

Climate warming drives invasion history of *Ambrosia artemisiifolia* in central Europe

Oteplování ovlivňuje invazi *Ambrosia artemisiifolia* ve střední Evropě

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It is thought that future climate change is likely to foster biological invasions, but effects of climate warming on invasions in recent decades are little explored. In this paper, we analyse the history of the spread of *Ambrosia artemisiifolia* (common ragweed) in central Europe in order to determine the effects of climate warming. In addition, we infer the likely history of this species' spread and current distribution from incomplete documentation. The area studied in central Europe includes Austria, the Czech Republic, Germany, Hungary, Liechtenstein, Slovakia, Slovenia and Switzerland. These countries were represented by a lattice of grid cells of size 5' × 3' (~ 6 × 6 km²), and we modelled this species' increase in range in this grid from 1900 to 2010 at an annual resolution. The spread was modelled to be driven by the spatio-temporal variation in environmental suitability of grid cells as determined by climatic conditions and land use, propagule production and dispersal from invaded cells, and 'background' introductions from unknown sources. A hierarchical Bayesian modelling approach accounted for lagged and incomplete records of occurrence and spatio-temporal variation in sampling intensity. We fitted models with different representations of climate variation over time, and further contrasted the hierarchical model to a simplified model, which assumed that records accurately reflected the species' actual spread. Climatic conditions were the most important determinants of environmental suitability for invasion, and suitability also increased with increase in the proportion of urban area and length of railways in grid cells. Temperature was, on average, 2.7 °C higher in the environmentally more suitable cells than in the less suitable cells. The pattern in the spread was determined by local range expansion from multiple, spatially scattered points of introduction. Assuming a linear trend in climate warming over the modelling period provided a better model fit than using annual weather conditions or the long-term average of the climate. The model estimated that by 2010 only about 60% of the actually invaded grid cells were recorded, and records lagged behind actual colonizations by years up to decades. Inferences of the hierarchical and simplified models differed quantitatively. We conclude that by using our modelling framework it is possible to separate spatial effects of climate on the spread of non-native species from temporal effects, and that climate warming has already promoted the spread of *Ambrosia artemisiifolia* in central Europe. The recorded distribution reflects only a part of this species' actual distribution. Properly accounting for incomplete records hence improves inferences about the dynamics of spread.

Key words: alien species, *Ambrosia artemisiifolia*, biological invasion, central Europe, climate change, climate warming, common ragweed, hierarchical Bayesian modelling, imperfect detection, propagule pressure, range expansion, spread

Introduction

The rate at which humans move species around the globe has greatly increased over the course of the 20th century. As a consequence, more than 1.5 species, on average, are currently establishing per day somewhere outside their native range (Seebens et al. 2017). Some of these species become invasive, i.e. they rapidly spread over large areas with potentially severe effects on native ecosystems or human societies (Vitousek et al. 1996, Pyšek & Richardson 2010, Vilà et al. 2011, Blackburn et al. 2014). These biological invasions are driven by a plethora of interacting factors, which essentially structure around biological traits of alien species and recipient communities, propagule pressure, biogeographical history and the environment of the invaded territory (Catford et al. 2009, Pyšek et al. 2017).

Climate is an ecologically important component of the environment. A changing climate, therefore, is likely to have ramifications for biological invasions. In particular, climate warming is expected to increase the likelihood and frequency of invasions (Dukes & Mooney 1999, Ward & Masters 2007). The mechanisms involved may include increased disturbances and destabilization of resident communities (Gilman et al. 2010, Diez et al. 2012), opening up new introduction pathways (Hellmann et al. 2008) or allow the survival and reproduction of potential invaders in areas that were previously climatically unsuitable for successful colonization (Ward & Masters 2007, Walther et al. 2009, Mainka & Howard 2010). While a pronounced climate warming is expected in future decades, a clear trend of increasing temperatures was already recorded during the last decades of the 20th century and early 21st century (Stocker et al. 2013). However, while range shifts of native species in response to recent climate warming are well documented (Root et al. 2003, Parmesan 2006, Chen et al. 2011) and similar effects on alien species ranges are expected (Bradley et al. 2010, Dullinger et al. 2017), the actual imprint of this recent climate warming on the spread of biological invaders remains little explored (Walther et al. 2007). A likely reason for this is the difficulty of detecting ‘fingerprints of climate warming’ in the progress of an inherently dynamic invasion. In the course of biological invasions, continued introductions, local population build-up, the spread from established invasion foci and lag times (Sakai et al. 2001, Allendorf & Lundquist 2003) typically result in continuous changes in species distributions and local abundances for a long time, irrespective of changes in the environment. As many alien species frequently colonize disturbed habitats (Chytrý et al. 2008), the dynamics of spread may also be driven by changes in the environment other than climatic conditions, for example by changes in land use and disturbance regimes. Moreover, disentangling climate effects from those of other determinants of biological invasions is hampered by a commonly unsystematic and often biased recording of the development of spread (Delisle et al. 2003, Meinesz 2007). The actual spread and its documentation may be separated by variable spatio-temporal time lags (Aikio et al. 2010). As a result, available records are often of a spread in which the colonization dynamics and climatic trends are decoupled because of an erratic detection history.

A promising way of understanding the role of individual putative drivers in biological invasions is to model the documented spread in space and time (Hastings et al. 2005). In the case of incomplete documentation of spread, hierarchical modelling approaches, which represent actual spread and detection processes as separate model layers, are of particular interest (Wikle 2003, Bled et al. 2011, Broms et al. 2016). Here, we apply such an approach

to disentangle a possible signal of climate warming in the invasion history of *Ambrosia artemisiifolia* (common ragweed) in central Europe. For this purpose, we analyse how spatio-temporal variation in climate (temperature and precipitation) and land use (cropland area, urban area, length of motorway and railway networks) has driven this species' spread by changing the suitability of local environments for invasion. Moreover, we infer the imperfectly recorded, and hence unknown, actual distribution of this species. We hypothesize that (i) spatial gradients in climate and land use had a profound effect on the pattern of spread, (ii) recent climate warming has accelerated the invasion, and (iii) the documented species distribution represents only a part of the actual distribution. In addition, we assess the effect of lagged and incomplete records of occurrence on the conclusions drawn from the analysis by contrasting the inferences from the hierarchical model with those from a technically simplified model, which assumes perfect detection.

Materials and methods

Spread of Ambrosia artemisiifolia in central Europe

Ambrosia artemisiifolia L. (*Asteraceae*) is an annual herbaceous plant native to central North America, adapted to temperate climates (Bullock et al. 2012, Essl et al. 2015, and references therein). Individuals are from several centimetres up to 2.5 m in height. This species is wind-pollinated and monoecious, and strong self-incompatibility results in high levels of outcrossing (Friedman & Barrett 2008). *Ambrosia artemisiifolia* reproduces exclusively by seed. Seed ripening is terminated by autumn frost, which kills the adult plant, and seed dormancy is broken by winter temperatures (Chapman et al. 2014). The number of seeds produced per plant varies with region and habitat, but typically ranges from several hundred up to many thousand per plant (Fumanal et al. 2007, Essl et al. 2015). Seed dispersal by wind is restricted to the immediate vicinity of the mother plant, and dispersal by animals and water (e.g. along rivers or in floodwater) is of minor importance (Bullock et al. 2012). Most long-distance dispersal is mediated by human agency and occurs via trade in contaminated goods such as grain and other agricultural products, planting seed, bird seed (Chauvel et al. 2006, Chapman et al. 2016), seeds sticking to agricultural and mowing machinery (Karrer et al. 2011) and traffic in general (Essl et al. 2009). Seed persists in the soil seedbank for several decades and a site once colonized hence remains occupied for a long time (Fumanal et al. 2008). *Ambrosia artemisiifolia* is of considerable public health concern as this species' wind-blown pollen is highly allergenic (Smith et al. 2013).

Ambrosia artemisiifolia has been introduced into areas with temperate climates globally (Essl et al. 2015). In Europe, the first records are from the 19th century, but the species did not start to spread and naturalize until the first decades of the 20th century (Bullock et al. 2012, Essl et al. 2015, and references therein). Range expansion accelerated considerably in the late 20th century. In temperate Europe, this species occurs mainly in warmer lowland areas. Climatic conditions are an important invasion filter, in particular, where this species' potential distribution is limited by low temperatures in northern Europe and montane regions, and by moisture stress in southern Europe (Chapman et al. 2014, Leiblein-Wild et al. 2016). Climate warming in future decades is predicted to considerably enlarge the area in Europe where climatic conditions are suitable for invasion by

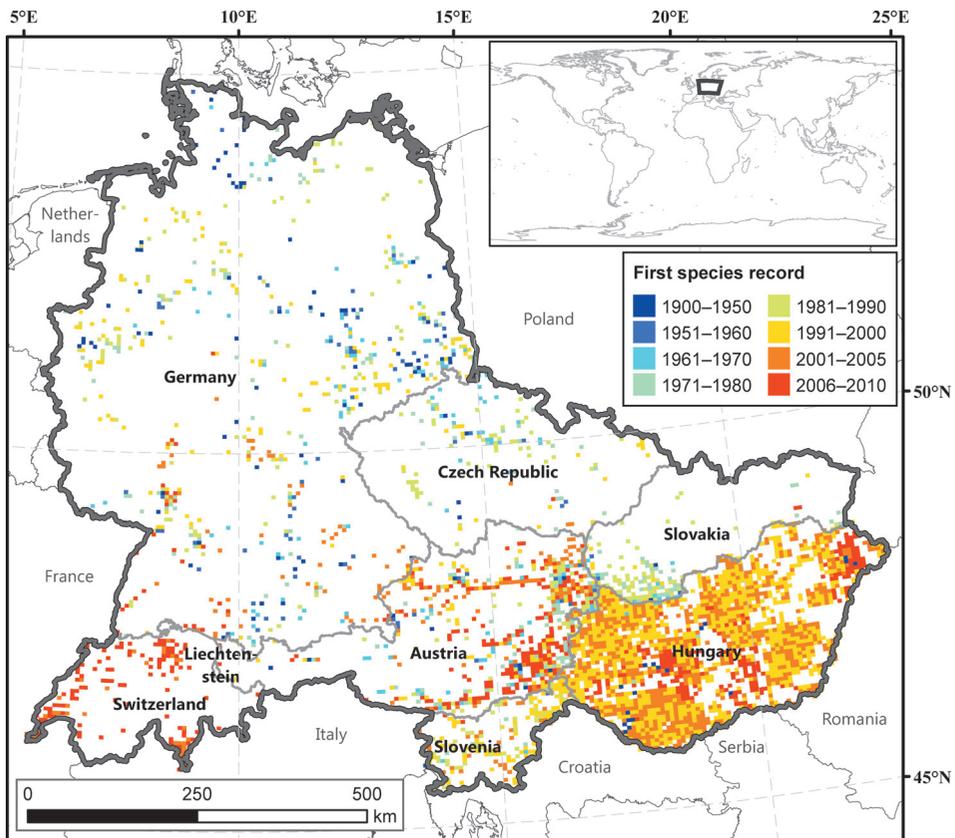


Fig. 1. – The chronology of the first records of *Ambrosia artemisiifolia* occurring in eight countries in central Europe during the period 1900–2010. Grid cell size is $5' \times 3'$ ($\sim 6 \times 6 \text{ km}^2$) and the study area spans over $700,000 \text{ km}^2$. Map projection: Lambert azimuthal equal-area.

A. artemisiifolia. Specifically, higher average temperatures during the growing season and later onset of autumn frost may cause an expansion in this species' range towards northern Europe (Cunze et al. 2013, Chapman et al. 2014, Storkey et al. 2014). *Ambrosia artemisiifolia* is a poor competitor (Leskovšek et al. 2012) and mainly thrives in disturbed open habitats in and around human settlements, agricultural fields, roadsides and along railway tracks (Essl et al. 2009, Pinke et al. 2011, Skálová et al. 2017). This species prefers nutrient-rich soils but can grow under a range of nutrient and salinity conditions (DiTommaso 2004, Skálová et al. 2015).

Study area and period

The area in central Europe studied includes Austria, the Czech Republic, Germany, Hungary, Liechtenstein, Slovakia, Slovenia and Switzerland (Fig. 1; see also Mang et al. (2018)). These countries span an area of over $700,000 \text{ km}^2$ and cover a range of temperate climates with more oceanic conditions in the north, lowland continental areas in the east and south-east, and cool montane to alpine climates in the Alps situated in the south and

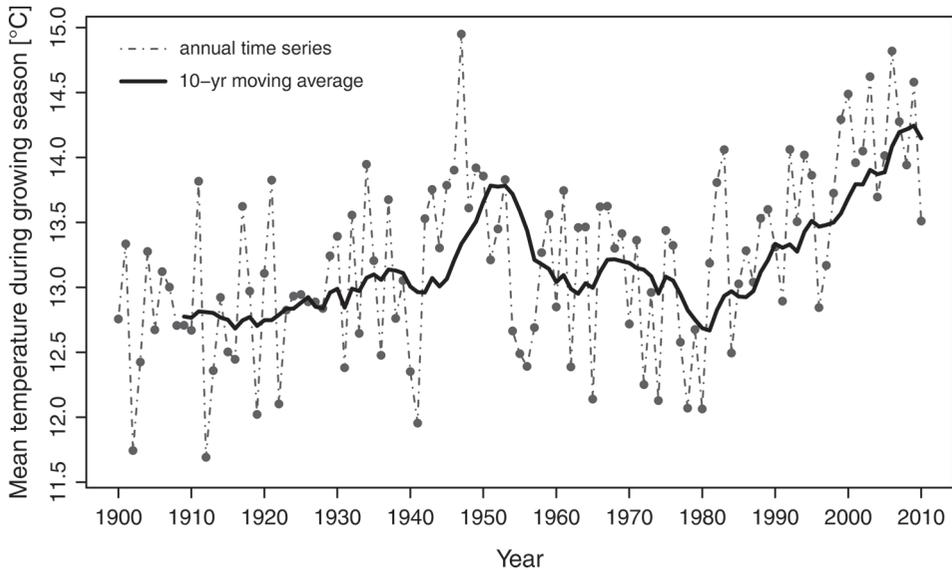


Fig. 2. – Annual time series (dot-dash line) and 10-year moving average (solid line) of the mean temperature recorded during the growing season (April–October) in the study area. The study area comprises eight countries in central Europe (see Fig. 1).

south-west in the study area. This area was represented by a lattice of grid cells of size $5' \times 3'$ ($\sim 6 \times 6 \text{ km}^2$) corresponding to the Central European Floristic Mapping Project (Niklfeld 1998), comprising a total of 22,451 cells. We modelled the spread of *A. artemisiifolia* in the study area from 1900 to 2010 at an annual resolution. In parallel with the global trend, in the late 20th century the average temperature in the study area also increased (Fig. 2). The mean temperature in the growing season (April–October) during the period 1980–2010 was $0.65 \text{ }^\circ\text{C}$ higher than during the period 1900–1979.

Species distribution data

Species records were compiled from many different sources (e.g. floristic publications, floristic mapping projects, major herbaria, unpublished records of the authors and of colleagues). The records were mapped to one of the 22,451 grid cells and the dates (years) of the records were extracted from the original source (Electronic Appendix 1). A total of 11,800 records indicate that 3,598 cells were invaded by this species by 2010 (Fig. 1, Table 1). Records were condensed to time of first detection in each grid cell by using the date of the earliest record for each cell.

Sampling intensity varied both in time and across the study area. Average sampling intensity differed across countries, and increased with the onset of the Central European Floristic Mapping Project in 1970 (Niklfeld 1998). Moreover, once this species was recognized to be a particularly detrimental invasive plant, there was a focus on recording *A. artemisiifolia* occurrences in select regions and years. In our modelling, this spatio-temporal variation in sampling intensity is explicitly represented.

Table 1. – The number of *Ambrosia artemisiifolia* records from 1900 until 2010 for the eight countries studied in central Europe, the number of grid cells for each of these countries in the models' lattice system and the number of grid cells with records.

Country	No. records	No. grid cells	No. grid cells with records
Austria	5,408	2,441	549 (22.5%)
Czech Republic	430	2,437	129 (5.3%)
Germany	1,076	11,422	618 (5.4%)
Hungary	3,406	2,747	1,825 (66.4%)
Liechtenstein	0	5	0 (0%)
Slovakia	414	1,490	141 (9.5%)
Slovenia	423	631	189 (30.0%)
Switzerland	643	1,278	147 (11.5%)
Study area	11,800	22,451	3,598 (16.0%)

Model overview

The model used in this study builds on a recently developed hierarchical modelling framework (Mang et al. 2017). In this framework, an invasion process layer represents the actual spread of the species by modelling the time of first invasion in each grid cell, and a separate observation process layer represents the history of the records by modelling the times when species occurrences were first detected (and recorded). In our model, we assume that the species persists in a grid cell once invaded, and that detection may lag behind the initial invasion by an unlimited period of time. Consequently, the first record for a particular cell is the latest possible time when this cell was actually invaded, and cells where the species has not been recorded so far may nevertheless already be invaded. The actual times of the initial invasion of the grid cells remain unknown but are inferred by means of statistical model fitting. For model details see Electronic Appendix 2.

Invasion process

Cells unoccupied at a given time are potential recipient cells exposed to an invasion risk. The magnitude of this invasion risk depends on the environmental suitability of a recipient cell for this species, the fecundity of populations in source cells (i.e. those cells that are already invaded at a given time) and the geographical distance between recipient cell and source cells. We further use 'background' introductions as a global propagule source that is independent of invaded source cells in the study area and represents, for example, introductions via international trade of planting and bird seed commodities that are known to be important in the case of *A. artemisiifolia* (Chapman et al. 2016).

In our model, environmental suitability of grid cells varies spatio-temporally and is given using a log-linear model component:

$$S_i(t) = e^{\mathbf{v}_{i,t} \cdot \boldsymbol{\beta}} \cdot \frac{a_i}{\bar{a}}, \quad (1)$$

where $\mathbf{v}_{i,t}$ is the vector of environmental attributes of cell i at time t , $\boldsymbol{\beta}$ is the vector of associated weighting parameters (to be estimated by model fitting), a_i is the cell's terrestrial area, and \bar{a} is the mean terrestrial area across all cells. In this representation, environmental

suitability is a relatively-scaled measure where $S_i(t) = 1$ is the threshold that separates negative from positive effects of cell attributes on suitability. Environmental attributes vary over time. In accord with this species' preferences we used the following six variables to characterize the environment: mean temperature and total precipitation during the growing season (April–October); the proportion of cropland area and of urban area; and the length (scaled relative to area) of motorway and railway networks (Dullinger et al. 2009, Joly et al. 2011). Non-climate variables were log-transformed to improve symmetry and reduce the effect of outlier values. All variables were standardized and the magnitudes of the obtained parameter estimates hence represent relative effect sizes. For details on data sources and data processing see Electronic Appendix 3.

Accounting for environmental suitability and the various propagule sources, for recipient cell i the invasion risk as a function of time is given by

$$g_i(t) = S_i(t) \cdot \left[\sum_{j \in \Omega(t-1)} R_j(t-1) \cdot \eta \cdot f_{2D}(d_{i,j}) + \lambda + \lambda_b \cdot \mathbf{1}(t = t_s) \right], \quad (2)$$

where $\Omega(t-1)$ is the set of cells already invaded at the given time (i.e. potential source cells; we use an offset of one year as *A. artemisiifolia* produces seed at the end of a growing season and germination occurs in spring), $R_j(t-1)$ is a source cell's estimated invasion level (see below) at that time, the parameter η is the propagule production rate of source cells per unit invasion level, $f_{2D}(d_{i,j})$ is the kernel function for dispersal from a source cell to the recipient cell in two-dimensional space dependent on the geographical distance between the cells, $d_{i,j}$ (the Euclidean centroid-to-centroid distance, in km), and the parameters λ and λ_b define the rate of background introductions. We used the approximation $R_j(t-1) = S_j(t-1)$ to reflect long-term average differences in invasion levels among cells, which differ in environmental suitability and, specifically, to represent differences in source strength among invaded cells. The parameter η scales the rate of spread from source cells to recipient cells at the grid cell level. To derive $f_{2D}(d_{i,j})$, we projected the one-dimensional kernel function $f_{1D}(d_{i,j}) = d_{i,j}^{-\alpha}$, where α is a shape parameter, into two-dimensional space and normalized it (Electronic Appendix 4). The parameter λ defines the generic background introduction rate, and the parameter λ_b provides an additional boost applicable only to the model start time, t_s (via the indicator function $\mathbf{1}$), to determine the number of initially invaded cells. In numerical terms, equation (2) defines a rate, with higher values of $g_i(t)$ corresponding to earlier expected invasion time (for details see Electronic Appendix 2 and Mang et al. (2017)).

Observation process

The observation process models the delay between first invasion of a grid cell and first detection of the species' occurrence in that cell (Mang et al. 2017). In our model, detection efficiency varies spatio-temporally. For invaded cell i detectability as a function of time is:

$$h_i(t) = \gamma \cdot R_i(t)^\varphi \cdot e^{\mathbf{m}_{i,t} \cdot \boldsymbol{\rho}}, \quad (3)$$

where the parameter γ defines the base detection rate, the parameter φ relates modelled invasion level to detectability, $\mathbf{m}_{i,t}$ is the vector of sampling intensity attributes of the cell at time t , and $\boldsymbol{\rho}$ is the vector of associated weighting parameters (to be estimated by model

fitting). We used the following variables to describe spatio-temporal differences in sampling intensity and thus to also account for spatio-temporal biases in the distribution data: (i) human population density in and around a given cell and year (log-transformed and standardized); (ii) whether a year was prior to the onset of the Central European Floristic Mapping Project in 1970 (a binary indicator variable); (iii) the degree of intensified sampling for *A. artemisiifolia* in particular regions and years, measured continuously in $[0,1]$ as a cell's share of the area in regions with intensified sampling; and whether (iv) a grid cell was in Germany, or (v) in the group Czech Republic, Slovakia and Slovenia (both variables measured continuously in $[0,1]$ as a cell's share of the area in these countries). In Austria, intensified sampling for *A. artemisiifolia* occurred in select political districts since 1996 and in additional districts since 2005. In Hungary and Switzerland, intensified sampling started in 1995 and 2005, respectively, but this information was only available at the country level. Intensified sampling resulted in a strong increase in the number of records from these countries. Effectively, the latter three variables make it possible to estimate separate detectability for (a) the set of countries composed of Austria, Hungary, Switzerland and Liechtenstein under either (a-1) non-intensified sampling (given implicitly by the base detection rate), or (a-2) intensified sampling; and further, the long-term average detectability for (b) Germany, and (c) the set of countries composed of the Czech Republic, Slovakia and Slovenia. For details on data sources and data processing see Electronic Appendix 3. In numerical terms, equation (3) defines a rate, with higher values of $h_i(t)$ corresponding to earlier expected detection time (for details see Electronic Appendix 2 and Mang et al. (2017)).

Non-hierarchical model

To investigate whether the observation process might affect the conclusions drawn from our analysis, we also used a simplified model that ignored observation issues and assumed that the documented spread accurately reflected the actual spread. In this model, record dates were thus directly used as the cells' invasion times. This simplified model uses only the invasion process layer and is therefore non-hierarchical. For model details see Electronic Appendix 2.

Model versions

The main purpose of our study was to detect a potential effect of recent climate change on the invasion history of *A. artemisiifolia* in the study area. To separate spatial effects of climate from temporal effects, we fitted three models with different representations of climate variation over time to the species' regional spread between 1900 and 2010. In the first model, climatic conditions in the individual cells were treated as constant over time and set to the average temperature and precipitation values recorded over the modelling period. Spatial climate variation was thus retained but temporal climate variation was eliminated. In the second model, climatic conditions were represented by an annual time series of temperature and precipitation values for each cell. This model integrates the available information at the most detailed level and is, therefore, henceforth called the 'main model'. In the third model, climate warming was represented in a simplified way, namely as a linearly interpolated trend series. For temperature, we used the (per cell) regression line from regressing annual temperature values against years. For precipita-

tion, to account for its negative correlation with temperature in the study area, we first assessed (per cell) the expected change in precipitation per change in temperature by using a linear regression of annual precipitation values against annual temperature values. For each year, we then calculated the difference between recorded and linearly regressed temperature values, used this difference to predict the expected change in precipitation, and offset the annual precipitation values accordingly. All other non-climatic descriptors of the environment were represented by annual time series of values in all three models.

Model fitting, comparison and validation

All models were fitted to the documented spread of *A. artemisiifolia* using a Bayesian inference approach with Markov chain Monte Carlo (MCMC) (Gelman et al. 2004, Brooks et al. 2011). In the hierarchical model, we thus inferred parameters of the invasion process and observation process, and the actual invasion times of all grid cells. In the non-hierarchical model, we inferred parameters of the invasion process. Vague (marginal) prior distributions were used for all model parameters (Electronic Appendix 5) and for each model the posterior distribution was therefore nearly all exclusively determined by the data. For each model we sampled 100,000 MCMC iterations after a burn-in period of 10,000 iterations. For the hierarchical model this required about nine days of computing time (per individual model). For further details on the MCMC sampling scheme see Electronic Appendix 5.

Estimates of the invasion process parameters and observation process parameters were summarized by the median and the 95% (central) credible interval of the respective (marginal) posterior distributions. The weighting parameters of environmental attributes and sampling intensity attributes, β and ρ , respectively, have 0 as the null-hypothesis value for a neutral effect and Bayesian kind of significance testing therefore assesses whether the credible interval overlaps this null-hypothesis value. Estimated actual invasion times of grid cells were summarized by (i) the median and the 95% (central) credible interval of the number of cells invaded by a given reference year; and (ii) the probability that a cell had already been invaded by a given reference year, calculated as the proportion of MCMC iterations in which the estimate of the actual invasion time of a particular cell was less than or equal to this reference year.

The three models with different representations of climate variation over time were compared for quality of fit using the Bayesian information criterion (BIC) (Hooten & Hobbs 2015). We used the median BIC value of the posterior distribution as reference. A lower BIC value represents a better fit.

For model validation, we also fitted models for the period 1900–2005 using only records up to 2005 and retained all subsequent records as independent data. We then used 10,000 draws from the respective posterior distributions (every tenth MCMC iteration), including cells' estimated actual invasion states by 2005, to simulate both the invasion process and the observation process further until 2010. For the hierarchical model, we calculated the probabilities of cells being invaded and detected as such by 2010 as the proportion of simulation runs in which invasion and detection occurred by 2010. For the non-hierarchical model, we calculated the probabilities of cells being invaded by 2010 as the proportion of simulation runs in which invasion occurred by 2010. For all cells that were not documented as already invaded by 2005 (19,374 cells in total), we then com-

pared these probabilities against the records from the period 2006–2010 using the area under the receiver operating characteristic (ROC) curve, AUC.

Results

Invasion process

In the ‘main model’, among the variables used to characterize the environmental suitability (ES) of grid cells for invasion by *A. artemisiifolia*, temperature, precipitation, the proportion of urban area per cell and the length of railway networks per cell were significant (Table 2). Of these variables, temperature was the most important (largest parameter magnitude), followed by precipitation. During the period 1980–2010, for cells with $ES \leq 1$ temperature (mean temperature during the growing season) was, on average, 11.9 °C, whereas for cells with $ES > 1$ temperature was, on average, 14.7 °C, and further 15.9 °C for the subset of cells with $ES > 2$ (Table 3). Precipitation was, on average, fairly similar across the gradient of ES values. However, as precipitation was negatively correlated with temperature in the study area, among cells with equal temperature the cells with more precipitation were more suitable. The proportion of urban area was, on average, 0.09 for cells with $ES > 1$ but only 0.02 for cells with $ES \leq 1$. For the (area-scaled) length of railways, this discrepancy was even more extreme with average values of 1.44 for cells with $ES > 1$ and 0.17 for cells with $ES \leq 1$. In general, cells with higher ES values were characterized by higher values of all environmental attributes except precipitation (Table 3).

Of the different climate regions in the study area, the lowland continental areas in and around the Pannonian Basin in the south-east and the surroundings of the warm Rhine valley in the west were identified as most suitable for invasion (Fig. 3A,B). Environmental suitability was lower in regions with an oceanic climate in the north of the study area and in montane regions. Finally, environmental suitability was minimal in the alpine regions (Fig. 3A,B). For the major part of the 20th century environmental suitability changed only marginally (Table 4A; median during the period 1900–1949: 0.94; and during the period 1950–1979: 0.97) and without a conspicuous spatial pattern (Fig. 3C). However, pronounced climate warming during recent decades triggered a strong average increase in environmental suitability (Table 4A; median during the period 1980–2010: 1.15) and so throughout the study area (Fig. 3D). As a result, the number of cells with suitable environmental conditions also increased strongly during the period 1980–2010 (Table 4B).

An invaded neighbouring cell was a stronger propagule source than background introductions in general, and particularly so in regions where suitable climate promoted source strength (Table 2). The spread pattern was therefore driven by the interplay of the establishment of scattered, initial invasion foci and subsequent local spread with exponential acceleration as progressively more cells were invaded and thus functioned as additional propagule sources. The dispersal kernel parameter estimate indicates that most dispersal occurred within a distance of a few cells (Fig. 4, Table 2).

Observation process

The modelled invasion level within a cell had a moderate effect on the detectability of species occurrences (Table 2). Detectability significantly increased with the human pop-

Table 2. – Parameter estimates of the invasion process and observation process for modelling the spread of *Ambrosia artemisiifolia* in central Europe. In the hierarchical model, the observation process accounts for lagged and incomplete records of occurrence. The non-hierarchical model assumes that records accurately reflect the species' actual spread and hence does not use the observation process. In both models an annual time series of temperature and precipitation values is used. Estimates are stated as median (top row) and 95% (central) credible interval (bottom row) of the marginal posterior distributions. Significance tests apply only to parameters of environmental suitability and sampling intensity, with significant results marked by *.

Parameter	Hierarchical model	Non-hierarchical model
Invasion process:		
Environmental suitability		
$\beta_{\text{temperature}}$	0.53* (0.48, 0.59)	0.66* (0.62, 0.69)
$\beta_{\text{precipitation}}$	0.37* (0.32, 0.41)	0.22* (0.19, 0.25)
$\beta_{\text{cropland area}}$	0.03 (-0.01, 0.07)	0.08* (0.04, 0.13)
$\beta_{\text{urban area}}$	0.10* (0.07, 0.14)	0.09* (0.05, 0.12)
$\beta_{\text{motorways}}$	0.01 (-0.01, 0.04)	0.02 (-0.01, 0.04)
β_{railways}	0.10* (0.07, 0.13)	0.09* (0.06, 0.12)
Dispersal, α	1.81 (1.69, 1.94)	1.08 (1.02, 1.15)
Source cells propagule production rate, η	0.022 (0.019, 0.025)	0.022 (0.020, 0.025)
Background introduction rate, λ	0.00017 (0.00010, 0.00024)	0.00011 (0.00009, 0.00013)
Background introduction start boost, λ_b	0.0071 (0.0042, 0.0109)	0.000088 (0.000009, 0.000294)
Observation process:		
Detection rate, γ	0.0075 (0.0064, 0.0087)	
Detection dependence on invasion level, φ	0.40 (0.26, 0.55)	
Sampling intensity		
$\rho_{\text{human population density}}$	0.53* (0.43, 0.63)	
$\rho_{\text{pre-1970}}$	-0.86* (-1.08, -0.66)	
$\rho_{\text{intensified sampling in Austria, Hungary \& Switzerland}}$	4.21* (3.98, 4.47)	
ρ_{Germany}	0.25 (-0.09, 0.59)	
$\rho_{\text{Czech Republic, Slovakia \& Slovenia}}$	0.78* (0.55, 1.02)	

ulation density in and around a cell. Moreover, detectability was significantly lower before the onset of the Central European Floristic Mapping Project in 1970. Among countries, detectability was lowest in Austria, Hungary, Switzerland and Liechtenstein under non-intensified sampling. Detectability in Germany was not different from these former countries, but was significantly higher in the Czech Republic, Slovakia and

Slovenia. Detectability peaked during the years of intensified sampling for *A. artemisiifolia* in Austria, Hungary and Switzerland (Table 2). Average expected delays between the actual invasion of a cell and the first record from this particular cell therefore ranged between almost instant detection up to decades.

Table 3. – Environmental attributes of grid cells in the study area, averaged for the period 1980–2010 and four categories of environmental suitability (ES) of grid cells for invasion by *Ambrosia artemisiifolia* according to the hierarchical model. The study area comprises eight countries in central Europe (see Fig. 1). ES is a relatively-scaled measure where an ES value of 1 is the threshold that separates negative from positive effects of environmental attributes on suitability. For each environmental attribute, the mean and standard deviation (in round brackets) were calculated using the attribute values of all grid cells in a given ES category. Number of grid cells in ES categories: $ES \leq 1.0$: 8,202 cells; $1.0 < ES \leq 1.5$: 8,226 cells; $1.5 < ES \leq 2.0$: 4,071 cells; $ES > 2.0$: 1,952 cells.

Variable	$ES \leq 1.0$	$1.0 < ES \leq 1.5$	$1.5 < ES \leq 2.0$	$ES > 2.0$
Temperature (mean Apr. – Oct.) [°C]	11.9 (2.8)	14.0 (1.1)	15.4 (1.4)	15.9 (1.3)
Precipitation (sum Apr. – Oct.) [mm]	562 (200)	491 (121)	496 (137)	577 (176)
Cropland area (proportion)	0.29 (0.28)	0.49 (0.28)	0.59 (0.27)	0.55 (0.27)
Urban area (proportion)	0.02 (0.03)	0.07 (0.08)	0.09 (0.12)	0.15 (0.17)
Motorways (area-scaled length)	0.66 (2.56)	1.72 (4.11)	2.26 (4.84)	3.98 (6.16)
Railways (area-scaled length)	0.17 (0.48)	1.06 (1.61)	1.58 (3.12)	2.73 (4.97)

Table 4. – Summary statistics of environmental suitability (ES) of grid cells for invasion by *Ambrosia artemisiifolia* according to the hierarchical model. The summary statistics were calculated for three different periods of modelling this species' spread in central Europe. (A) The p -quantiles of environmental suitability (for the 0.05 p -quantile, 5% of the grid cells have an ES value less than the given value; and so forth). (B) The number of grid cells (out of 22,451 grid cells in total) in four ES categories.

Statistic	1900–1949	1950–1979	1980–2010
(A)			
0.05 p -quantile	0.48	0.48	0.55
0.25 p -quantile (= first quartile)	0.73	0.75	0.89
0.50 p -quantile (= median)	0.94	0.97	1.15
0.75 p -quantile (= third quartile)	1.26	1.29	1.54
0.95 p -quantile	1.89	1.87	2.18
(B)			
No. grid cells where $ES \leq 1.0$	12,612 (56.2%)	12,024 (53.6%)	8,202 (36.5%)
No. grid cells where $1.0 < ES \leq 1.5$	6,557 (29.2%)	7,074 (31.5%)	8,226 (36.6%)
No. grid cells where $1.5 < ES \leq 2.0$	2,506 (11.2%)	2,629 (11.7%)	4,071 (18.1%)
No. grid cells where $ES > 2.0$	776 (3.5%)	724 (3.2%)	1,952 (8.7%)

Actual spread

Throughout the modelling period, the number of cells recorded as invaded was substantially lower than the number of cells that were estimated to be actually invaded (Fig. 3E,F, Fig. 5). This discrepancy increased continuously, peaked in the late 20th century and stabilized in recent years when intensified sampling for *A. artemisiifolia* was implemented in particular regions. For the year 2010, the model estimated that invaded cells outnumber those with records by a factor of 1.66 (Fig. 3F, Fig. 5).

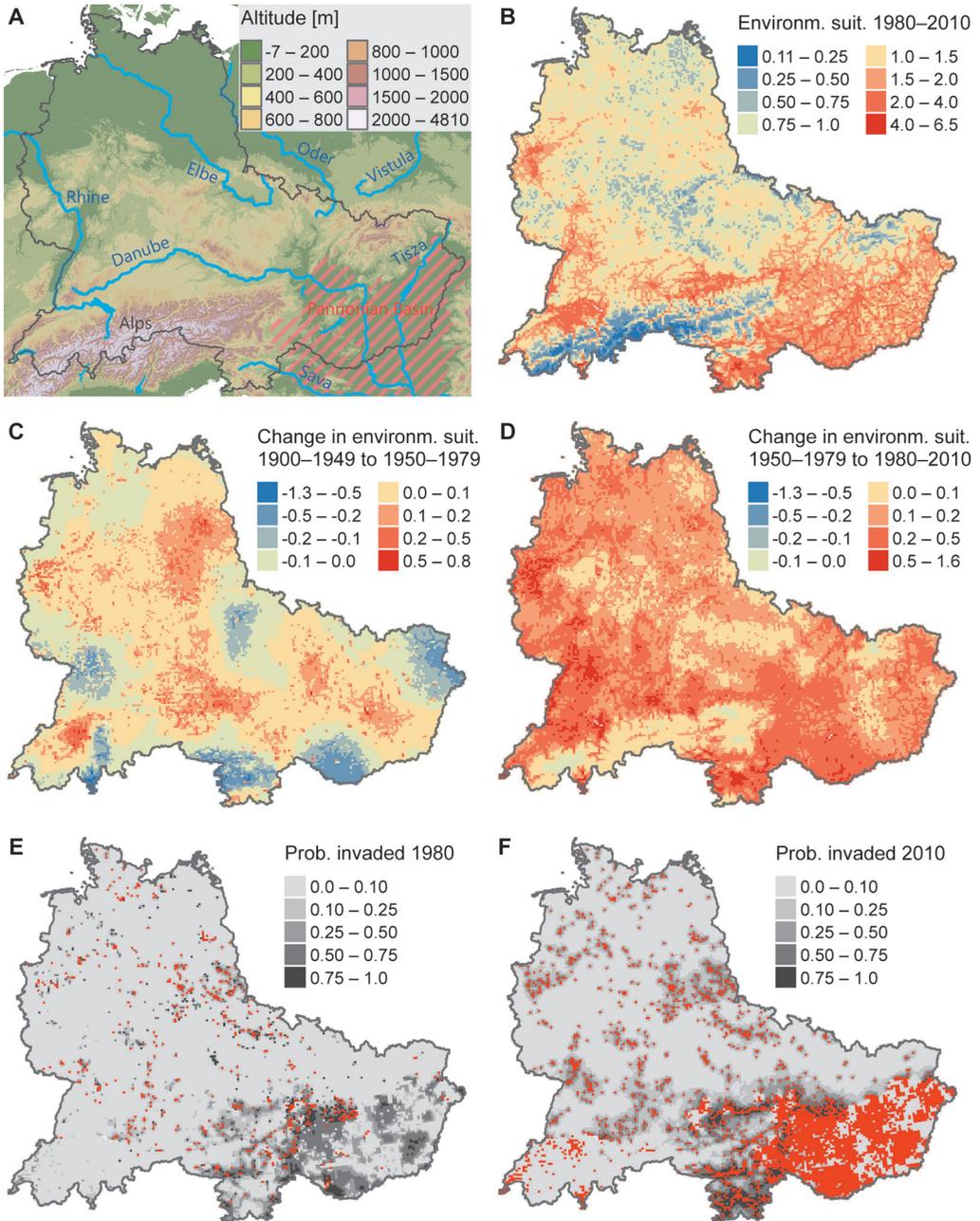


Fig. 3. – (A) Physical geography of central Europe. The dark grey line delimits the study area (see Fig. 1). (B) Environmental suitability of grid cells for invasion by *Ambrosia artemisiifolia* during the period 1980–2010 according to the hierarchical model of this species' spread in central Europe. (C) Change in environmental suitability from the period 1900–1949 to the period 1950–1979 (median: 0.02), and (D) from the period 1950–1979 to the period 1980–2010 (median: 0.16). Model-estimated probabilities of grid cells being invaded by *A. artemisiifolia* (E) by 1980, and (F) by 2010; grid cells in which the occurrence of this species has been documented by records up to the given year are shown in red.

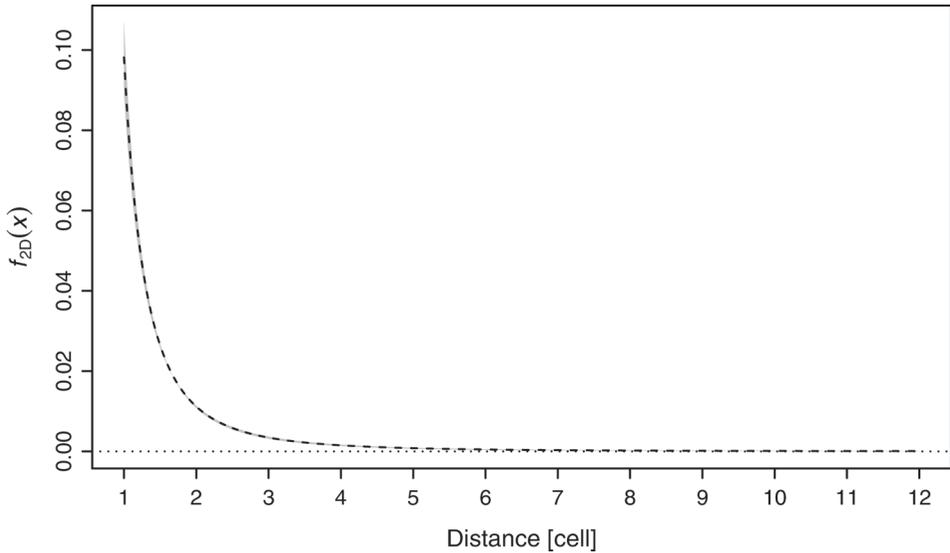


Fig. 4. – The kernel function for dispersal from invaded source cells to unoccupied recipient cells in a two-dimensional lattice system according to the hierarchical model of the spread of *Ambrosia artemisiifolia* in central Europe. The dashed line shows the function for the median of the marginal posterior distribution of the shape parameter α (see Table 2). The curve is very similar for the 95% credible interval of α , which is shown as the shaded area in the background of the dashed line.

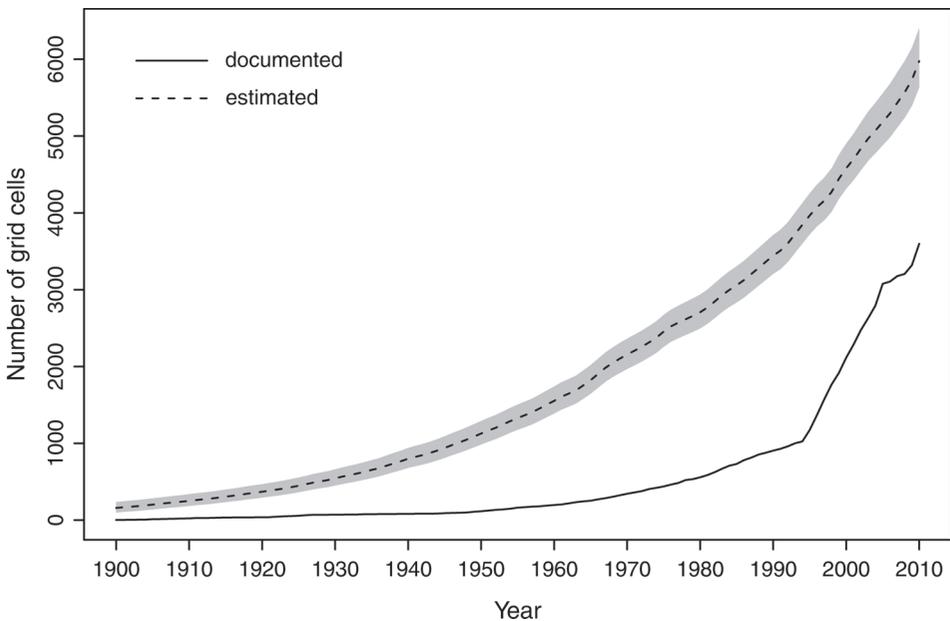


Fig. 5. – Cumulative number of grid cells documented as invaded by records (solid line), and estimated to be invaded (dashed line) according to the hierarchical model of the spread of *Ambrosia artemisiifolia* in central Europe. The dashed line shows the median and the shaded area the 95% credible interval of the marginal posterior distribution. The study area in central Europe includes a total of 22,451 grid cells.

Table 5. – Model statistics contrasting three model versions (MV) with different representations of the variation in climate over time for modelling the spread of *Ambrosia artemisiifolia* in central Europe. Each model version was fitted using both the hierarchical model that accounts for lagged and incomplete records of occurrence, and the non-hierarchical model that assumes that records accurately reflect the species' actual spread. For both the hierarchical model and the non-hierarchical model, the model version with the lowest Bayesian information criterion (BIC) value provides the best fit (note that the BIC cannot be used to compare the hierarchical model with the non-hierarchical model). For model validation, the area under the receiver operating characteristic curve (AUC) was calculated using records from the validation period 2006–2010, which were not used for model fitting.

Statistic	MV annual time series of temperature and precipitation values	MV linear trend in climate warming	MV long-term climate average
Hierarchical model			
BIC	313835.4	312274.0	314061.7
AUC	0.889	0.890	0.888
Non-hierarchical model			
BIC	39743.9	39242.4	39311.6
AUC	0.835	0.839	0.837

Different representations of climate variation

The version of the model with the linear trend in climate warming provided the best fit (Table 5). The ‘main model’ with annual time series of temperature and precipitation values was ranked second, and the model with the long-term climate average was ranked last. However, for all three models, and in particular for the two top-ranking ones, the estimates of the individual parameters were fairly similar (Table 2, Electronic Appendix 6).

Differences between hierarchical and non-hierarchical models

In comparison with the hierarchical ‘main model’, in the non-hierarchical model the shape parameter α of the kernel function for dispersal was much lower (Table 2), thereby yielding a more fat-tailed function with dispersal over greater distances (several cells) inferred to occur with a substantially greater frequency (Electronic Appendix 7). Moreover, in the non-hierarchical model temperature was by far the dominant determinant of environmental suitability, whereas in the hierarchical model temperature and precipitation differed less in relative importance. Finally, the parameter estimate of the boost of background introductions for the model start time, λ_b , was higher in the hierarchical model as this model estimated that in 1900 many actually invaded cells were unrecorded. Despite these discrepancies between the two models, the parameter uncertainty as expressed by the respective credible intervals was rather low within each model (Table 2).

Fitting the non-hierarchical model to the data resulted in altered ranking of the three different representations of climate variation: while the model with the linear trend in climate warming still performed best, the version with the long-term climate average yielded a better fit to the data than the one with annual time series of temperature and precipitation values (Table 5).

Model validation

For the hierarchical model, the AUC-values were 0.89 for all three model versions with different representations of climate variation. For the non-hierarchical model, the AUC-values for the three model versions were between 0.83 and 0.84 (Table 5). All fitted models could therefore well distinguish invaded cells (and documented as such in the case of the hierarchical model) in 2010 from unoccupied cells.

Discussion

Climate as driver of spread

In this study, we tracked a century of *A. artemisiifolia* spread over a large area and long altitudinal gradient. Variation in climate in the area, together with a relatively fine spatio-temporal grain, improved the model's ability to detect the role of climate in driving this spread. In line with previous studies (Dullinger et al. 2009, Chapman et al. 2014, Leiblein-Wild et al. 2016, Skálová et al. 2017), we found that geographical variation in climatic, and especially in temperature conditions had a pronounced effect on the pattern of this species' occurrence in the area. Compared to spatial variation, the change in climate over time was, however, fairly weak, even if temperatures have significantly increased during the most recent decades. As a consequence, detecting signals of climate warming in the documented pattern of spread was challenging and required separating spatial effects of climate from temporal effects.

Nevertheless, our model provides a strong indication that the trend in climate during the 20th and early 21st century affected the regional spread of *A. artemisiifolia*. In both the hierarchical and the non-hierarchical model configurations, accounting for climate change yielded models that explained more of the changes in occurrence than models that used only spatial variation in the climate. The warming climate likely enhanced the spread of this species via two different processes. First, warmer temperatures have resulted in the potential distribution extending into previously inhospitable montane regions. And second, more favourable climatic conditions accelerated the infilling of gaps within already occupied regions in the study area. For *A. artemisiifolia*, the rate and speed of germination (Leiblein-Wild et al. 2014), the growth of seedlings, leaf development and the accumulation of biomass (Deen et al. 1998, Skálová et al. 2015) are promoted by temperatures higher than those prevailing in central Europe. Climate warming thus makes it more likely that this species successfully completes its life cycle. Larger plants also produce more seed (Fumanal et al. 2007), which in terms of spread enhances source strength of existing populations and thus facilitates colonization of unoccupied sites.

Contrary to our expectations, however, fitting the documented spread to an annual time series of temperature and precipitation values did not provide a better fit than a linear interpolation of the climatic trend. As a likely reason, we assume that even an annual plant is buffered to a certain extent against the effect of inter-annual climatic fluctuations. For *A. artemisiifolia*, the most important means of buffering is the persistent seedbank that enables in situ survival in less suitable years (Fumanal et al. 2008, Essl et al. 2015). Here, we only partially included the effects of the seedbank since source strength of invaded cells did not consider the role of environmental conditions in local seedbank

build-up over years. In a model of the historical spread, such simplification is less problematic if annual climatic fluctuations are smoothed by a linear time series. As a corollary, a more accurate analysis of climatic signals in this species' spread probably requires that the seedbank is expressed as a function of local climatic and colonization history. Indeed, in the model of Chapman et al. (2016) seedbank dynamics play an important role in the response of this species to a changing climate.

Land use as driver of spread

Our model showed that the spatio-temporal occurrence of *A. artemisiifolia* in central Europe was also determined by the amount of urban area and the extent of railways in grid cells. These findings match the habitat preferences of this species in Austria and the Czech Republic, where most occurrences are found in settlement and industrial areas, and along railway tracks and roads (Essl et al. 2009, Skálová et al. 2017). *Ambrosia artemisiifolia* prefers these habitats for various reasons: first, this species is a poor competitor and its occurrence is therefore often confined to habitats that are characterized by a high frequency of disturbance (Joly et al. 2011, Leskovšek et al. 2012); second, anthropogenic activities in these habitats promote species introductions (Chapman et al. 2016); and third, traffic corridors facilitate dispersal by means of vehicle airflow or the mowing of roadsides (Karrer et al. 2011, von der Lippe et al. 2013). However, according to our model neither the proportion of an area that is cropland nor the length of motorways significantly affected the occurrence of this species. Previous studies report that fields and roads are relevant habitats for *A. artemisiifolia* (Essl et al. 2009, Pinke et al. 2011, Skálová et al. 2017), but the importance of these habitats varied substantially among studies and can be modified by small-scale variation in environmental conditions, such as soil properties or type of crop grown (Pinke et al. 2011). Consequently, we hypothesize that the spatial resolution of our model was too coarse to detect possible effects of fields and motorways on this species' pattern of occurrence. Nevertheless, our findings provide evidence that land use co-determined the occurrence of *A. artemisiifolia* in central Europe albeit, at the scale of this study, climatic conditions were most important. Since the extent of built-up areas and traffic networks increased during the period of this study, it is likely that changes in land use have further promoted the spread of this species in addition to climate change.

Imperfect records of occurrence

For species that expand their range, delayed detection of new populations could introduce several systematic biases into analyses of the dynamics of spread (Mang et al. 2017). Our results demonstrate, however, that explicitly accounting for lagged and incomplete records of occurrence can considerably improve inferences on the dynamics of spread. The most important discrepancy in the inferences of the hierarchical model accounting for imperfect records of occurrence and its otherwise equivalent non-hierarchical model was the indicated number of grid cells invaded by this species at a particular time. Mismatches between actual and recorded distributions of an invasive alien species may be critical for an accurate assessment of the impact of the biological invasion or for developing efficient management strategies. In the case of *A. artemisiifolia*, substantial efforts are being undertaken in Europe to control the spread of this species because of its effect

on human health and the associated economical costs (Bullock et al. 2012, Richter et al. 2013). These efforts may benefit from advanced modelling inferences about the actual distribution of this species. Regarding the individual drivers of the pattern of this species' spread, the hierarchical and the non-hierarchical models yielded some quantitative differences but qualitatively the inferences were fairly robust. This suggests that for studies that can make use of large distribution data sets, using the non-hierarchical model as an ad-hoc tool may be sufficient for qualitatively disentangling the role of particular drivers of the pattern in spread. For more accurate assessments of these drivers, and estimates of the actual distribution and detection efficiency, using the hierarchical model is likely to be more rewarding. Indeed, in our study the inferences of the particular role of climate depended more on accounting for imperfect records of occurrence than on the precise way of how to represent climate variation over time.

Spatio-temporal modelling framework and data requirements

Many models have been used to track and/or forecast the spread of organisms (Hastings et al. 2005, Gallien et al. 2010). These models cover the full range from purely correlative to mechanistic approaches, with the implicit trade-off between data requirements and tractability on the one hand and causal understanding and realism on the other hand. Within this model continuum, our approach represents a kind of compromise in being process-based (Dormann et al. 2012) though not mechanistic, and statistical with 'standard' records of species occurrence being sufficient for model fitting. These properties make the model a flexible and powerful tool for analysing the history of spread. Its flexibility depends on the possible integration of various different kinds of processes. As an example, Chapman et al. (2016) recently demonstrated that at the continental scale, international trade of seed commodities is an important driver of the spread of *A. artemisiifolia* in Europe. By contrast, our study analyses the spread of this species at a regional scale, where local range expansion dominates. Propagule input from abroad was thus represented by a generic rate of background introductions. It would, however, be theoretically straightforward to define this rate of background introductions more precisely by a sub-model that accounts for the variation in the associated propagule pressure, e.g. via a land cover map. Similarly, changes in the species' niche via possible genetic adaptation (Gallien et al. 2016) could be represented by making the parameters of environmental suitability, β , themselves spatio-temporally variable. Obviously, the more such processes are included, the more kinds of different data, amount of data and higher accuracy of these data will be needed for sensible model parameterization. In our model, we made efficient use of simple occurrence records with date information. Such data can often be collected retrospectively from different sources, and hence enables an analysis of the history of spread over long time frames.

A disadvantage of these 'simple' data, however, is that the model does not consider transient population dynamics within grid cells. In fact, in the context of analysing putative effects of climate change on range dynamics, using abundance data would be more powerful than using occurrence data. If spatio-temporal abundance data are available, recently developed dynamic range models enable accurate tracking of changes in population size over space and time (Pagel & Schurr 2012, Zurell et al. 2016). However, currently dated records of the occurrence of non-native species are much more frequent than

time series of species abundances. Similarly, dynamic occupancy models can represent local extinction (Bled et al. 2011, Broms et al. 2016) but require presence-absence information from site surveys and are hence considerably more demanding with respect to data quality than our modelling approach.

Conclusions

Our results show that climate is an important factor in the spread of *A. artemisiifolia* in central Europe and that recent climatic trends have already further promoted the spread of this species. These results corroborate previous concerns that 21st century climate warming could result in continuation of the spread of *A. artemisiifolia* in Europe (Chapman et al. 2014, Storkey et al. 2014) and hence increase the pollen load and associated human health costs (Richter et al. 2013, Hamaoui-Laguel et al. 2015). They further provide evidence that this species is already more widespread than available data suggest and deliver spatially explicit information on undocumented occurrences. As a corollary, measures to reduce further spread will likely be more efficient if spatial prioritization of management is informed by a hierarchical model that accounts for imperfect records of the occurrence of this species.

See www.preslia.cz for Electronic Appendices 1–7.

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Souhrn

Navzdory předpokladu, že budoucí změna klimatu ovlivní invaze rostlinných druhů, je tato problematika dosud nepříliš často studována. V článku se tomuto tématu věnujeme prostřednictvím analýzy historie šíření druhu *Ambrosia artemisiifolia* ve střední Evropě, na území zahrnujícím Rakousko, Českou republiku, Německo, Maďarsko, Lichtenštejnsko, Slovensko, Slovinsko a Švýcarsko, a predikce vlivu, jaký bude mít změna klimatu na další průběh této invaze. Šíření bylo modelováno v síti o velikosti čtverců $5' \times 3'$ ($\sim 6 \times 6 \text{ km}^2$) pro roky 1900 až 2010 a odráželo časoprostorové změny v klimatických podmínkách, využívání krajiny a produkci diaspor a jejich rozšiřování z invadovaných čtverců; tyto parametry určovaly pravděpodobnost, že bude čtverec invadován. Klimatické podmínky měly největší vliv na invazi, jejíž pravděpodobnost stoupala s mírou městské zástavby a délkou železničních tratí ve čtverci. Ve čtvercích příhodných k invazi byla v průměru o $2,7 \text{ }^\circ\text{C}$ vyšší teplota než tam, kde byla pravděpodobnost invaze malá. Model ukázal, že v roce 2010 bylo zaznamenáno jen zhruba 60 % skutečně existujících výskytů a zpoždění v přesnosti záznamů se pohybuje na úrovni desetiletí. Je proto důležité tuto chybu kvantifikovat a počítat s ní v predikcích dalšího vývoje.

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