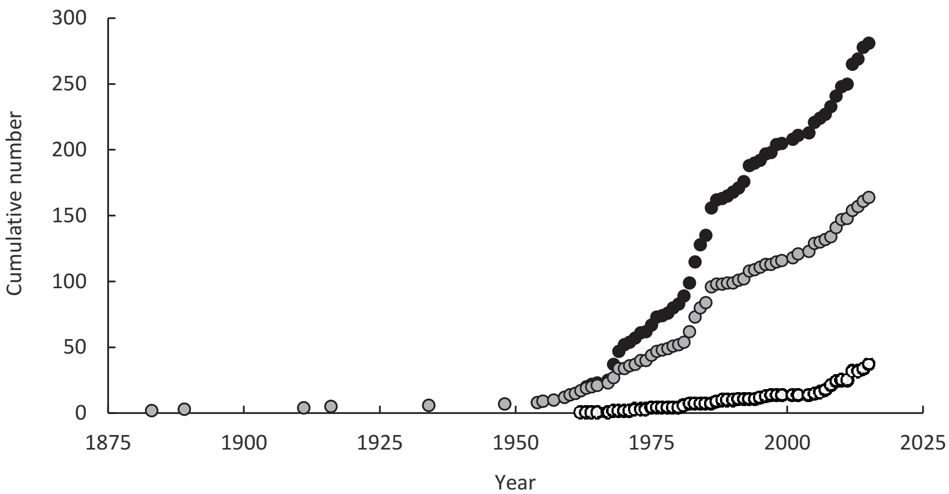

Fig. 1. – Cumulative number of ● records, ● occupied grid cells and ○ grid cells with naturalized populations (i.e. with populations of more than 50 individuals or records for 5 or more years; or records from 5 sites or more within the cell; or records from 3–4 years and from 3–4 sites within a cell) of *Ambrosia artemisiifolia* in the Czech Republic since the first record up to 2016.

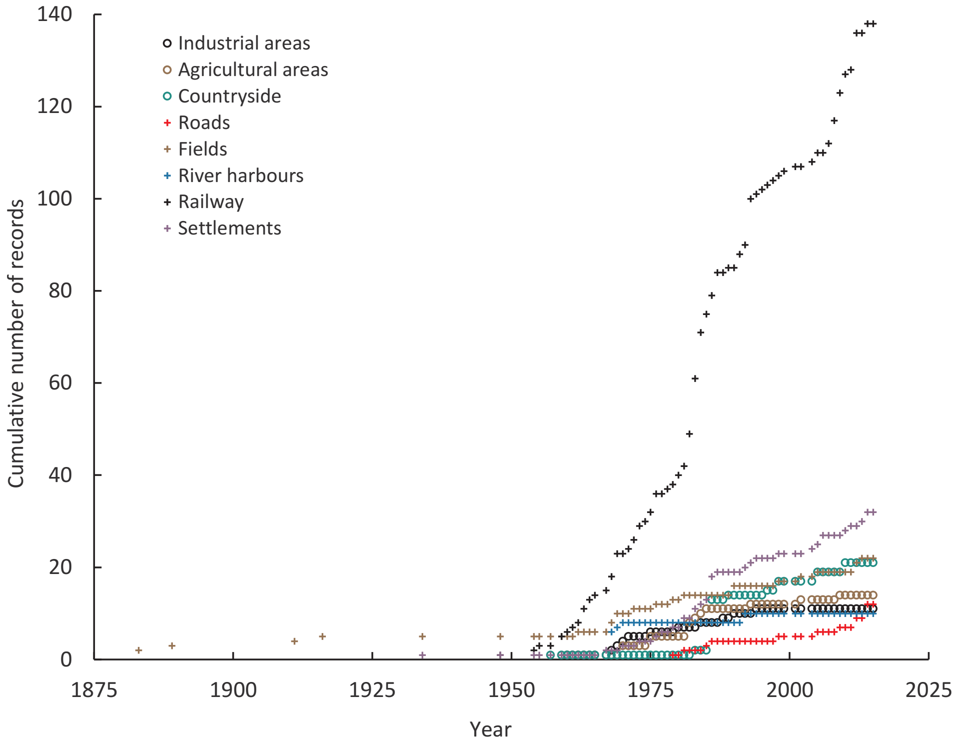

Fig. 2. – Cumulative number of records of *Ambrosia artemisiifolia* from particular habitats in the Czech Republic up to 2016.

Factors shaping the distribution of Ambrosia artemisiifolia

A conditional inference tree identified the proportion of industrial, commercial and transport areas within cells as the strongest predictor of *A. artemisiifolia* presence (Fig. 3, Electronic Appendix 3). *Ambrosia artemisiifolia* is highly likely to be present in grid cells with more than 3.1% of their area covered by this type of habitat. The pattern is fine-tuned by the relative influence of other covariates; regardless of the proportion of industrial, commercial and transport areas, grid cells with a high density of railway network are more likely to harbour *A. artemisiifolia* populations than those with fewer railways. Another important influence on whether populations remain as casual or become naturalized is the annual temperature. Populations in grid cells with a mean annual temperature above 9.4 °C and dense railway networks, or mean temperatures above 9.1 °C and moderately dense rail networks in areas with less than 30% of agricultural landscapes, are likely to become naturalized. Populations in grid cells below these thresholds are likely to be casual occurrence(s) (Fig. 3).

Within grid cells where the proportional area of industrial, commercial and transport units are below 3.1% and the railway network is sparse, there is an extremely low probability of the occurrence of *Ambrosia* if the total length of water streams and January

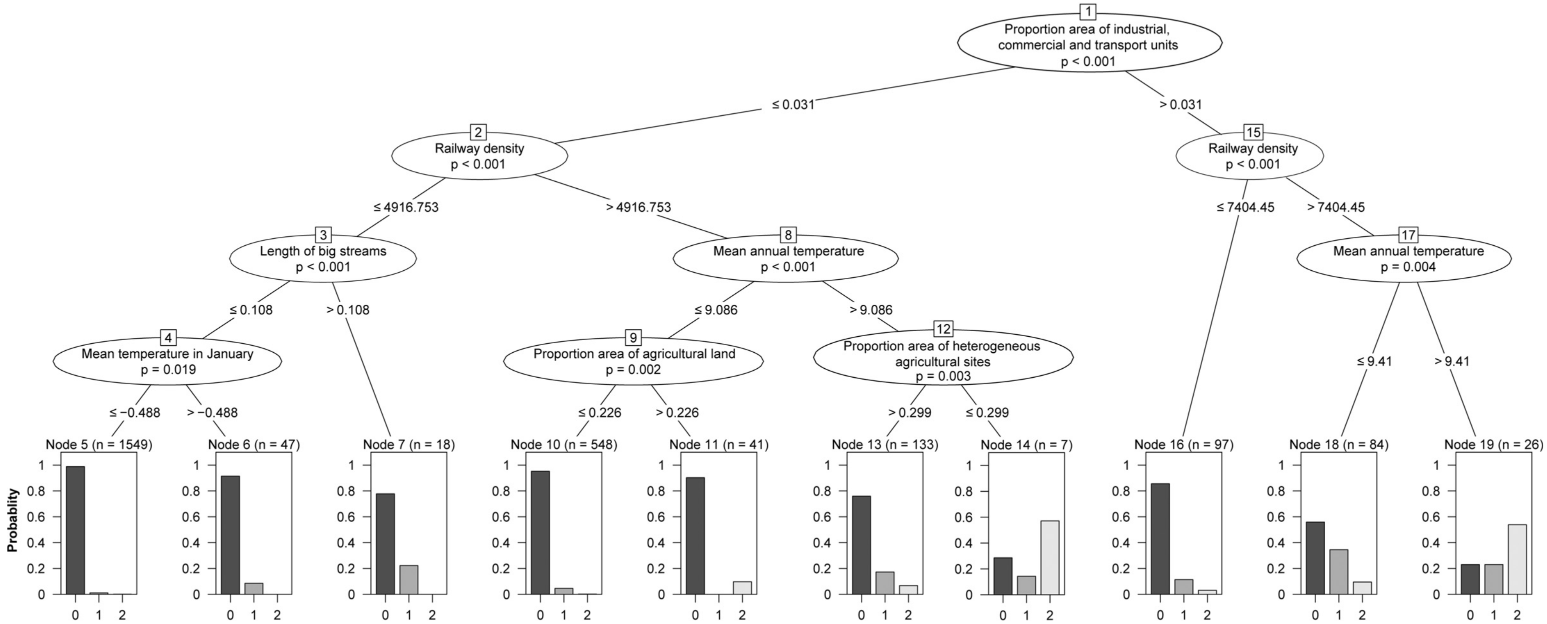

Fig. 3. – Factors shaping the distribution of *Ambrosia artemisiifolia* in the Czech Republic, identified using a conditional interference tree. The variables in ovals split the grid cells with different categories of occurrence (0 – absence; 1– casual occurrence; and 2 – naturalized populations). P-values were derived from a Bonferroni-corrected significance test; the numbers of observations (n) are given at each terminal node. The y axis is the probability of a grid cell belonging to the given category of occurrence, and the inside bars indicate the proportions of observations in the individual occurrence categories. The numbers in squares indicate the order of nodes.

temperature are low (Fig. 3). Moreover, the proportion of industrial, commercial and transport area below 10.2%, in combination with low density of railways, results in zero probability of harbouring naturalized populations (Electronic Appendix 3). As a result, most *A. artemisiifolia* populations, especially naturalized ones, are recorded along the Labe river (eastern, northern and central Bohemia), south-east of Brno (southern Moravia) and close to the town of Ostrava (north-eastern Moravia and Silesia) (Fig. 4).

Potential distribution of Ambrosia artemisiifolia in the Czech Republic

The prediction model (Fig. 5) revealed more than half of the country (56% of grid cells; Table 1) is of very low suitability for *A. artemisiifolia*. However, the model also indicates that many grid cells with suitable conditions are currently unoccupied; more than half of those with the most suitable conditions are not colonized, and only about one quarter of these cells host naturalized populations. Many unoccupied grid cells in close proximity to occupied cells were assessed as having a high suitability (Fig. 5). This suitability is especially true for cells in northern, central and eastern Bohemia along the Labe river, in eastern Moravia along Morava and Odra rivers, in northern and central Bohemia in the surroundings of big cities such as Ústí nad Labem and Prague, respectively, and in north-eastern and southern Moravia in the surroundings of Ostrava and Brno. However, some highly suitable cells are rather far from currently occurring populations, especially those in western Bohemia along the Ohře river and west of the city of Plzeň, and also in southern Bohemia close to České Budějovice. In contrast, suitable cells that are far from currently occurring populations are rather rare in Moravia.

Table 1. – Percentage of grid cells in the Czech Republic within individual probability categories as revealed by the prediction model, percentage of cells within the categories that are occupied by *Ambrosia artemisiifolia* and percentage of cells with naturalized populations.

Occurrence probability category	% total cells	% occupied	% with a naturalized population
0.04–0.2	56.3	0.3	0.1
0.2–0.4	17.1	3.9	0.0
0.4–0.6	14.1	8.1	0.6
0.6–0.8	5.0	24.6	6.4
0.8–0.94	7.5	43.5	15.7

Discussion

Total number of records and frequency in particular habitats

Ambrosia artemisiifolia was first recorded in the territory of the present-day Czech Republic in the same year as it was in the territory of the present-day Austria (Essl et al. 2009). However, the rate of spread in the Czech Republic was considerably slower than in Austria. Despite the countries being of comparable size, the current number of records and occupied grid cells in the Czech Republic is only about 40% of those recorded in Austria up to 2009 (Essl et al. 2009). Although it is not possible to make a detailed

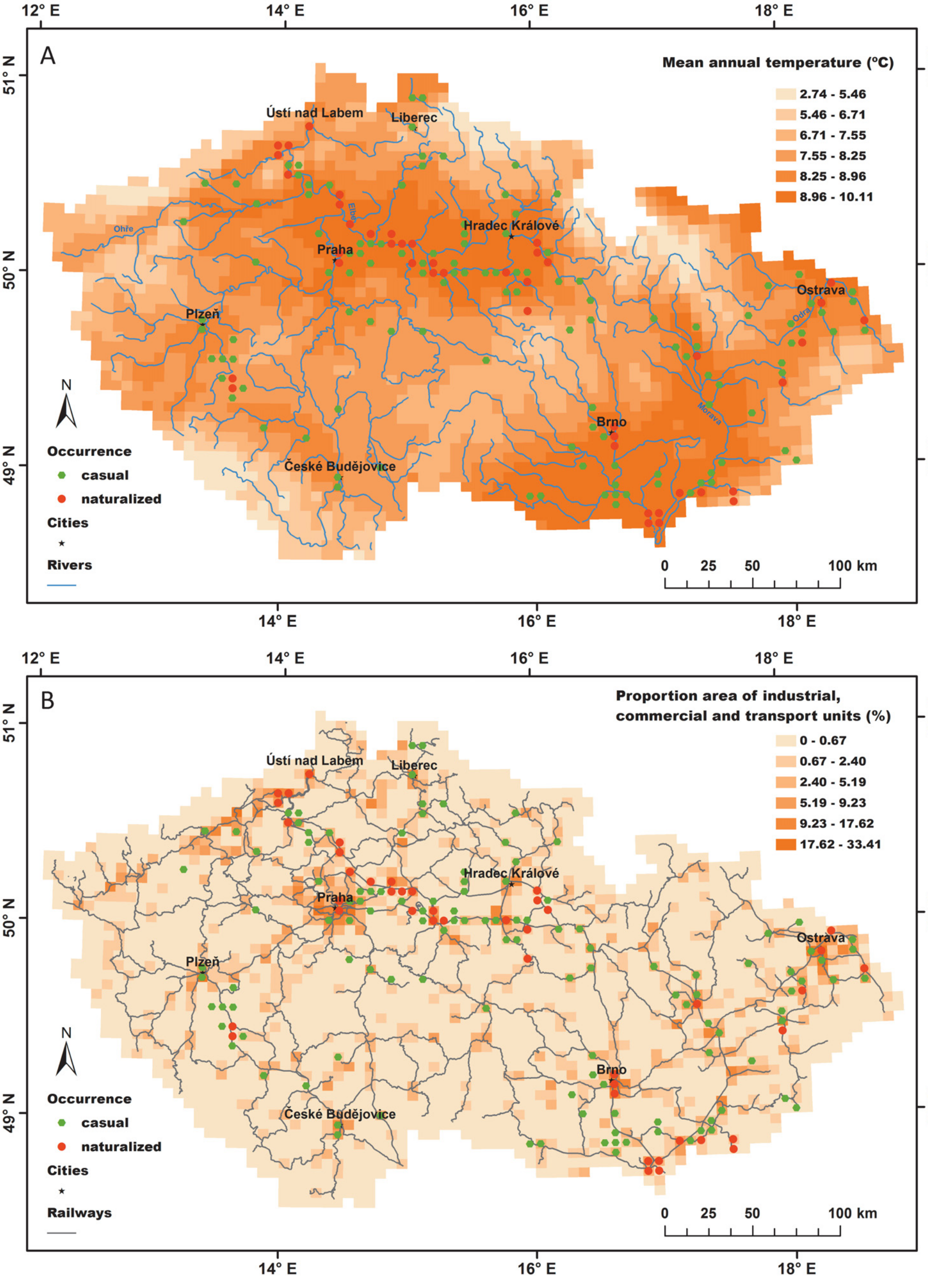

Fig. 4. – Map showing the distribution of *Ambrosia artemisiifolia* in the Czech Republic displayed together with (A) distribution of mean annual temperature in 5' × 3' grid cells and river networks, and (B) distribution of proportional area of industrial, commercial and transport units in 5' × 3' grid cells and railway networks.

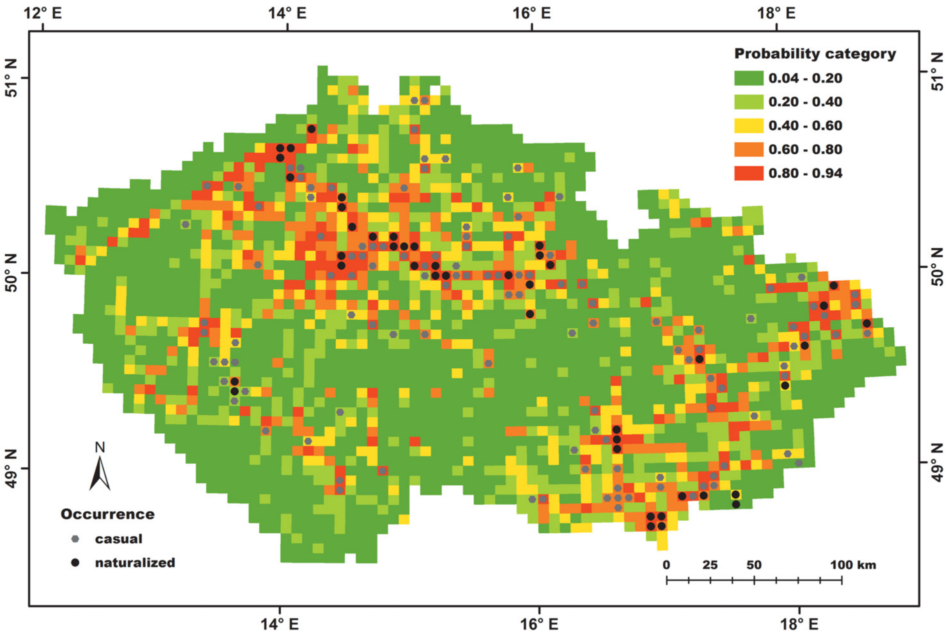

Fig. 5. – Potential distribution of *Ambrosia artemisiifolia* in grid cells (5'× 3') in the Czech Republic based on factors revealed by the conditional interference tree as shaping the species distribution with up to now recorded occurrences represented by dots.

comparison with other countries due to the absence of detailed data, it is clear that the extent of the area colonized in the Czech Republic is considerably less than in Hungary, Croatia and Serbia (Kazinczi et al. 2008).

The high number of records associated with transport corridors, railways and roads, is typical of the occurrence of *A. artemisiifolia* in the Czech Republic, Slovakia and Austria. The Czech Republic has more records from railway corridors and there was about a 10-year delay in the start of the rapid spread along roads. These routes seem to have become the main transport pathway of *A. artemisiifolia* in the Czech Republic just as in other central-European countries (Vitalos & Karrer 2009, Jolly et al. 2011, Medvecká et al. 2012, Milakovic et al. 2014, Essl et al. 2015b, Hrabovský et al. 2016, Milakovic & Karrer 2016). The situation may be similar to Slovakia where the number of ragweed records started to increase markedly around 2010, namely along highways and main roads (Hrabovský et al. 2016). The spatiotemporal pattern in the Czech Republic also supports the view of reported long-distance dispersal as a contaminant of crops or bird feed, direct transport of contaminated litter or soil or attached to construction- or agricultural machinery (Bullock et al. 2012). Populations in arable fields are now rather scarce. This could be a result of rather low propagule pressure due to the existence of a limited number of really extensive populations in the Czech Republic, lower seed production compared to other countries (Moravcová et al. 2010, Essl et al. 2015b) and still low abundance along roads that may serve as a stepping stone for the invasion of fields. However, the situation may soon change due to the ongoing spread of *A. artemisiifolia* along roads that are managed using agricultural machinery for cutting the roadsides and cleaning ditches. If populations become established on arable land, further spread by agricultural machinery seems inevitable, and may follow the trend reported from Hungary where *A. artemisiifolia* became the most abundant weed in less than 50 years and is now present in all grid cells (Pinke et al. 2011). The large-scale establishment of *A. artemisiifolia* in this habitat poses a major threat due to the increase in propagule pressure, which consequently is likely to accelerate the invasion in climatically suitable areas at the regional scale. Another possible stepping stone in this invasion could be forest nurseries where plants were recently recorded (J. Doležal, personal observation). *Ambrosia artemisiifolia* seed and seedlings can be easily distributed with young trees.

Factors shaping the distribution of Ambrosia artemisiifolia

Predominance of records from sites with frequent, mainly anthropogenic disturbance reflects the poor competitive ability of *A. artemisiifolia* (Leskovšek et al. 2012). The poor resistance of the species to spontaneous succession (Gentili et al. 2015) and population decline at disturbance-free sites indicates the crucial role of disturbance in maintaining the populations. In our analysis, the role of disturbance manifests itself through the association with particular types of habitats, with the proportion of area that is industrial, commercial and related to transport being the most important variable shaping the current distribution of *A. artemisiifolia* in the Czech Republic. Its effect is further fine-tuned by factors related to human-related dispersal and climate, such as density of the railway network and temperature, respectively. This fact should be taken in account when constructing models of its future distribution. Surprisingly, the anthropogenic factors are rarely included in models of *A. artemisiifolia* distribution (but see Richter et al. 2013a, b), despite their importance demonstrated in previous studies of common ragweed (Essl et al. 2009) and other species (Stratonovitch et al. 2012, Guo et al. 2013). Anthropogenic factors may explain the differences in distribution predicted by our models and those of other authors who identified the western part of the Czech Republic as the most suitable area (Cunze et al. 2013, Storkey et al. 2014), or did not predict the occurrence of the species in northern Moravia (Leiblein-Wild et al. 2016).

Although temperature is not the most important factor influencing the distribution of *A. artemisiifolia*, it played a key role in the past in determining the invasion pathways and the likelihood of naturalization once sites are colonized. This factor was identified as the main splitter between the two stages of the invasion process (following the terminology of Richardson et al. 2000, Blackburn et al. 2011). This is in accordance with experimentally demonstrated effect of low temperature in slowing down the rate of seed germination (Leiblein-Wild et al. 2014) and development of seedlings (Skálová et al. 2015) and leaves (Deen et al. 1998). The negative effect of low temperature may be partly compensated by an increased nutrient availability (Skálová et al. 2015), which may explain the occurrence at disturbed sites (where nutrient availability is usually high) and facilitate further spread into arable fields.

Potential distribution of Ambrosia artemisiifolia in the Czech Republic

Our models indicate that not all sites suitable for *A. artemisiifolia* are already invaded. Further spread within the Czech Republic is thus probable. At the local scale it is likely that populations will colonize suitable areas in the proximity of sites of current occurrence, but there is also a great potential for long-distance spread to remote areas. In some areas the spread might be limited by low precipitation as this was revealed as a limiting factor in previous studies (Pinke et al. 2011, Jacob et al. 2013). The occurrence of a single plant does not necessarily result in the establishment of a population due to pollen limitation and strong self-incompatibility (Essl et al. 2015b). However, the presence of additional individuals may result in stable populations and the formation of a viable, long-lived seed bank (Darlington 1922). This provides an opportunity for populations to survive over time (Gioria et al. 2012, Gioria & Pyšek 2016). At such sites the vegetation cover should not be destroyed as more disturbed, open habitats allow ragweed populations to recover (H. Skálová & L. Moravcová, personal observation). The spread may be slowed down by the eradication of newly emerging individuals or populations. At infested sites disturbance should be avoided and sowing of seed mixtures composed of competitively strong species is recommended (Gentili et al. 2015). Populations at permanently disturbed sites such as roadsides should be managed by precisely timed cutting, which is reported to reduce seed production (Milakovic et al. 2014).

See www.preslia.cz for Electronic Appendices 1–3

Acknowledgments

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Souhrn

Analyzovali jsme dynamiku šíření jednoho z nejnebezpečnějších invazních druhů, *Ambrosia artemisiifolia*, který je znám svým dopadem na lidské zdraví. Studovali jsme ji s ohledem na biotopy a faktory, které určují jeho současné rozšíření, a vytipovali jsme oblasti, které jsou ohroženy jeho dalším šířením. Analýza vychází z dosavadních 281 záznamů výskytu získaných do roku 2016, situovaných ve 164 mapovacích polích, z nichž 37 hostí naturalizované populace a 127 populace přechodně zavlečené. Nejvíce záznamů pochází z blízkosti železničních koridorů (49 %), za nimiž následují lidská sídla (11 %). Zaznamenali jsme nárůst výskytu druhu podél silnic během posledních let. Analýza pomocí dedukčního regresního stromu ukázala, že rozšíření druhu je nejvíce ovlivněno procentním zastoupením průmyslových, komerčních a transportních ploch v mapovacím poli. Vliv mají také faktory související s transportem diaspor zprostředkovaným lidskou činností, jako je hustota železniční sítě, a z klimatických faktorů průměrná teplota v mapovacím poli. Predikční model ukázal, že zdaleka ne všechna vyhovující pole jsou již obsazena. Značná část těchto polí se nachází v těsné blízkosti těch již obsazených, ale identifikovali jsme i pole, která splňují stejná kritéria jako ta již obsazená a přitom se od nich nacházejí ve značné vzdálenosti. V České republice lze proto předpokládat další šíření ambrózie peřenolisté.

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