Changes in the spatio-temporal patterns and habitat preferences of *Ambrosia artemisiifolia* during its invasion of Austria

Změny v rozšíření a vazbě na stanoviště v průběhu invaze *Ambrosia artemisiifolia* v Rakousku

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The invasion of Austria by the alien vascular plant *Ambrosia artemisiifolia* (*Asteraceae*) is analysed in detail, based on a survey of available records. In total, 697 records were collated. The first record for Austria is a herbarium specimen collected in 1883. Up to the end of the 1940s, records were rare and only of casual populations resulting from long-distance dispersal. Since the 1950s, the number of records has increased exponentially, and more than one third of all records (242) were collected in the last 5-year period (2001–2005) included in the survey. The first naturalized population was recorded in 1952, nearly 70 years after the first record of a casual population. Recently, the number of naturalized populations increased considerably faster than that of casual populations. Several pathways (contaminated crops and bird seed, agricultural machines, transport of soil) have contributed to the high levels of propagule pressure and this successful invasion. *Ambrosia artemisiifolia* has undergone a niche expansion during the invasion process. Up to 1950, most records were from sites along railway routes, whereas in the period 1950–1974 it was mostly ruderal habitats, not associated with traffic infrastructure, which were colonized. Since the 1970s, records from roadsides have increased strongly and now dominate. Fields were colonized first in the 1970s and since then have gained in importance. The distribution of naturalized populations was related to environmental and climatic variables by means of a generalized linear model. Their distribution in Austria is closely related to temperature. Landscape variables, describing aspects of habitat availability (topography, land use, major street density) also significantly explain the current distribution of *A. artemisiifolia*. Suitable habitats currently occur mainly in the eastern and southeastern lowlands. We conclude that global warming will disproportionally enhance the invasion success of *A. artemisiifolia* in Austria, even if there is only a slight increase in temperature, as significant areas of agricultural land in Austria are currently only slightly too cool for *A. artemisiifolia*. The widespread occurrence of this species will have serious consequences for human health and agriculture.

Keywords: climate change, human health, introduction history, invasion, naturalization, niche expansion, species distribution models, spread

Introduction

Biological invasions are an acknowledged major threat to global biodiversity (Williamson 1996, McNeely et al. 2001). In Europe, a recent review identified 5789 alien vascular plants, and this number is growing rapidly (Lambdon et al. 2008). A better understanding of the causes and underlying mechanisms of invasions is hence of prime importance. Conducting detailed analyses of the invasion history of one or a few alien species is a well-established way of gaining new insights into biological invasions (Trepl 1984, Pyšek & Prach 1993, Pyšek & Hulme 2005, Essl 2007). Such analyses are also crucial for developing strategies for successful management of invasive alien species (Williamson 1996, Kowarik 2003a).

During the invasion of a species, changes in the importance of factors governing the spatio-temporal pattern of spread might occur. These changes may affect the relative importance of the pathways and habitats colonized, the persistence and size of populations and the role of environmental and climatic variables or land use (Trepl 1984, Kowarik 2003a, Pyšek & Richardson 2006). Habitat shifts or expansions of alien plants have been documented in Central Europe several times (e.g., Trepl 1984, Kowarik 1995, 2003a). Habitat shifts can enhance competitiveness of an invading species and may increase its geographic distribution, as well as its impact on native biota. However, as several factors can contribute to habitat shifts or expansions (Jakobs et al. 2004, Broennimann et al. 2007), this phenomenon can usually only be studied by retrospective analysis.

Species distribution models (SDM; Guisan & Zimmermann 2000, Guisan & Thuiller 2005) have become an important tool for assessing the potential range of species under current as well as predicted future environmental conditions. SDMs use sample data to relate the occurrence, or abundance, of species to a range of mostly abiotic site conditions by means of a variety of statistical techniques (Elith et al. 2006).

Ragweed, *Ambrosia artemisiifolia,* is a wind-pollinated annual plant native to the central USA. It invaded Central Europe late in the 19th century. Recently, it has greatly increased in range and abundance (Chauvel et al. 2006, Kiss & Beres 2006, Brandes & Nitzsche 2007). Ragweed is of particular concern because many people develop an allergic reaction to its pollen, which causes problems for public health (Taramarcaz et al. 2005).

Records of the presence of *A. artemisiifolia* in Austria up to the year 2005 were extracted from a wide range of data sources. This dataset was previously used to analyse other effects related to invasion history, propagule pressure and spatial autocorrelation (Vogl et al. 2008, Dullinger et al. 2009). Here, the distribution data and a large set of variables describing climate, environmental factors (e.g., bedrock, topography) and land use, were used to address the following questions: (i) How did the pattern of spatio-temporal spread and the proportion of naturalized and casual populations change during the invasion? (ii) Which factors govern the current distribution pattern of *A. artemisiifolia*? (iii) How did habitat preferences of *A. artemisiifolia* change during the invasion?

Material and methods

Study area

Austria is a landlocked country in Central Europe, covering an area of 83,858 km^2, with a population of slightly more than 8 million inhabitants mainly living in the lowlands and major valleys in the Alps. Two thirds of Austria consists of mountainous regions. The landscape at low to medium altitudes is shaped by a long tradition of human land use. About 27% of the flora of Austria consists of neophytes (post-1500 aliens), which have been well studied (Essl & Rabitsch 2002, and references therein).

Study species

Ambrosia artemisiifolia L. (common ragweed; *Asteraceae*), is a wind-pollinated annual herb germinating in spring and setting fruit in autumn. As a pioneer species, it mainly thrives in open semi-arid habitats in its native range and in ruderal and segetal habitats in invaded regions (Basset & Crompton 1975, Chauvel et al. 2006). Its native range is restricted to parts of central USA. Since the middle of the 19th century, and especially over the last few decades, it has invaded several temperate regions of the world, including SE and SW Europe, where it has greatly increased in range and abundance since the mid-20th century (Chauvel et al. 2006, Kiss & Beres 2006, Brandes & Nitzsche 2007).

Besides its economic impact on crop yields (Reinhardt et al. 2003, Sheppard et al. 2006), the strongly allergenic pollen of ragweed is causing considerable problems for public health (Taramarcaz et al. 2005). Hence, the species is receiving considerable and increasing attention from European ecologists (Song & Prots 1998, Genton et al. 2005, Chauvel et al. 2006) as well as immunologists (Jäger 2000, Taramarcaz et al. 2005) and national strategies for preventing its further spread have been developed (Bohren et al. 2006).

Distribution data and data analyses

All the records of the presence of *A. artemisiifolia* in Austria up to 2005 were collected. This information was gathered from many different sources: the database of the Floristic Mapping project of Austria (FMA; Niklfeld 1998), public and many private herbaria, the literature and unpublished records.

All records were assigned to a grid cell (5 × 3 geographic minutes, ca 30 km^2) of the FMA. The date (= year) of each record was obtained from the original source. Data on the habitat colonized was obtained from original data sources. Habitats were classified using a simplified version of the Austrian habitat catalogue (Umweltbundesamt 2005); the following categories were used: roadsides, ruderal habitats associated with railways, waste sites, bird feeding places, other ruderal habitats not associated with the above sites, cultivated fields and gardens. We analysed invasion curves (Pyšek & Prach 1993) across habitat types by calculating the cumulative number of records and invaded grid cells per habitat.

For each record the status of the respective population – whether naturalized or non-naturalized – was assessed either by the observer or by us 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 naturalized if at least two records in consecutive years were reported. Populations that observers had not explicitly rated as either naturalized or non-naturalized and which we could not classify unambiguously based on information given in the original source were also classified as non-naturalized. Non-naturalized records hence include a continuous range from casual to small populations.

Altitude of the records was obtained from the original sources or by reference to the Austrian Map (BEV 2008). We calculated altitudinal ranges for naturalized and non-naturalized populations and for different time periods separately to determine whether climatic constraints act differently at different stages during the invasion.

Species distribution model

Spatially explicit data on climatic conditions, topography and land use were collected from various sources (Table 1). All GIS data were pre-processed to match the resolution of the FMA raster (Table 1), i.e. aggregation by means of averaging (topographical data) or summarizing (street length). For calibrating the SDM, records of *A. artemisiifolia* were partitioned into those of naturalized and non-naturalized populations (Dullinger et al. 2009). The distribution of naturalized populations was then related to the environmental variables by means of a generalized linear model (GLM) with a binomial error distribution and a logistic link function, i.e. *A. artemisiifolia* was recorded as present only in FMA cells where there were naturalized populations and absent from all other cells. This was motivated by the assumption that the distribution of naturalized populations is more likely to reflect the habitat requirements of the species (Richardson et al. 2000). Indeed, models that only include naturalized populations are more accurate than those that include all the records (Dullinger et al. 2009). Using a backward elimination procedure, i.e. elimination of individual variables and ANOVA comparisons of full and restricted models, predictors were retained in the model at a threshold P-level of 0.05. Non-linear effects of the individual predictors were tested separately by means of restricted cubic spline functions with three knots (Harrell 2001). Non-linear terms were kept in the model using the same threshold P-level.

Following the recommendations by Liu et al. (2005), prevalence (= ratio of infested grid cells vs total number of grid cells) was chosen as a threshold for presence/absence predictions. To present a graduated habitat suitability map we constructed three habitat suitability classes – with the threshold (0.14) itself falling into the middle one: ‘low habitat suitability’ (< 0.08), ‘high habitat suitability’ (0.08–0.15), ‘very high habitat suitability’ (> 0.15).

The nomenclature of vascular plants follows Fischer et al. (2005). Statistical analyses were carried out in R, version 2.5.1 (R Development Core Team 2006).

Table 1. – Environmental variables used to calibrate the model of the distribution of *Ambrosia artemisiifolia* in Austria.

Category	Variable	Source	Original scale
Climate: Temperature	mean annual, winter, summer and monthly temperatures, and number of frost days	Austrian Institute for Meteorology and Geodynamics	250 × 250 m grid
Climate: Precipitation	mean annual and seasonal precipitation	Austrian Institute for Meteorology and Geodynamics	250 × 250 m grid
Topography	standard deviation of curvature	Digital elevation model of the Austrian Mapping Agency	250 × 250 m grid
Land use	proportion of area occupied by human settlements and agricultural fields	CORINE Land cover	map with min. 25 ha polygons
Bedrock	percentage of the area with a calcareous substrate	Geological survey of Austria	1: 1 000 000 map
Human traffic	length of major roads	Tele Atlas N.V. (© 2005)	–

Results

Introduction history and distribution

In total 697 records of *A. artemisiifolia* from 366 FMA cells were obtained from more than 30 sources (Fig. 1). In 10 FMA cells there were at least 5 records (maximum: 17 records). The first record of *A. artemisiifolia* in Austria is a herbarium specimen collected in 1883. Up to the end of the 1940s, records of this plant were very rare (on average between zero and 0.6 records per decade) and scattered, and were only of small casual populations, mostly in large cities.

Since the 1950s, the number of records has increased exponentially (Fig. 2). The number of cells for which there were records increased from 122 in 1980 to 366 in 2005, with occurrences of naturalized populations nearly quadrupling (25 in 1980 to 97 in 2005) and non-naturalized populations nearly tripling (104 in 1980 to 318 in 2005). More than 1/3 of all records (242) were collected in the last 5-year period (2001–2005) included in this study. The first record of a naturalized population was in 1952, nearly 70 years after the first record of a casual population in Austria. In the period 2001–2005, the number of naturalized populations increased to 85, which is 35% of all the records in this period. Hence, the number of naturalized populations has recently been increasing considerably faster than that of casual populations.

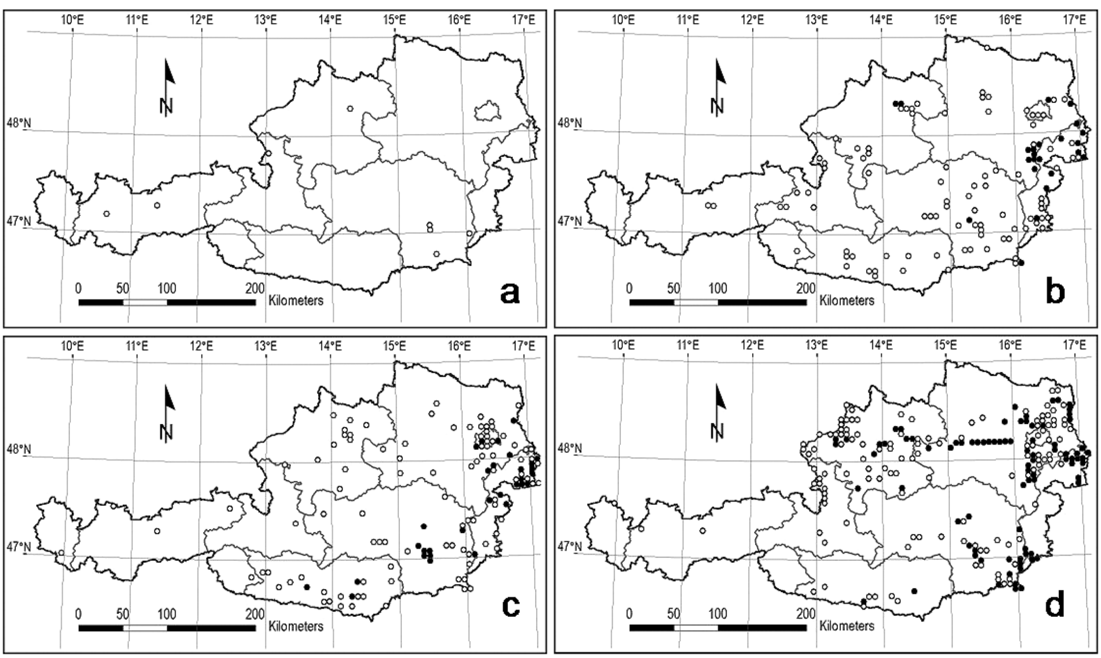


Fig. 1. – Grid distribution maps of *Artemisia artemisiifolia* in Austria for the periods 1883 to 1949 (a), 1950 to 1979 (b), 1980 to 1994 (c) and 1991 to 2005 (d). Naturalized populations are represented by black circles, casual ones by open circles. Points symbolize at least one record in each cell of the grid.

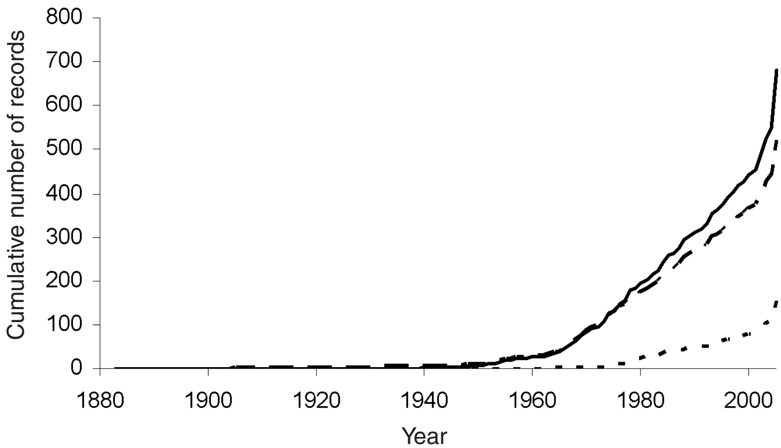


Fig. 2. – Cumulative number of records of *Artemisia artemisiifolia*. Records naturalized (dotted line) and casual (dashed line), and the sum of all records (solid line) are shown.

Habitat preference over time

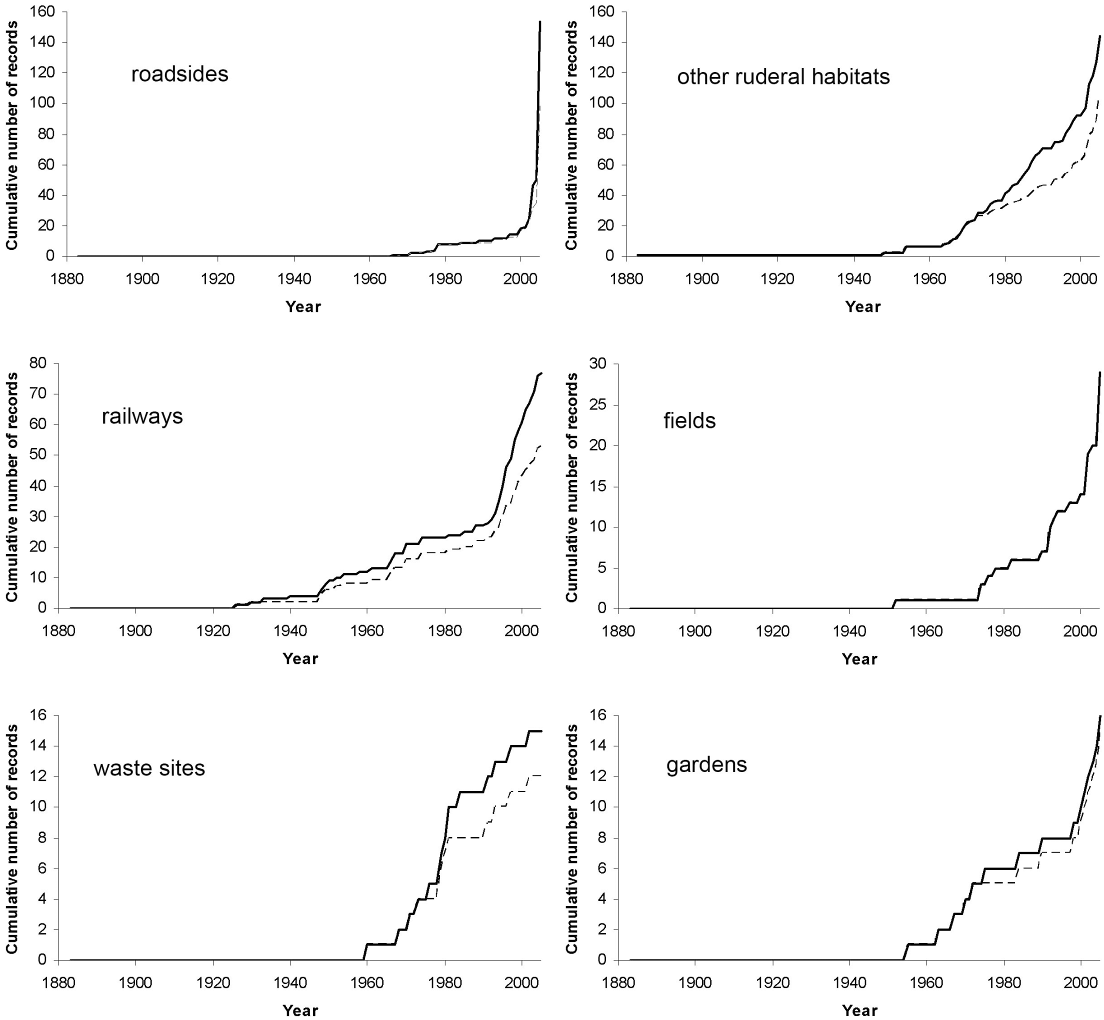
The habitat preference of *A. artemisiifolia* changed and broadened considerably during the invasion (Fig. 3, Table 2). Until 1950, most records were associated with railways, whereas in the period 1950–1974 they were for ruderal habitats not associated with traffic infrastructure. Since the 1970s, and especially in the last few years included in this study, records from roadsides increased strongly and became dominant. Fields were first colonized in the 1970s and have gained in importance since then. Habitats associated with bird feeding places and gardens peaked in the period 1950–1979, but have since become less important.

The cumulative number of grid cells with records for a particular habitat type generally follows the pattern of the invasion. For several habitats, the number of grid cells for which there are records is identical (fields) or only marginally lower than the number of individual records (roadsides, gardens, waste sites), whereas for the other habitats (railways, other ruderal habitats, bird feeding places) it is considerably lower than the number of individual records.

Factors promoting and limiting spread

The distribution of the naturalized populations of *A. artemisiifolia* across the FMA raster in Austria is closely related to temperature (Table 3). The mean temperature of the hottest month (July) predicts the distribution slightly, but significantly, better than the mean annual temperature. Interestingly, its distribution is not associated with precipitation. Landscape variables describing aspects of habitat availability are weakly, but significantly associated with the current distribution. The variables are: topography, land use and denisty of major roads. With a bootstrap-validated Somers' Dxy of 0.85 and a R^2 of 0.41, the calibrated SDM is a good predictor (Guisan & Harrell 2000).

In general, records, particularly those of naturalized populations, are still most frequent in the E and SE lowlands of Austria (Fig. 4), the warmest parts of the country. More than



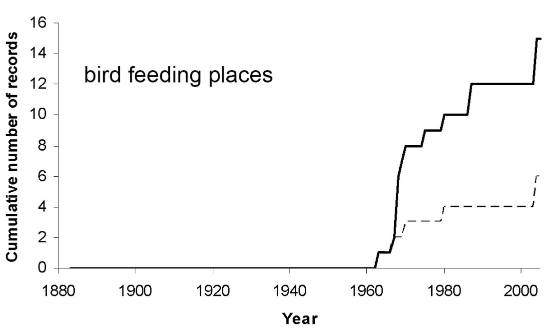


Fig. 3. – Invasion curves (sensu Pyšek & Prach 1993) of *Artemisia artemisiifolia* for different habitats in Austria. Results are expressed as the cumulative number of records (solid line) and cumulative number of grid cells (dashed line) of the project 'Floristic Mapping of Austria' (5' × 3', ca 30 km^2) with records. Note, that both lines are identical for fields.

Table 2. – Habitats colonized by *Ambrosia artemisiifolia* during the different periods of its invasion. Numbers of records for each habitat are shown followed by its percentage contribution to the total number of records in the given period (n = 450); for 247 records habitat data were not available. The category “other ruderal habitats” includes all ruderal habitats not associated with traffic infrastructure, waste sites or bird feeding places.

Period	Roadsides	%	Railways	%	Other ruderal habitats	%	Fields	%	Waste sites	%	Bird feeding places	%	Gardens	%	Total
1883–1949	0	0.0	8	80.0	2	20.0	0	0.0	0	0	0	0	0	0.0	10
1950–1979	2	3.1	15	23.4	27	42.2	3	4.7	4	6.3	8	12.5	5	7.8	64
1980–1994	10	10.8	12	12.9	46	49.5	9	9.7	9	9.7	4	4.3	3	3.2	93
1995–2005	142	50.2	42	14.8	69	24.4	17	6.0	2	0.7	3	1.1	8	2.8	283
Total	154	34.2	77	17.1	144	32.0	29	6.4	15	3.3	15	3.3	16	3.6	450

Table 3. – Variables retained in the distribution model of *Ambrosia artemisiifolia* and their Wald χ^2 statistics. d.f. – degrees of freedom.

Variable	d.f.	÷2	P-value
Mean July temperature	1	68.11	< 0.0001
Length of major roads	1	15.35	0.0001
Curvature	1	15.16	0.0001
Proportion of the area made up of human settlements and agricultural fields	1	9.35	0.0022

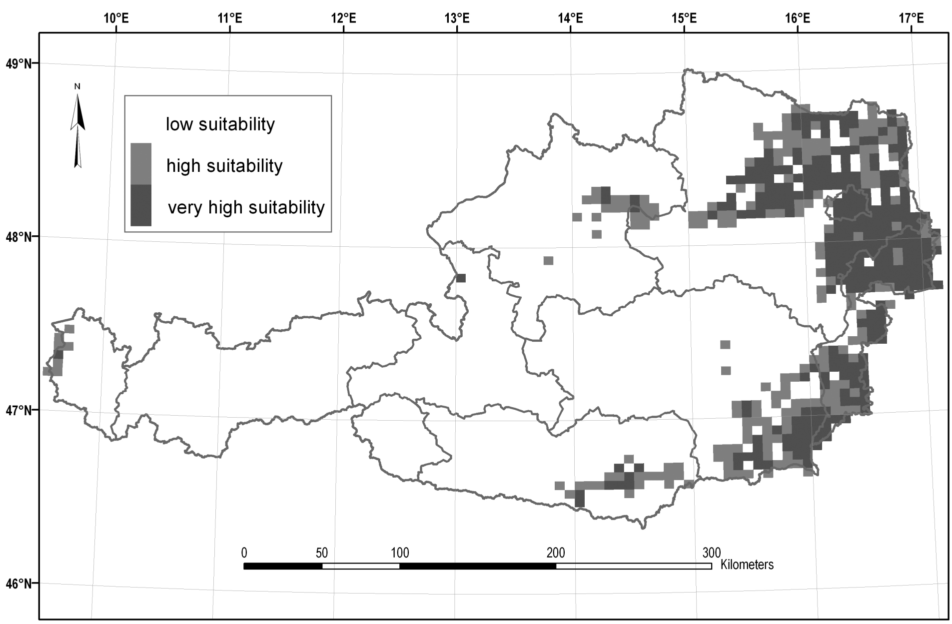


Fig. 4. – Habitat suitability map for *Artemisia artemisiifolia* under current climatic conditions based on a generalized linear model calibrated using the distribution of naturalized populations in 2005. A prevalence of 0.14 was chosen as a threshold for presence/absence predictions: ‘low habitat suitability’ (< 0.08), ‘high habitat suitability’ (0.08–0.15), ‘very high habitat suitability’ (> 0.15). The squares are the cells of the ‘Floristic Mapping of Austria’ (5' × 3', ca 30 km^2).

50% of the records are for locations below 400 m s.l., which includes only 37% of Austria. On average, casual populations are recorded at much higher average altitudes (395 m s.l.) than naturalized populations (301 m a.s.l.). The highest altitude for a casual population was 1100 m a.s.l.

Discussion

Quality of the information on distribution and its interpretation

Distribution data based on herbaria specimens (e.g., Pyšek & Prach 1993, Delisle et al. 2003, Chauvel et al. 2006, Lavoie et al. 2007) or floristic mapping projects (e.g., Mandák et al. 2004, Rich 2006) have been used successfully to reconstruct patterns of spread. However, these data are not usually based on a constant sampling effort, which could result in significant errors when reconstructing patterns of spread (Delisle et al. 2003, Pyšek & Hulme 2005, Rich & Karran 2006). However, this seems to be unlikely in the present case. First, *A. artemisiifolia* is a conspicuous and because of its allergenic effects a well-known species, which for a long time has been included in Central European standard floras. Second, Austria has a long and very strong tradition of floristic research dating back to the first half of the 19th century, which makes the Austrian flora one of the best documented in the world. And third, the integration of a couple of different data sets should mitigate any spatio-temporal variation in sampling effort. Indeed, the compilation of different data sets significantly improved data coverage, as each of the sources provided a considerable number of unique records. The majority of the records were extracted from the database of the FMA (ca 250 records), followed by floristic literature (ca 170 records), herbarium specimens (ca 150 records) and unpublished records (ca 130 records).

History of the introduction and distribution pattern

The first records of *A. artemisiifolia* in Europe are from the second half of the 19th century: France (1863; Chauvel et al. 2006), Germany (1863; Brandes & Nitzsche 2007) and the Czech Republic (1883; Pyšek et al. 2002b). Interestingly, from Hungary, where *A. artemisiifolia* is omnipresent now, it was not reported until 1922 (Balogh et al. 2008). The first records of *A. artemisiifolia* in Austria are nearly all for several larger cities and are probably related to repeated human-assisted long-distance dispersal. Only after the occurrence of the first naturalized populations and the associated local spread of populations to adjacent grid cells of the FMA did a more compact invasion range in the eastern lowlands emerge. This spatio-temporal picture of spread corresponds to stratified dispersal processes consisting of long-distance movements and local diffusion (Kowarik 2003b, Gilbert et al. 2004, Hastings et al. 2005, Nehrbass et al. 2007).

An alien species has to overcome several barriers if it is to become a successful invader (Richardson et al. 2000). Our post hoc analysis shows that the invasion of Austria by *A. artemisiifolia* exhibits four stages:

I. Rare introductions (1883–1949): All records of *A. artemisiifolia* are of small populations scattered across the Austrian territory; spread is mediated exclusively by anthropogenic long-distance dispersal and repeated introductions (80% of all records are associated with railways).

II. Incipient spread and local naturalization (1950–1979): numbers of records increase considerably, although *A. artemisiifolia* continues to be rare; reproduction within Austria and short distance dispersal gain importance; first naturalized populations are recorded in the most favourable areas of E and SE Austria, fields are colonized for the first time.

III. Increased spread and regional naturalization (1980–1994): number of records increases, especially of naturalized populations in the cooler and wetter lowland areas in N Austria; short distance dispersal is dominant.

IV. Rapid spread (1995-ongoing): a great increase in the numbers of records, *A. artemisiifolia* is naturalized in increasingly larger fraction of the lowlands of Austria; spreading mainly along major roads and the first very large populations recorded.

In Austria, there was a lag phase of ca 70 years between first records of casual populations of *A. artemisiifolia* and its incipient spread and local naturalization. The saturation phase of the invasion – i.e. when the rate of invasion of new areas slows down (Pyšek & Hulme 2005) – has apparently not been reached in Austria, in terms of the number of records or number of grid cells (ca 30 km^2) colonized. In other Central European countries there is a similar ongoing rapid expansion in the range of *A. artemisiifolia*, e.g. in Switzerland (Bohren et al. 2006), W Ukraine (Song & Prots 1998) and N France (Chauvel et al. 2006), whereas in Hungary (Balogh et al. 2008) and in S France (Chauvel et al. 2006) this species has achieved saturation phase and is omnipresent.

Genetic analyses have shown that *A. artemisiifolia* was independently (and unintentionally) introduced into Europe several times (Genton et al. 2005). Invasion patterns in Austria, which are characterized by scattered casual occurrences during the first decades, are well in line with these marker-based reconstructions. The seed of *A. artemisiifolia* is not adapted for dispersal by wind or animals (Bassett & Crompton 1975), long-distance dispersal is mostly dependent on man. Several pathways (contaminated crops and bird seed, agricultural machines, transport of soil) contributed to high levels of propagule pressure (Chauvel et al. 2006, Brandes & Nitzsche 2007, Vitalos & Karrer 2008) and a successful invasion.

Habitats and habitat change

Our results suggest that the habitat preferences of *A. artemisiifolia* changed during its invasion of Austria, as it has recently successfully colonized roadsides and fields, which were not initially colonized until the 1950s. In Quebec, *A. artemisiifolia* similarly invaded a wider range of habitats in the later stages of its spread (Lavoie et al. 2007). In Germany, colonization of fields is also a recent phenomenon (Brandes & Nitzsche 2007). In contrast, it colonized clover fields in France very early as contaminated clover seed from the US was widely used (Chauvel et al. 2006). As the colonization of fields and field margins offers a potentially very large new niche for *A. artemisiifolia* (Bazzaz 1974), we expect that if the recent spread continues, the majority of ragweed populations will in the near future grow in fields and associated habitats. In Hungary, *A. artemisiifolia* is ubiquitous in fields and the most common weed nationally (Mihály & Botta-Dukát 2004, Balogh et al. 2008) and has colonized several habitats there that it has not yet invaded in Austria (e.g., dry grassland, sand dunes – Mihály & Botta-Dukát 2004). Interestingly, the invasion rates for some habitats in Austria determined using numbers of records and colonized grid cells differ, whereas for other habitats they are similar. We argue that this can partly be attributed to different spatio-temporal invasion patterns; e.g. invasion of roadsides occurred only recently and due to the connectivity of this habitat spread across grid cells very fast.

More widespread alien plant species have a wider niche breadth in Central Europe (Kühn et al. 2004). Our results show that an increase in niche breadth may occur only during the later stages of an invasion. Niche shift or expansion is one of the main factors that make ex-ante risk analyses of biological invasions so difficult (Ruiz & Carlton 2003); hence a better understanding of this phenomenon is needed. Several factors contribute to habitat change, including evolutionary processes within an alien species (Jakobs et al. 2004), alterations in the recipient habitats (Broennimann et al. 2007, Lavoie et al. 2007) or historical circumstances, which may prevent the alien species immediately colonizing the whole range of suitable habitats e.g., due to spatial mismatch. As in Quebec (Lavoie et al. 2007), the increase in network density might have fostered the recent spread along roads in Austria.

Environmental factors, habitat corridors and habitat availability

The current distribution of *A. artemisiifolia* is strongly linked to climate, which is indicated by the importance of mean July temperature in the species distribution model. This result is in line with the general pattern of invasions in Europe, which is characterized by a pronounced latitudinal and altitudinal gradient in the risk of invasion (Pyšek et al. 2002a, Pyšek & Richardson 2006) and where the current distribution of many alien plants is mainly limited by climatic constraints (Pyšek et al. 2002b, Walther 2003, Vilà et al. 2007). Assuming no climate change, the future spread of *A. artemisiifolia* in Austria will primarily lead to increased frequency in already suitable areas across the eastern and south-eastern lowlands, with mostly casual populations occurring in the Alpine foothills and low-lying valleys of the Alps.

Global warming will greatly enhance the invasion success of *A. artemisiifolia* in Austria, even under moderate climate change scenarios. Currently, large areas of agricultural land in Austria are only slightly too cool for *A. artemisiifolia*. The current distribution pattern in Europe underpins our results, as ragweed is widespread in adjacent areas with a slightly warmer climate, e.g. Hungary (Balogh et al. 2008). The expansion of *A. artemisiifolia* in the last decades into the E and SE Austrian lowlands has probably also been fostered by an increase in the annual mean temperature of ca 1° C since the 1950s. Precipitation does not significantly influence current distribution and is therefore not included in the SDM. However, if temperature increases were to be coupled with significant decreases in precipitation during the vegetation period, this might impose constraints on the future invasion process, as *A. artemisiifolia* is not competitive in mediterranean-like climatic conditions, where dry summers prevail (Chauvel et al. 2006).

Linear corridors such as the network of major roads and railways facilitate the invasion of weedy alien species (Christen & Matlack 2006). In Austria, the invasion by *A. artemisiifolia* is strongly associated with railways and, since the 1970s, roadside habitats, i.e. human transportation activities (Christen & Matlack 2006, von der Lippe & Kowarik 2007). Major roads with their specific disturbance and temperature regime represent a well-connected habitat network and were invaded by *A. artemisiifolia* in the 1970s (Table 2). Colonization of roadsides might have been facilitated by its high tolerance of the saline conditions that resulted from the widespread use of salt for de-icing the roads (Di

Tommasso 2004) in Austria since the 1960s. Mowing of roadsides enhances its spread, as significant numbers of seeds stick to mowing machines (Vitalos & Karrer 2008). Interestingly, in Quebec *A. artemisiifolia* initially spread along river corridors and only recently has spread via the road network (Lavoie et al. 2007). This delay in the spread along roads is mainly attributed to the increase in the number of roads and the increased application of salt for de-icing.

Effects on human health and agriculture

The strongly allergenic pollen of ragweed is having an adverse effect on the health of many people in Europe (Jäger 2000, Taramarcaz et al. 2005). The recent spread of *A. artemisiifolia* in Central Europe is also reflected in the significant increase of ragweed pollen in pollen traps (Jäger 2000, Bohren et al. 2006). Exposure to high levels of pollen of *A. artemisiifolia* leads to an increasing number of people developing allergic reactions. Hence, in Hungary, 80% of all allergies caused by pollen are to ragweed pollen, compared to only 30% in Vienna and 1.25% in Germany (Jäger 2000, Reinhardt et al. 2003). The annual economic cost of the ragweed invasion of Germany is estimated to be 32 million €, nearly entirely due to the increased cost incurred by the health sector (Reinhardt et al. 2003).

The economic impact of *A. artemisiifolia* on crop yields can be significant (Reinhardt et al. 2003, Sheppard et al. 2006). In heavily infested maize fields crop losses of up to 70% are recorded in Hungary (Balogh et al. 2008). Not surprisingly the biological control of *A. artemisiifolia* in Europe is considered to be of top priority (Sheppard et al. 2006). In Austria, infestations of fields are a rather recent phenomenon and hence this weed currently has little effect on crop yield. However, if the current rate of spread continues it will have a negative impact on agriculture in the near future.

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Souhrn

V práci je podrobně analyzován průběh invaze druhu *Ambrosia artemisiifolia* (*Asteraceae*) v Rakousku. Druh je znám z celkem 697 lokalit, prvním údajem je herbářová položka z roku 1883. Do 40. let 20. století byl druh poměrně vzácný a vyskytoval se v podobě přechodně zavlečených populací, jež vznikaly dálkovým šířením. Od 50. let 20. století počet zjištěných lokalit rostl exponenciálně a více než třetina údajů pochází z let 2001–2005. První naturalizovaná populace byla zaznamenána v roce 1952, více než 70 let poté, co byl druh v Rakousku nalezen poprvé. V současné době roste počet naturalizovaných populací rychleji než počet přechodně se vyskytujících populací. Druh je zavlékán jako příměs osiv a ptačího zobu, se zemědělskou technikou a při přemisťování půdy. Během invaze druh pronikal do postupně širšího spektra stanovišť; do roku 1950 byla většina lokalit zaznamenána na železnici, v letech 1950–1974 se rozšířil na ruderální stanoviště. Of 70. let 20. století jsou převládajícím stanovištěm okraje silnic. Rozšíření *A. artemisiifolia* v Rakousku úzce souvisí s teplotními poměry, průkazný vliv má typ stanoviště, hustota silniční sítě a topografie. Lze předpokládat, že probíhající oteplování povede k většímu rozšíření *A. artemisiifolia*, neboť v současné době je druh v mnoha zemědělských oblastech omezován nízkými teplotami.

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