

Invasion dynamics of three allergenic invasive Asteraceae (*Ambrosia trifida*, *Artemisia annua*, *Iva xanthiifolia*) in central and eastern Europe

Invazní dynamika tří allergenických hvězdnicovitých druhů (*Ambrosia trifida*, *Artemisia annua*, *Iva xanthiifolia*) ve střední a východní Evropě

Swen Follak¹, Stefan Dullinger^{2, 3}, Ingrid Kleinbauer³, Dietmar Moser⁴
& Franz Essl⁴

¹Austrian Agency of Health and Food Safety, Spargelfeldstraße 191, A-1220 Vienna, Austria, e-mail: swen.follak@ages.at; ²University of Vienna, Rennweg 14, A-1030 Vienna, Austria, e-mail: stefan.dullinger@univie.ac.at; ³Vienna Institute for Nature Conservation and Analyses, Giessergasse 6/7, A-1090 Vienna, Austria, e-mail: ingrid.kleinbauer@vinca.at; ⁴Environment Agency Austria, Spittelauer Lände 5, A-1090 Vienna, Austria, e-mail: franz.essl@umweltbundesamt.at, dietmar.moser@umweltbundesamt.at

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We analyzed the history of the invasion, spread dynamics and habitat affiliation of three allergenic wind-pollinated species (*Ambrosia trifida*, *Artemisia annua*, *Iva xanthiifolia*; tribe Heliantheae, Asteraceae) in central and eastern Europe (CEE) using distribution data from a wide range of sources. In addition, we used niche-based ensemble modelling techniques to assess current invasion risk of the region studied. We collated 1804 records of *A. annua*, 1063 of *I. xanthiifolia* and 324 of *A. trifida*. All species were first recorded in the 19th century, remained rare until the middle of the 20th century, but have spread rapidly in recent decades. *Iva xanthiifolia* spread the fastest followed by *A. annua*. The latter species is now abundant in northern Italy, along the Elbe river in Germany and the Danubian Lowland in Slovakia and Hungary, while *I. xanthiifolia* occurs most frequently in the warm and continental parts of CEE. *Ambrosia trifida* spread slowly and its current distribution consists of relatively few and mostly isolated localities in CEE. *Ambrosia trifida* and *I. xanthiifolia* occur primarily in ruderal habitats, whereas *I. xanthiifolia* has also increasingly invaded fields. Initially confined to ruderal habitats, *A. annua* has expanded its habitat niche during the invasion and has invaded riverine vegetation and (semi-)natural habitats. Ensemble species-distribution models show that the current distribution of *A. trifida* and *A. annua* in CEE is closely related to temperature and precipitation, whereas land use is only important for *I. xanthiifolia*. Under the current climate, substantial fractions of the study area provide suitable habitat for these species: *A. trifida* (16% of CEE), *A. annua* (28%) and *I. xanthiifolia* (26%). Because of their significant potential impact on public health, future spread of these species should be monitored and management strategies (e.g. raising awareness, early control) should urgently be implemented.

Key words: allergy, distribution, habitats, human health, impact, invasion history, invasive alien species, species distribution models, spread

Introduction

Plant invasions are a significant component of global change with far-reaching consequences for biodiversity, land use and human well-being (Lambdon et al. 2008, Vilà et al. 2011). Some alien plant species are of particular concern for human health due to their allergenic pollen. In Europe, *Ambrosia artemisiifolia* L. (common ragweed) is the most

widespread allergenic alien plant species that has attracted considerable interest from European ecologists and immunologists (Taramarcz et al. 2005, Dullinger et al. 2009, Smolik et al. 2010, Richter et al. 2013). Recently, the annual cost of the invasion of this species in Germany was estimated to be 32 million €, which is almost entirely due to increased costs in the human health sector (Reinhardt et al. 2003). However, several species with high allergenic potential in the same genus (*Ambrosia trifida* L., giant ragweed) and closely related genera (*Iva xanthiifolia* Nutt., burweed marshelder; *Artemisia annua* L., annual wormwood) within the same tribe (*Heliantheae*) are not native in Europe. Their invasion has received much less attention and has so far not been investigated systematically. However, evidence suggests that *A. trifida*, *A. annua* and *I. xanthiifolia* have increased in abundance and range in some parts of central and eastern Europe (CEE) (Follak 2009, Medvecká et al. 2012, Pyšek et al. 2012). Given this trend, it seems likely that these species may create significant problems for human health in the medium term.

Comprehensive retrospective analyses of invasion histories provide a better understanding of patterns and processes affecting the spread of a species and may provide ways of testing hypotheses in invasion ecology. For instance, by analysing spatio-temporal distribution patterns it is possible to assess the importance of introduction pathways, to identify invasion foci and whether the speed and nature of the invasion process has changed over time (Pyšek & Prach 1993, Mandák et al. 2004, Follak & Essl 2013). Information on habitat preferences and habitat shifts provides further data on spread dynamics and dispersal vectors (Lavoie et al. 2007, Essl et al. 2009). Distribution and rates of spread of invasive plants are controlled by the interplay of environmental, climatic and anthropogenic factors. In this respect, niche-based distribution modelling (e.g. species distribution models, SDMs, Guisan & Thuiller 2005, Elith et al. 2006) has become an important tool for identifying environmental factors affecting a species' distribution and for assessing the species' potential range under current and potential future environmental and climatic conditions (e.g. Thuiller et al. 2005, Essl et al. 2009, Kleinbauer et al. 2010, Gallien et al. 2012). In addition, a proper understanding of a species' behaviour in its new range is a prerequisite for the evaluation of management options to halt or slow down its future spread (Richter et al. 2013).

In this study, we extracted distribution records of *A. trifida*, *A. annua* and *I. xanthiifolia* in CEE up to the year 2011 from a wide range of data sources to analyse their invasion dynamics. In particular, we address the following questions: (1) What is the spatio-temporal pattern in their spread? (2) Which habitats are predominately colonized and did habitat preferences change during the invasion? (3) Which parts of the region are currently most at risk of being invaded? (4) What are the implications for future spread, impact and management?

Material and methods

Study region

The region studied is a large contiguous area encompassing most of the areas where the study species are currently found in central and eastern Europe. It includes Austria, Czech Republic, Germany, Hungary, Slovakia, Slovenia, Switzerland and northern parts of more southerly countries like Croatia, Italy (i.e. the regions Aosta Valley, Friuli-Venezia Giulia, Liguria, Lombardy, Piedmont, Trentino–Alto Adige, Veneto) and Serbia (Vojvodina, parts

of central Serbia). The climate is mostly temperate to submediterranean in the southernmost parts (northern Italy), with a pronounced gradient towards a more continental climate in the eastern part of the region. Lowlands are dominated by agriculture and the major centres of population are located there. Cooler mountainous regions dominated by forests and grasslands are prominent in the Alps and Carpathian Mountains (e.g. in parts of Austria, Czech Republic, Slovakia, Switzerland).

Study species

Besides being phylogenetically closely related, the study species share a range of traits (wind-pollinated herbaceous plants of open habitats with vigorous growth) and introduction characteristics (e.g. accidental introduction into CEE, invasion started in the 19th century).

Ambrosia trifida is a summer annual species 30–150 (–400) cm in height. This species is characterized by rapid growth and relatively low seed production (Abul-Fatih & Bazzaz 1979a, b). *Ambrosia trifida* is a native of the United States where it occurs on riverbanks and lakeshores north of the Ohio River (Basset & Crompton 1982). Currently, this species occurs mainly in New England and further south, the Ohio and Mississippi River valleys and in southern Canada (Basset & Crompton 1982, FNA Editorial Committee 2006).

Artemisia annua is an annual species 30–200 (–250) cm in height. It has a pioneer strategy characterized by a high degree of morphological and reproductive plasticity and massive seed production (Brandes & Müller 2004). This species is a native of East Asia, most probably Inner Mongolia in China, where it is part of the grassland and steppe vegetation (Ferreira et al. 1997). *Artemisia annua* has become widespread in temperate regions worldwide (FNA Editorial Committee 2006).

Iva xanthiifolia is also an annual species 30–200 (–300) cm in height. It is characterized by rapid growth and high seed production (Hunyadi et al. 1998, Hodi & Torma 2002). *Iva xanthiifolia* is a native of the North American prairies (Jackson 1960) where it occurs on sandy and silty river alluvials, in river and stream beds and occasionally as a weed in moist places. The species' range has been increased by human means and currently covers large fractions of the lower United States and parts of southernmost Canada (Jackson 1960, FNA Editorial Committee 2006). Further, it has been introduced into Europe and western Asia (Pruski 2005).

Distribution data and data analyses

We collected all the records of *A. trifida*, *A. annua* and *I. xanthiifolia* in CEE up to 2011 from a wide range of sources (Electronic Appendix 1). We searched global (Global Biodiversity Information Facility; <http://www.gbif.org>), national (floristic mapping projects of Austria, Croatia, Czech Republic, Germany, Switzerland) and subnational (floristic mapping projects of Trentino, South Tyrol, Bergamo, Brescia, Friuli-Venezia Giulia) databases and important national herbaria (BP, FR, GZU, LI, SAV, SLO, STU, W, WU). These data were supplemented by an exhaustive search of the literature using appropriate keywords in indexed (Web of Science, CAB Abstracts, Agris, AGRICOLA) as well as in non-indexed journals, monographs and the internet. Additionally, we contacted 38 key country and regional experts for further records (see Acknowledgements). Given the strong tradition of floristic research in countries of CEE, the inclusion of floristic literature and unpublished data of key experts proved to be particularly important. Further, the

integration of different data sets should at least mitigate spatio-temporal variation in the effort put into sampling underlying each specific source.

We cross-checked all records to avoid double entries of identical records in different data sources. All records were assigned to a grid cell (5×3 geographic minutes, $\sim 33 \text{ km}^2$) of the Floristic Mapping Project of Central Europe (= FMCE; Niklfeld 1998). The date (= year) of the records was extracted from the original source. If a time period of several years was given, we used the arithmetic mean. To document the early phase of the invasion, we identified and mapped the first three records for each species in each country in CEE (Electronic Appendix 2). For each record the status of the respective population, whether established or casual, was assessed either by the observer or by using information in the original data source. Our post-hoc classification was mainly based on the size of the population, using a threshold of 100 reproductive individuals. Smaller populations were only classified as established if at least two records in consecutive years were reported. Populations that observers had not explicitly rated as either established or casual and which we could not classify unambiguously based on the information in the original source were also classified as casual. Data on the types of habitats colonized in CEE were extracted from original data sources and were assigned to the following categories: ruderal habitats, ruderal habitats associated with transport infrastructure like roads and railways, riverine vegetation, fields and (semi-)natural habitats (incl. urban parks and gardens, wood edges, dry grassland). We analyzed the invasion of the three species over time in CEE and of the different habitats. We constructed invasion curves by calculating the cumulative number of records plotted against time (sensu Pyšek & Prach 1993). To compare the rate of spread of the three species the regression slopes b of the cumulative number of all records over time were tested for the period 1950 to 2011, i.e. the beginning of rapid spread of each species. The data was analyzed using a general linear model with species as a factor and year as a covariate (Mandák et al. 2004). Statistical analyses were performed using IBM® SPSS® Version 20.

Species distribution models

Spatially explicit data on climatic conditions (selected bioclimatic variables from WorldClim, <http://www.worldclim.org/bioclim>), major infrastructure (highways) and natural (rivers) networks, which represent potential invasion corridors, and land use were collected from various sources (Table 1). All GIS data were pre-processed to match the resolution of the raster of the FMCE, i.e. aggregation by means of averaging (topographical data) or summarizing (street and river length). For calibrating the SDMs, records of the species studied were partitioned into those of established and casual populations (Dullinger et al. 2009, Essl et al. 2009). This was motivated by the assumption that the distribution of established populations is more likely to reflect the habitat requirements of the species (Richardson et al. 2000). Indeed, models that only include established populations are more accurate than those that include all the records (Dullinger et al. 2009).

We used SDMs (Guisan & Zimmermann 2000) to identify the factors governing the current distribution of the species studied. The proliferation of statistical modelling tools has led to the availability of various methods, each with strengths and caveats (Elith et al. 2006). Hence, the use of several modelling techniques (ensemble forecasts) is recommended (Araújo & New 2007). We used the BIOMOD-framework implemented in the R

Table 1. – Environmental variables used to calibrate the distribution models of *Ambrosia trifida*, *Artemisia annua* and *Iva xanthifolia* in central and eastern Europe.

Category	Variable	Source	Original scale
Land use	Proportional area of human settlements and agricultural fields	CORINE Land cover	map with min. 25 ha polygons
Highway	Length of major streets	Tele Atlas N. V. (© 2005)	–
River	Length of major rivers	Various sources	–
Temperature	Temperature seasonality (BIO4), minimum temperature of coldest month (BIO6), mean summer temperature (BIO10)	WorldClim (www.worldclim.org) (Hijmans et al. 2005)	2.5 × 2–5 arc minutes
Precipitation	Precipitation seasonality (BIO15), mean summer precipitation (BIO18)	Selected bioclimatic variables from WorldClim (www.worldclim.org) (Hijmans et al. 2005)	2.5 × 2–5 arc minutes

software (R Development Core Team 2012) for fitting SDMs. BIOMOD allows combinations of several modelling techniques in an ensemble forecast (Thuiller et al. 2009). Here, we used a combination that included generalized linear models (GLM, McCullagh & Nelder 1989), generalized boosting models (GBM, Friedman 2001), generalized additive models (GAM, Hastie & Tibshirani 1990) and multiple adaptive regression splines (MARS, Friedman 1991). Different models were evaluated separately and combined in the ensemble forecast using a weighted approach that ranks the models using their evaluation score, i.e. models with better evaluation statistics were regarded as more reliable and got higher weights in the ensemble procedure (Thuiller et al. 2009). We used a random subset (70%) of the distribution data for fitting the models and the remainder to evaluate the models. Moreover, pseudo-absences were created using a random sample of 1000 data points in a squared neighbourhood around the presences. We used the average of 10 repetitions of each model. In the GLMs, we used ordinary polynomial terms and in the GAMs the degrees of freedom were set to three. In GBMs we used a maximum of 3000 trees. We performed a tenfold cross-validation using the area under the curve (AUC) of a receiver-operating characteristic curve for model accuracy evaluation. AUC is a composite measure of model performance, with values ranging from 0 to 1, where 1 is a perfect fit. Useful models produce AUC values of 0.7–0.9, and models with “good discriminating ability” produce AUC values > 0.9 (Swets 1998).

Following the recommendations of Liu et al. (2005), prevalence (= ratio of occupied grid cells vs total number of grid cells) was chosen as a threshold for presence/absence predictions. Projected occurrence probabilities were transformed into presence/absence predictions per grid cell, based on the threshold that maximizes model accuracy. To assess the importance of variables in explaining the current distribution of a study species and to assure comparability among models, BIOMOD provides a permutation procedure to extract a measure of relative importance for each predictor variable that is independent of the model. High values imply high importance of the predictor variable (Thuiller et al. 2009).

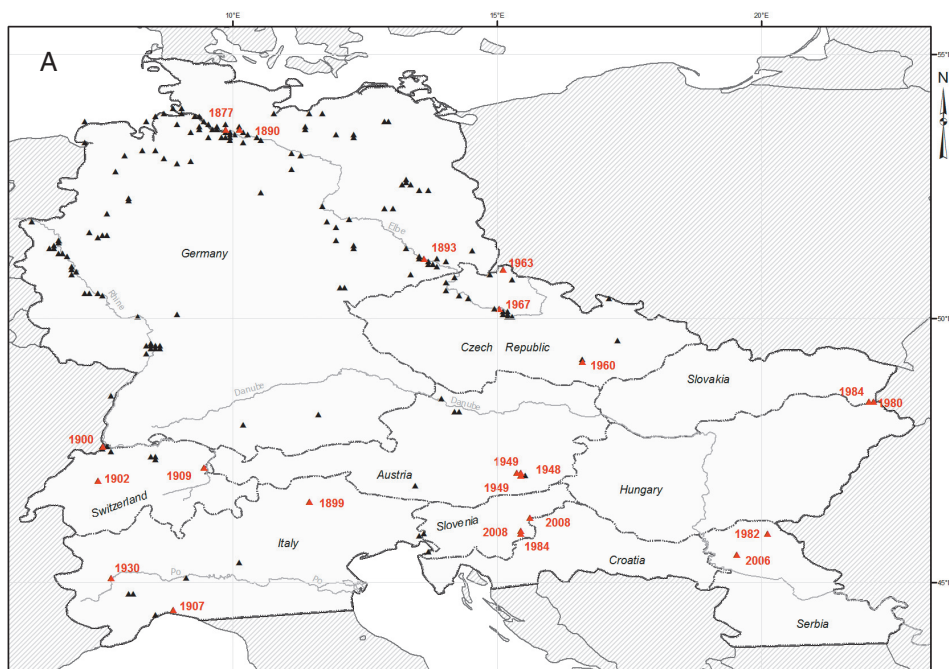
Results

Introduction and invasion history

In total, we collated 324 records of *A. trifida* in CEE (Fig. 1A, Electronic Appendix 3). The first records are for 1877 (Hamburg, Germany), 1899 (Atzwang, South Tyrol) and 1900 (Basel, Switzerland). In the other countries *A. trifida* was first recorded substantially later. First record for Austria is 1948 (Graz), the Czech Republic 1960 (Brno) and Slovakia 1980 (Čierna nad Tisou). In Serbia, *A. trifida* was first found in 1982 at Vojvodina (Čoka) and in the late 1980s in Slovenia. There are currently no records for Hungary and Croatia.

In total, we collected 1804 records of *A. annua* in CEE (Fig. 1B, Electronic Appendix 3). The presence of *Artemisia annua* was noted in Rochel's "Plantae Banatus rariores, iconibus et descriptionibus illustratae" published in 1828, but no definite records were provided. First tangible records are for 1852 (Stara Gradiška, Croatia) and 1871 (Bački Petrovac, Serbia). Subsequently, the species was first recorded in Austria (1867, Vienna) and Switzerland (1871, Zurich), followed by Germany (1882, Wandersleben), Hungary (1882, Budapest), the Czech Republic (1891, Znojmo) and Slovakia (1916, Komárno). In the south-western CEE, *A. annua* was intentionally introduced as an ornamental and medicinal plant in the 18th century. Thus, this species might have already escaped before the first records. In northern Italy, the first record of *A. annua* was for 1909 (Bozen, South Tyrol) and for Slovenia it was 1928 (Ljubljana).

There are a total of 1063 records of *I. xanthiifolia* in CEE (Fig. 1C, Electronic Appendix 3). This species was recorded for the first time in Germany near a botanical garden in 1858 (Potsdam). In the other countries it was recorded substantially later. The first record



for Switzerland was 1902 (Basel). In Slovakia, this species was first collected in 1934 (Šurany & Čiky), in Austria in 1942 (Vienna), the Czech Republic in 1948 (Prague), Hungary in 1950 (Mezőhegyes), Serbia in 1966 (Novi Sad) and Slovenia as late as 1970 (Škofije). The most recent first national record was for 1976 in Croatia (Đurđancima).

Distribution

Ambrosia trifida is recorded at markedly fewer localities than *A. annua* and *I. xanthiifolia* (Fig. 1A). It is most widespread in northern parts of CEE, in particular Germany, Switzerland and the Czech Republic, where it is mainly recorded in large cities along the rivers Rhine and Elbe (i.e. Basel, Dresden, Hamburg, Mannheim Ruhr; Fig. 1A). There are currently a few established populations, e.g. in Serbia (South Bačka district, Vojvodina), Italy (Pavia, Lombardy) and the Czech Republic (Kolín district).

Artemisia annua is present in all the countries of the region studied, but the distribution is very uneven with several regions where it is very abundant (Fig. 1B). The invasion hotspots are mostly associated with large river valleys. In Germany, the species forms extensive stands along the rivers Elbe and Saale, and in Slovakia and Hungary it is widespread along the Danube river. *Artemisia annua* is also common on the plains and in river valleys of northern Italy, in particular in the regions Lombardy, Piedmont and Trentino–Alto Adige. However, this species is rare or absent along the Austrian and German section of the Danube river and other rivers systems (i.e. Oder, Tisza, Rhine). Populations can be found in large cities and their vicinities in the Czech Republic (Olomouc, Prague), Germany (Ruhr, Berlin, Erfurt), Hungary (Budapest) and northern Italy (e. g. Torino), but there are few records for the rest of CEE (western Germany, Hungary, northern Serbia, Croatia).

Iva xanthiifolia is most widespread in warm continental lowlands in the eastern part of the region studied (Fig. 1C). Here, *I. xanthiifolia* has spread from points of introduction into the Danubian Lowland and the Pannonian Basin. Invasion hotspots are in southern and eastern Slovakia (districts Bratislava, Nitra, Košice), northern Serbia (Vojvodina), south-eastern Hungary (counties Csongrád and Békés), the easternmost part of Austria (Burgenland, Lower Austria) and eastern Germany (e.g. Dresden Basin). Throughout most of the other parts of CEE, *I. xanthiifolia* is uncommon except for some large cities and areas along the rivers Rhine (Ruhr, Mainz, and Mannheim) and Elbe (Hamburg). In mountainous regions in the Alps (Switzerland, western Austria) and Carpathians the three species studied are rare to absent.

Spread dynamics

The cumulative number of records of *A. trifida*, *A. annua* and *I. xanthiifolia* has increased over time since their introduction into CEE (Fig. 2). The rate of spread of *A. trifida* was moderate. The number of records peaked in the periods 1951–1970 (104 records) and 1971–1990 (98 records) and thereafter decreased strongly to 33 records. The first established population was recorded at the end of the 19th century in Germany. Since then, the percentage of established populations has not increased (Fig. 2A). Casual populations prevail, whereas only 27% of all records are currently classified as established (*A. annua*: 58%; *I. xanthiifolia*: 35%). For *A. annua*, there was a constant but slow increase of records from the 1890s up to the 1970s. Then there was a marked increase in the number of records and rate of spread became particularly pronounced after 1995 when the number of records

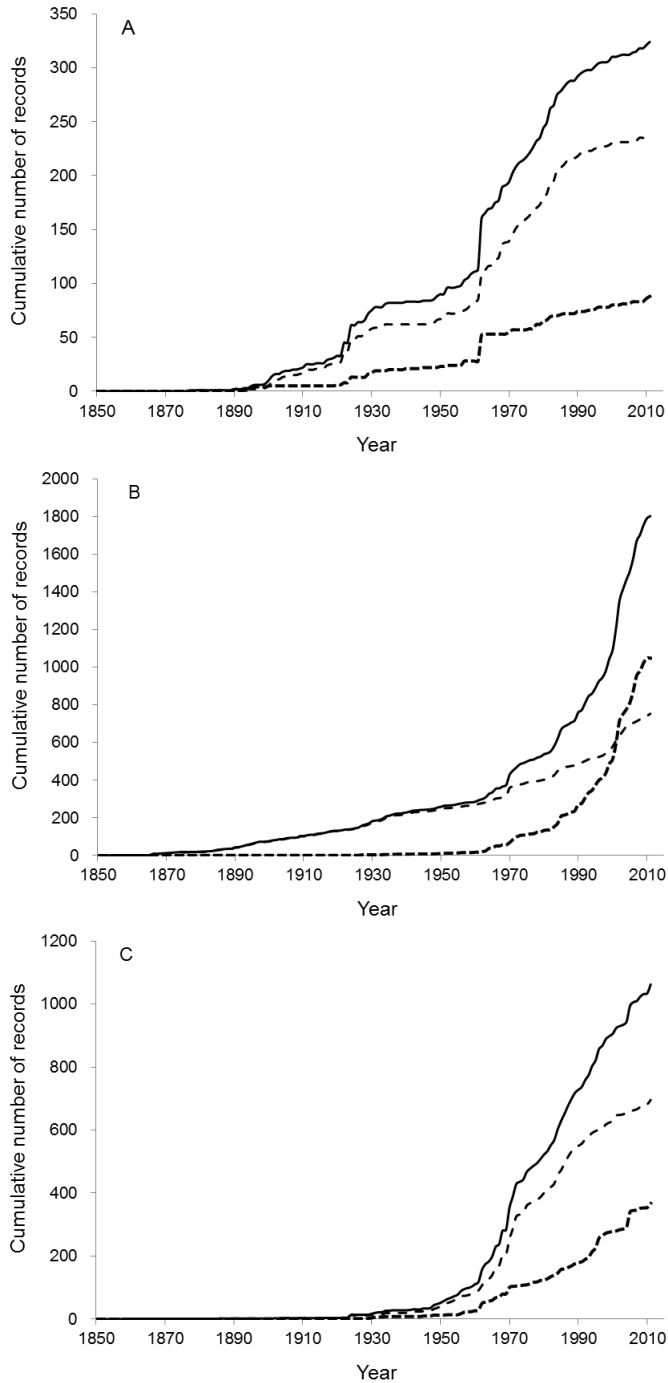


Fig. 2. – Curves of the colonization (i.e. cumulative number of records) by *Ambrosia trifida* (A), *Artemisia annua* (B) and *Iva xanthifolia* (C) of central and eastern Europe. Sum of all records (solid line) and records of casual (dashed line) and established populations (dotted line) are shown.

more than doubled from 872 (1995) to 1804 (2011) (Fig. 2B). The majority of the early records of *A. annua* were for populations categorized as of casual status, but the percentage of established populations increased after 1960. Recently, the number of established populations has increased much faster than that of casual populations (Fig. 2B). Our data indicate a distinct lag phase for *I. xanthiifolia*, since records were scarce until 1950, but have sharply increased since then (> 80% of all the records are for after 1950) (Fig. 2C). The first established population was recorded in the mid-1920s, nearly 50 years after the first record of a casual population. Since then casual populations have outnumbered established ones, but from 1991–2011 the number of established populations have doubled whereas that of casual populations increased by less than one and a half. The cumulative number of all records over time for each species was best fitted by linear models that explained 93% of the variance ($F = 527.647$, $df = 5$; $P < 0.001$). The slopes for the different species differed significantly ($F = 82.945$, $df = 2$, $P < 0.05$). The rate of spread (expressed as the regression slope b) during the period 1950 to 2011 (i.e. the beginning of the rapid spread of each species) was highest for *I. xanthiifolia* ($b = 0.0245$) followed by *A. annua* ($b = 0.0145$) and *A. trifida* ($b = 0.0095$).

Habitat preference

Ambrosia trifida occurs only in a limited range of habitats (Table 2, Fig. 3). This species primarily colonizes ruderal habitats as of the total number of records more than two-thirds are for this habitat. Records in ruderal habitats associated with railway areas increased markedly since the 1950s and peaked in the 1990s. Less than 10% of all records for which habitat information is available were for non-ruderal habitats (i.e. fields, riverine vegetation).

In contrast, *A. annua* has a broader habitat niche (Table 2, Fig. 3). It regularly occurs in ruderal habitats associated with transport infrastructure like roads and railways. Since the 1990s, and especially in the last few years, records for these two habitats greatly increased and became dominant. Moreover, *A. annua* is now a typical element of the riverine vegetation of several river systems in CEE (Table 2, Fig. 3), which has led Burkart (2001) to denote this species ‘a river corridor plant’. Indeed, almost one fifth of all records were associated with riverine vegetation, mostly that of the rivers Elbe, Danube, Adige and to a lesser extent the Sava and Drava. Whereas *A. annua* rarely occurs in fields, there are several records in (semi-)natural habitats. Early records are for urban parks and gardens, which indicate it most likely escaped from cultivation. Since 1990, it has been recorded in woodlands, shrubberies and semi-dry grasslands. Such records are mainly for northern Italy.

Table 2. – Habitat preferences of *Ambrosia trifida*, *Artemisia annua* and *Iva xanthiifolia* in central and eastern Europe. Given are the number of records for which habitat information was available and the percentage of occurrences per habitat. See text for information on the different habitats.

Species	Roads		Railway		Ruderal habitats		Riverine vegetation		Fields		(Semi-)natural habitats	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
<i>A. trifida</i> (n = 144)	–	–	33	22.9	93	64.6	14	9.7	4	2.7	–	–
<i>A. annua</i> (n = 1152)	292	25.4	78	6.8	452	25.4	220	19.1	24	2.1	86	7.4
<i>I. xanthiifolia</i> (n = 555)	45	8.1	96	17.3	349	62.9	9	1.6	56	10.1	–	–

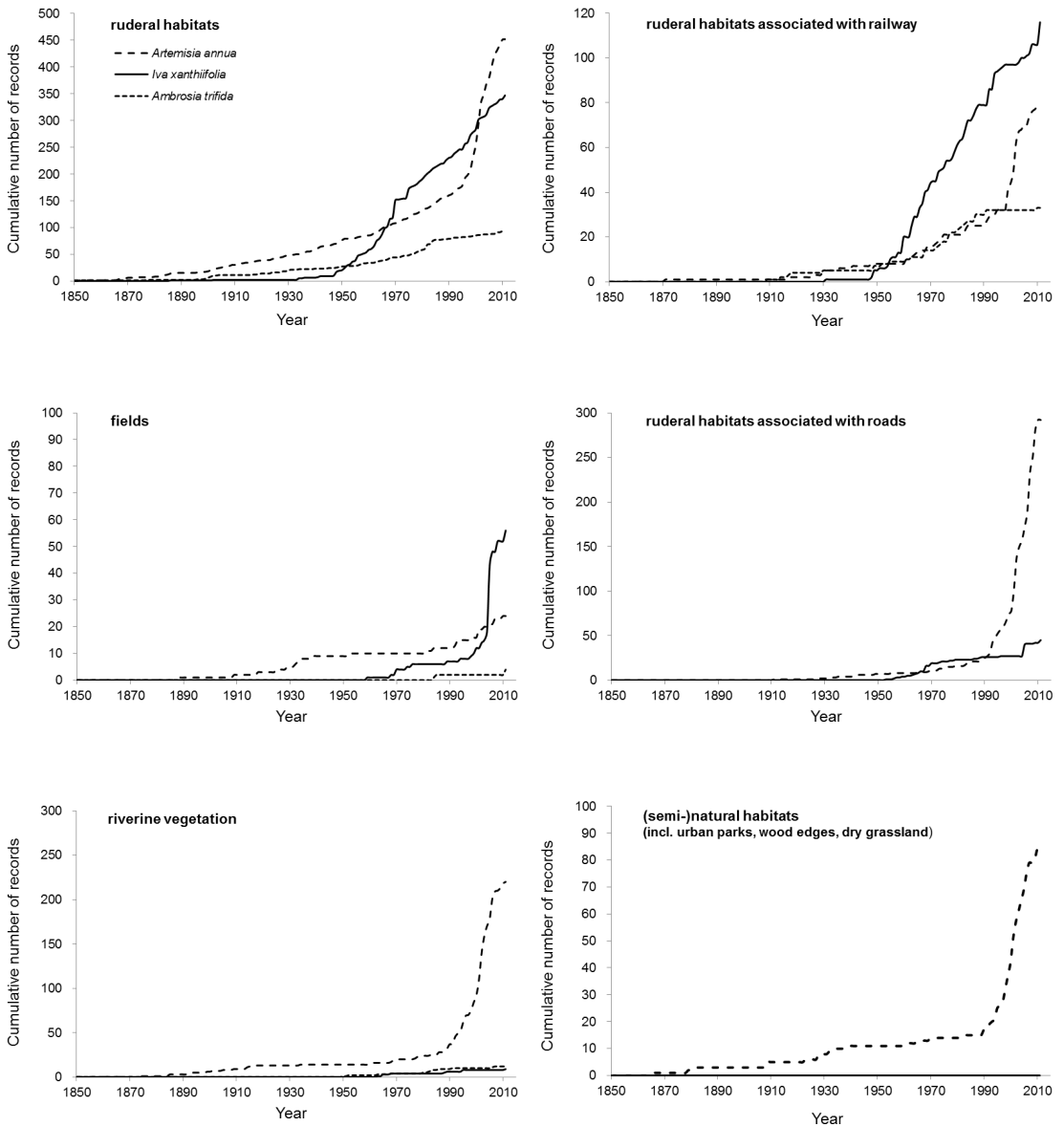


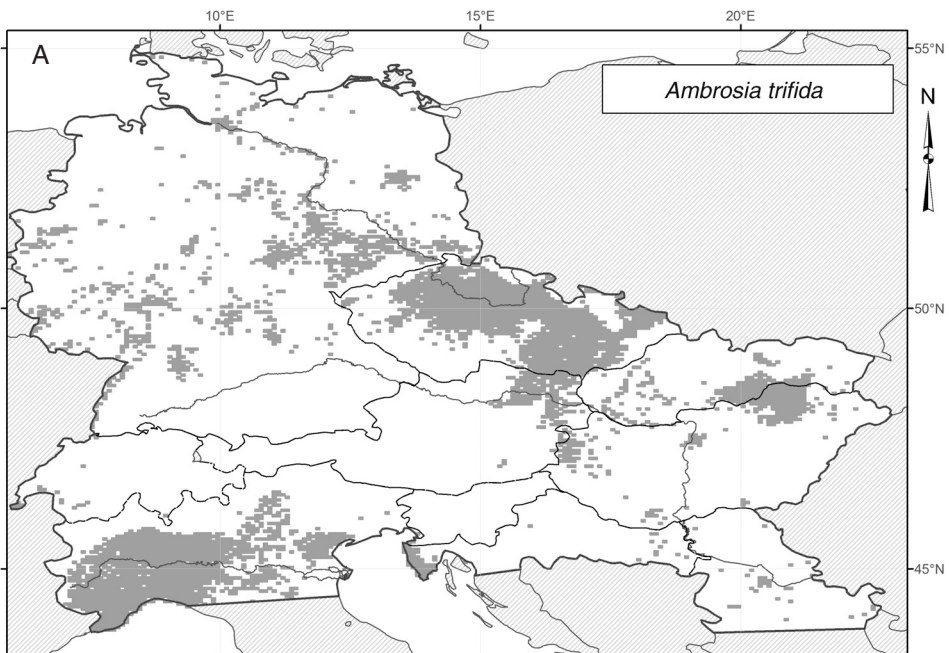
Fig. 3. – Curves of the colonization (i.e. cumulative number of records) by *Ambrosia trifida*, *Artemisia annua* and *Iva xanthiifolia* of different habitats in central and eastern Europe. Note, that there are no records for (semi-)natural habitats for *A. trifida* and *I. xanthiifolia* and roads for *A. trifida*.

Early records of *I. xanthiifolia* are associated with ruderal habitats but now it is recorded in other habitats (Table 2, Fig. 3). From the 1950s onwards, this species was collected increasingly in ruderal habitats associated with transport infrastructure. At present,

railway habitats make up 17% of the total number of records for which habitat information is available and the colonization of railway areas is ongoing as indicated by the increase in the number of records in the last decade (Fig. 3). However, roadside habitats seem to be of less importance (8% of all records). *Iva xanthiifolia* started to invade fields in the late 1950s in Germany. First records in fields were reported in 1968 for Slovakia (Šurany), 1970 for Hungary (Battonya) and 1974 for Serbia (Šajkaš). It has become an important agricultural weed in these countries, in the Slovakian Danubian Lowland, Vojvodina and the Southern Great Plain in Hungary, whereas in the other countries it only occasionally colonizes fields. Approximately 10% of all the records of *I. xanthiifolia* are for fields, more than 80% of these after 2000 (Table 2, Fig. 3). Other habitats are only very rarely colonized.

Potential distribution under current climate

All the distributions for the three species studied produced by the ensemble modelling approach have AUC values > 0.8 , and most have AUC values > 0.9 , indicative of “good discriminating ability” (Swets 1998) (Table 3). Currently, these three species occupy less than 1.5% of all the potentially suitable grid cells of the FMCE raster across CEE. However, SDMs show that under current climatic conditions 16%, 28% and 26% of all grid cells are suitable for *A. trifida*, *A. annua* and *I. xanthiifolia*, respectively. The spatial pattern of suitable habitats in CEE is rather similar for these three species (Fig. 4), with lowland regions in the east and south being most suitable. In contrast, cool mountainous regions in the Alps and most parts of western Germany and Croatia are not currently suitable for these species.



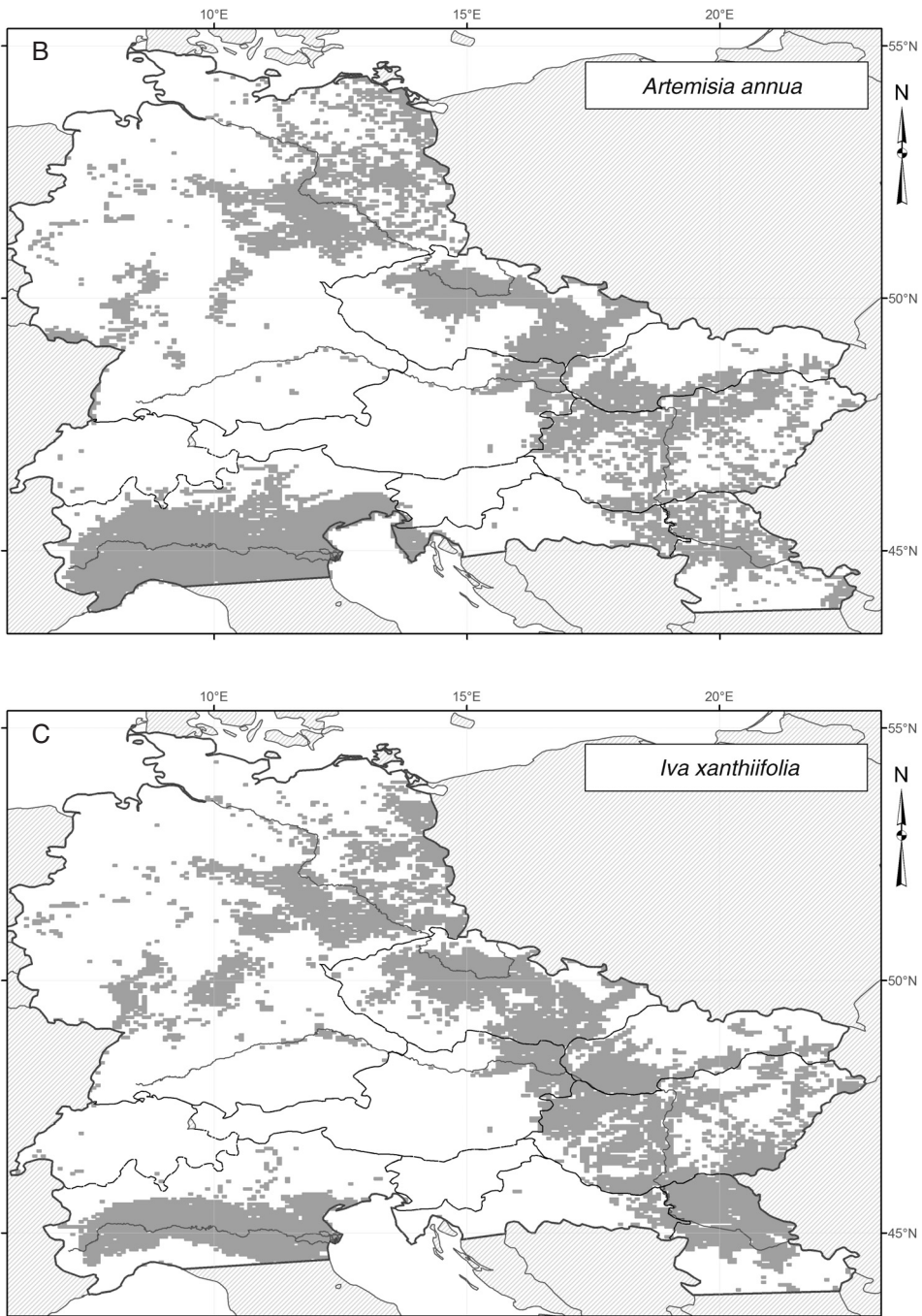


Fig. 4. – Maps of habitat suitability for *Ambrosia trifida* (A) *Artemisia annua* (B) and *Iva xanthiifolia* (C) under current climatic conditions in central and eastern Europe based on an ensemble modelling approach using four regression techniques (GAM, GBM, GLM, MARS) as implemented in the BIOMOD-framework. Suitable grid cells are given in grey, unsuitable ones in white. Projected occurrence probabilities were transformed into presence/absence predictions per grid cell based on the threshold that maximizes model accuracy.

Table 3. – Evaluation of the predictive accuracy (as measured by the AUC) of distribution models of *Ambrosia trifida*, *Artemisia annua* and *Iva xanthiifolia*. GAM = generalized additive models, GBM = generalized boosting models, GLM = generalized linear models, MARS = multiple adaptive regression splines.

Study species	GAM	GBM	GLM	MARS
<i>A. trifida</i>	0.842	0.903	0.857	0.864
<i>A. annua</i>	0.881	0.903	0.870	0.891
<i>I. xanthiifolia</i>	0.901	0.888	0.898	0.891

Table 4. – Single predictor variable importance in the four different regression models of the distribution of *Ambrosia trifida*, *Artemisia annua*, and *Iva xanthiifolia* in central and eastern Europe. GAM = generalized additive models, GBM = generalized boosting models, GLM = generalized linear models, MARS = multiple adaptive regression splines. Variable importance was measured by evaluating how predictions for validation data change as a consequence of their removal from the models (Thuiller et al. 2009). Possible values range from 0 (lowest) to 1 (highest). Empirical values higher than 0.25 are highlighted in bold.

A. *Ambrosia trifida*

	GAM	GBM	GLM	MARS
Highway	0	0.181	0.316	0.046
River	0	0.018	0	0.037
Land use	0	0.374	0	0.069
Temperature seasonality	0	0.023	0	0.261
Minimum temperature of coldest month	0	0.004	0	0.087
Mean summer temperature	0	0.007	0	0.065
Precipitation seasonality	0.356	0.492	0.268	0.84
Mean summer precipitation	0.752	0.045	0.50	0.094

B. *Artemisia annua*

	GAM	GBM	GLM	MARS
Highway	0.069	0.011	0.068	0.045
River	0.03	0.001	0.03	0
Land use	0.062	0.039	0.059	0.111
Temperature seasonality	0.909	0.001	0.791	0.147
Minimum temperature of coldest month	1.045	0.001	0.873	0.263
Mean summer temperature	0.438	0.307	0.386	0.259
Precipitation seasonality	0.192	0.431	0.269	0.503
Mean summer precipitation	0.155	0.075	0.138	0.242

C. *Iva xanthiifolia*

	GAM	GBM	GLM	MARS
Highway	0	0.002	0	0.042
River	0	0	0.022	0
Land use	0.369	0.579	0.302	0.32
Temperature seasonality	0.208	0.065	0.24	0.149
apdefaultMean temperature of coldest month	0	0.002	0	0
Minimum summer temperature	0	0.047	0	0.128
Precipitation seasonality	0.086	0.021	0.131	0.387
Mean summer precipitation	0.312	0.205	0.352	0.1

The importance of the predictor variables for the species studied identified by the four regression techniques differed. The current distribution of *A. trifida* is closely associated with the seasonality of precipitation and summer precipitation, whereas land use and landscape structure were of little importance, or were only important in one model (Table 4A). In contrast, the distribution of *A. annua* is closely associated with summer temperature and seasonality of temperature, but again, seasonality of precipitation proved to be important (Table 4B). Land use and landscape variables are of little importance. Interestingly, land use (i.e. proportion of area occupied by human settlements and fields) was the most important predictor in all models for *I. xanthiifolia* (Table 4C). Climatic variables were of lower importance, and the importance of temperature and precipitation identified by the different regression techniques differed.

Discussion

Invasion history, distribution and spread dynamics

The early invasion of CEE by *A. trifida* was mediated by anthropogenic long-distance dispersal via contaminated grain and oil-seeds from North America as it was found exclusively in larger cities along the rivers Elbe and Rhine and locally in small populations in cities with railway stations and re-loading facilities in other regions of CEE (e.g. Jehlík 1998). In an early study, Stebler (1906) indicated that seeds of *A. trifida* were introduced into Germany from abroad in spring wheat seed. Jehlík & Dostálek (2008) demonstrated that *A. trifida* was introduced into eastern Slovakia (Čierna nad Tisou, Fig. 1A), because North American grain was imported via the former USSR. In contrast to the other two species studied, the low number of established populations and invaded habitats (> 85% of all records were associated with ruderal habitats and railway areas) imply that the spread of *A. trifida* still depends largely on repeated introductions and the species may suffer most from decreasing propagule pressure via contaminated grain and oil-seeds due to improved seed cleaning. Furthermore, *A. trifida* has a relatively low fecundity, a transient seed-bank and a high percentage of non-viable or low-survivorship seeds (Harrison et al. 2007), features which may have constrained its establishment and spread.

The invasion of *A. annua* shows three distinct stages. After an initial phase of slow spread (before 1960) the cumulative number of records increased considerably (1961–1994), but still linearly, until the species entered a phase of rapid exponential spread (after 1995). Early records consisted of small casual populations scattered across CEE and spread was mediated mostly by anthropogenic long-distance dispersal and repeated introductions. After the establishment of stable populations (after 1961, Fig. 2B), a more compact invasion range emerged particularly in northern Italy and along the Elbe river, as short-distance dispersal gained importance and populations of *A. annua* colonized adjacent grid cells (Fig. 1B). *Artemisia annua* spread mainly along riverbanks as shown by Brandes & Sander (1995) and Burkart (2001) for the rivers Saale and Elbe. In northern Italy, cultivation of *A. annua* for medicinal use and its spread into adjacent habitats may have contributed to its extensive expansion (Banfi & Galasso 2010).

The pattern of spread of *I. xanthiifolia* in CEE is characterized by two main stages, namely a distinct time-lag of ~100 years until 1950, followed by spreading at a steady rate coincident with the occurrence of established populations. Like *A. trifida*, it was

frequently found along the rivers Rhine and Elbe where ship ports were often the points of entry. This indicates it was mainly introduced into CEE via grain and oil-seeds from North America before World War II (Jehlík 1998; Fig. 1C). Later, imports of grain by railway from infested sites in its secondary range in the former USSR (Święs & Soroka 1998) led to several new introductions and contributed to a scattered distribution in the eastern part of the area studied (e.g. Slovakia, Czech Republic, eastern Germany; Jehlík & Hejný 1974, Jehlík 1995). Short-distance spread from these invasion foci led to the substantial contemporary acceleration of the rate of spread, particularly into ruderal habitats (Figs 2C, 3). The invasion proceeded at highest rates in the eastern countries of the region studied in the years following World War II (Fig. 1C). This expansion might have been fostered by the extensive availability of suitable habitats (urban wastelands, agricultural changes due to collectivization) as shown by Krippelová (1969), Święs (1993) and Święs & Soroka (1998). Several pathways (soil transport, seeds attached to harvesters, agricultural machines and vehicles) particularly enhanced the dispersal of *I. xanthiifolia* (Krippelová 1969, Jehlík & Hejný 1974).

Habitats colonized and temporal changes in habitat preference

Our results suggest that *A. annua* and *I. xanthiifolia* have both undergone a habitat shift and expansion during their invasion, which may have contributed to their more extensive colonization of CEE than *A. trifida*. In general, more widespread alien plant species have a wider niche breadth in central Europe (Kühn et al. 2004). Habitat shift and concurrent range expansion is a common phenomenon and already documented in CEE for prominent alien plant species like *Impatiens glandulifera* (Pyšek & Prach 1993) and *A. artemisiifolia* (Essl et al. 2009). *Ambrosia trifida* has remained largely restricted to ruderal habitats, which might be one of the reasons for its slow spread in CEE. Outside of the region studied, *A. trifida* occurs in several habitats that it has only rarely or not yet invaded in CEE. In its native range, it can also be found in fields (Harrison et al. 2001) and riverine vegetation (Sickels & Simpson 1985). In CEE, there are a few records of *A. trifida* occurring along the Elbe river (Jehlík & Hejný 1974) and in fields (Rydlo et al. 2011) (Fig. 3). In its introduced range in Korea and Japan, *A. trifida* has even successfully colonized (semi-) natural habitats (Miyawaki & Washitani 1996, Lee et al. 2010). The wider niche breadth of *A. annua* in CEE was already apparent at the beginning of its invasion (e.g. the first record in fields was 1888), but only in the later stages of its spread did this species colonize roadsides, railways and riverine vegetation (after 1970, Fig. 3). *Artemisia annua* is a pioneer species and tolerant of a wide range of ecological conditions (Brandes & Müller 2004), i.e. an opportunistic plant preadapted to roads and railways with their specific disturbance and temperature regimes. River systems were colonized by *A. annua*, probably because of their dynamic hydromorphology, which results in the creation of open pioneer habitats after flooding (Brandes & Müller 2004). Canalization and artificial regulation of water flow (e.g. by construction of groynes in the Elbe river; Brandes 1998) may have additionally aided the spread along river systems. *Iva xanthiifolia* is still largely confined to ruderal habitats, but in contrast to *A. trifida* it has also colonized railway habitats and fields to a certain extent (Fig. 3, Jehlík 1995, Marisavljević et al. 2007, Vrbničanin et al. 2009). The colonization of these habitats may have aided its spread, as railways and fields are well connected.

Current and possible future invasion risk

The current distribution of the species studied is strongly linked to climate, which is indicated by the importance of precipitation and temperature variables in the SDMs. However, even under current climatic conditions, the SDMs and the ongoing spread of these species suggest that there is a substantial potential for further range expansion and increase in abundance in already colonized regions.

It is very likely that even moderate climate warming will result in a considerable increase in the distribution of these three species in CEE, as temperatures are only slightly below the species' requirements in significant proportions of this area. However precipitation is also an important variable explaining the current distributions of all three species. Uncertainties related to changes in precipitation under climate change are much greater than they are for temperature, and regional climate change models for Europe suggest that it is likely that there will be significant regional differences in the changes in precipitation (IPCC 2007). Current land use is an important determinant of the current distribution of *I. xanthiifolia*, but less so for the other two species, whereas variables which represent potential invasion corridors in these models (i.e. rivers, road network) are of little importance for all three species. We hypothesize that this apparent contradiction between the habitat and the landscape scale analysis is actually a consequence of different spatial grains and extents: the coarse-scale SDMs mainly reveal the species' dependence on the pronounced climatic gradients within the study area, while only individual observations allow for identifying local-scale habitat preferences. In addition, colonization of riverine vegetation by *A. annua* is uneven within CEE, with it abundant along some rivers but not yet present along others. This non-equilibrium situation has probably lowered the detectable impact of rivers for *A. annua* in the SDMs.

Impacts and implications for management

The three species studied produce pollen, which can induce allergic diseases (Gergen et al. 1987, Leng & Ye 1987, Weber 2002). Current pollen concentrations of these species in CEE and other European countries are poorly monitored. However, the spread of *I. xanthiifolia* in Lublin (Poland) and *A. annua* in Marseille (France) was reflected in the concomitant recording of significant concentrations of airborne pollen (Spieksma et al. 1980, Weryszko-Chmielewska et al. 2003). To our knowledge, specific pollen hypersensitivity studies for CEE are not available for any of the three species studied (Mari et al. 2009). Given their near-absence in fields, it is not surprising that there are no records of the effect of *A. trifida* and *A. annua* on crops in CEE. In contrast, *I. xanthiifolia* locally invades several crops and may cause substantial yield losses as reported by Hodi (2005).

At present, it seems that all three species do not represent an urgent threat for human health and land use across CEE. However, our results suggest that these species have not fully realized their invasion potential, particularly *A. annua* and *I. xanthiifolia*. The likely associated effects on human health call for the development of proactive management strategies focused on systematic prevention and early control. A starting point might be to use our data to apply the EPPO prioritization process (EPPO 2012) in order to assess whether these species are still containable using appropriate measures and their potential for further spread in CEE or each country. Special attention should be given to regions for which the SDMs indicate a high invasion potential (Fig. 4). Any management strategy

must incorporate a way of increasing the awareness of landowners, farmers and municipal authorities (road managers, water authorities). Based on pathways for long-distance dispersal, our results propose that new populations are most likely to become established in locations like harbours, reloading points, warehouses or along roadsides and hence these locations should be regularly surveyed by authorities and landowners. It is also suggested that emphasis should be placed on treating incipient populations (Richter et al. 2013) with herbicides, hand weeding or mowing in order to eliminate potential invasion foci. Once a soil seed bank has formed, control becomes increasingly difficult and time-consuming. In areas with established populations, more intensive and strategic control efforts ('action plan') are needed (e.g. repeated mowing, establishment of a dense cover of vegetation, change in crop rotation and application of specific herbicides; e.g. Marisavljević et al. 2006). Management should concentrate on limiting the species' spread into previously uncolonized areas. For example, machinery operators should be educated on the ways of avoiding transporting propagules attached to vehicles and agricultural machinery.

See <http://www.preslia.cz> for Electronic Appendix 1–3

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Souhrn

V práci jsme analyzovali historii invaze, dynamiku šíření a stanovištní preference tří alergenních, větrem opylovaných druhů z čeledi *Asteraceae* (*Ambrosia trifida*, *Artemisia annua* a *Iva xanthiifolia*) ve střední a východní Evropě. Pomocí kombinace prediktivních modelů rozšíření, založených na konceptu niky, jsme také vyhodnotili současná rizika spojená s invazí těchto druhů. Celkem jsme ve studované oblasti zjistili 1804 lokalit *A. annua*, 1063 lokalit *I. xanthiifolia* a 324 lokalit *A. trifida*. Všechny tři druhy byly poprvé zaznamenány v 19. století, do poloviny 20. století byly vzácné, ale v posledních desetiletích se rychle šíří; nejrychleji se šířila *I. xanthiifolia*, o něco pomaleji pak *A. trifida*, která je nyní hojná v severní Itálii, podél Labe v Německu a v Podunajské nížině na Slovensku a v Maďarsku. *Iva xanthiifolia* je nejhojnější v teplých a kontinentálních oblastech střední a východní Evropy. *Ambrosia trifida* se šířila pomalu a v současnosti je známa jen z několika málo, většinou izolovaných lokalit. *Ambrosia trifida* a *I. xanthiifolia* se vyskytují primárně na ruderálních stanovištích, druhý druh však stále častěji invaduje i na polích. *Artemisia annua* byla původně vázána také na ruderální stanoviště, v průběhu invaze se však rozšířila i do pobřežních a (polo)přirozených porostů. Modely rozšíření ukázaly, že současný výskyt *A. trifida* a *A. annua* ve střední Evropě závisí na teplotě a srážkách, zatímco v případě *I. xanthiifolia* je jeho nejvýznamnějším prediktorem způsob využití krajiny. V současných podmínkách je poměrně velká část studovaného území klimaticky vhodná pro výskyt všech tří druhů; *A. trifida* nachází příznivé klimatické podmínky na 16 % území střední a východní Evropy, *A. annua* na 28 % a *I. xanthiifolia* na 26 %. Vzhledem k významnému dopadu těchto druhů na zdraví lidské populace by mělo být jejich další šíření monitorováno a co nejrychleji by měla být vypracována účinná strategie, která by zabránila jejich dalšímu šíření.

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