**ORIGINAL ARTICLE**

# Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant

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## ABSTRACT

**Aim** We demonstrate how to integrate two widely used tools for modelling the spread of invasive plants, and compare the performance of the combined model with that of its individual components using the recent range dynamics of the invasive annual weed *Ambrosia artemisiifolia* L.

**Location** Austria.

**Methods** Species distribution models, which deliver habitat-based information on potential distributions, and interacting particle systems, which simulate spatio-temporal range dynamics as dependent on neighbourhood configurations, were combined into a common framework. We then used the combined model to simulate the invasion of *A. artemisiifolia* in Austria between 1990 and 2005. For comparison, simulations were also performed with models that accounted only for habitat suitability or neighbourhood configurations. The fit of the three models to the data was assessed by likelihood ratio tests, and simulated invasion patterns were evaluated against observed ones in terms of predictive discrimination ability (area under the receiver operating characteristic curve, AUC) and spatial autocorrelation (Moran's *I*).

**Results** The combined model fitted the data significantly better than the single-component alternatives. Simulations relying solely on parameterized spread kernels performed worst in terms of both AUC and spatial pattern formation. Simulations based only on habitat information correctly predicted infestation of susceptible areas but reproduced the autocorrelated patterns of *A. artemisiifolia* expansion less adequately than did the integrated model.

**Main conclusions** Our integrated modelling approach offers a flexible tool for forecasts of spatio-temporal invasion patterns from landscape to regional scales. As a further advantage, scenarios of environmental change can be incorporated consistently by appropriately updating habitat suitability layers. Given the susceptibility of many alien plants, including *A. artemisiifolia*, to both land use and climate changes, taking such scenarios into account will increasingly become relevant for the design of proactive management strategies.

**Keywords**

*Ambrosia artemisiifolia,* **Austria, conservation biogeography, dispersal, habitat suitability, invasion, invasive alien species, spatial autocorrelation, species distribution model, spread model.**

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## INTRODUCTION

Invasive alien species pose major threats to ecosystems, particularly regarding their biodiversity and the services they provide. Forecasting the potential spatial spread of these species from invasion foci can assist proactive management in as yet uncolonized areas. Since the pioneering work of Fisher (1937) and Skellam (1951), such forecasts have typically been

based on reaction–diffusion models. More recently, integro-difference frameworks have been used to accommodate the often leptokurtic shape of empirical dispersal data (Kot *et al.*, 1996). However, both reaction–diffusion and integrodifference modelling frameworks have traditionally assumed homogeneous environments. Environmentally dependent spread rates can be incorporated by varying model parameters, for example local growth rates, diffusivity or dispersal kernels, according to habitat type (e.g. Shigesada & Kawasaki, 2002; Hastings *et al.*, 2005; Drury & Candeleria, 2008). In spite of this, the complex spatial habitat patterns of many real landscapes cannot easily be accounted for in these modelling frameworks, although such patterns may profoundly influence invasion processes at least on local to regional scales (e.g. Higgins *et al.*, 1996; Havel *et al.*, 2002; With, 2002; Rouget & Richardson, 2003; Meentemeyer *et al.*, 2008). Despite a lack of generality, approaches that operate on spatially explicit representations of landscape structure hence seem to be more promising if the task is to predict the spread of individual invasive species in real landscapes.

Among such approaches, interacting particle systems (IPSs), including cellular automata as a special case, are the most common (e.g. Higgins *et al.*, 1996, 2003; Gilbert *et al.*, 2004). In an IPS the landscape is usually represented as a contiguous two-dimensional grid of sites. The spread of an invasive species through this landscape is driven by local demographic rates and a dispersal kernel that delivers per-cell infestation probabilities at time-step $t+1$ as a function of the distances to cells already occupied at time-step $t$. The shape of the dispersal kernel is supposed to be the main determinant of spread velocity (Higgins & Richardson, 1999; Gilbert *et al.*, 2004). In contrast, spatial variation in habitat suitability is often either completely ignored or represented on a binary scale only (e.g. Higgins *et al.*, 2003; Pearson & Dawson, 2005). In many real systems, and particularly in the case of plants, however, habitat suitability will not be a binary variable, but will vary continuously across the landscape (Murphy & Lovett-Doust, 2004). Species distribution models (SDMs, see Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) offer a tool with which to describe such variation. SDMs use statistical relationships between species occurrence and environmental conditions to predict the potential distribution of a species across an area of interest and have repeatedly been applied to identify regions likely to become invaded by exotic taxa (e.g. Weber, 2001; Kriticos *et al.*, 2003; Rouget *et al.*, 2004; Thuiller *et al.*, 2005a; Mercado-Silva *et al.*, 2006).

The combination of IPSs and SDMs into hybrid models hence seems to offer an appropriate framework for simulating invasive spread as both dispersal- and habitat-driven (cf. Thuiller *et al.*, 2008). Such combinations are indeed beginning to be developed in the context of both climate change research and invasion biology, either using hypothetical dispersal estimates (e.g. Midgley *et al.*, 2006), or as complex models with explicit representations of local population dynamics and data-based dispersal kernels (Dullinger *et al.*, 2004; Pearson & Dawson, 2005; Keith *et al.*, 2008; Pitt *et al.*, 2009).

In this paper we demonstrate a comparatively simple approach to establishing such a hybrid model for species invasions and to estimating the necessary parameters from data. In order to verify whether or not the integrated model predicts empirical invasion patterns more precisely than a purely dispersal- or a purely habitat-driven alternative, we compare the simulations of three IPSs with the recent empirical invasion history of *Ambrosia artemisiifolia* L. (ragweed) in Austria. In the first set of simulations, the range expansion of the species is driven only by a spread kernel, relating new infestation events to the spatial distance to already occupied cells; in the second set of simulations, spatial spread is assumed to be unlimited, and hence the geography of the invasion is determined solely by the habitat suitability patterns; in the third set, finally, spread kernel and habitat suitability information jointly control simulations.

## MATERIALS AND METHODS

The basic idea of this work is to combine two different modelling tools, which are mostly used separately in ecological applications, into one framework to achieve improved predictions of the spatio-temporal dynamics of invading species.

### Species distribution model

Species distribution models are now a widely applied tool in ecology, biogeography, conservation biology, and global change research (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Basically, SDMs relate the occurrence or abundance of species to a suite of mostly abiotic site conditions by means of a variety of statistical tools (Elith *et al.*, 2006). The calibrated statistical functions are then applied for spatial or temporal extrapolation; that is, to predict the occurrence or occurrence probabilities of species at sites that have not been surveyed yet but for which information on site conditions is available, or under scenarios of environmental change. Here, we use generalized linear models (GLMs, McCullagh & Nelder, 1989) and generalized additive models (GAMs, Hastie & Tibshirani, 1990), both with a binomial error distribution and a logistic link function, to relate species distributions to site conditions. The two methods differ in that a GLM assumes a parametric relationship between response and predictor variables and is hence equivalent to logistic regression with the above specifications. In contrast, GAMs use nonparametric regression methods, essentially smoothing techniques, to relate response and predictor variables.

The (rescaled, see below) predictions of these two statistical models will henceforth be called habitat suitabilities, denoted by $H(\mathbf{x})$.

### Interacting particle system

Interacting particle systems (IPSs), also called stochastic spatial models (Durrett & Levin, 1994), are a popular method for investigating biological spread processes (see e.g. Durrett,

1988; Czárán & Bartha, 1992; Durrett & Levin, 1994; Czárán, 1998; Gilbert *et al.*, 2004). IPSs are spatially explicit and usually operate on a regular grid of discrete cells, each of which represents an individual site. At any given discrete time-step, each cell is characterized by one of a number of states. Model performance is controlled by rules, or state transition functions, specifying how the state of a cell is changed at each time-step, depending on its own previous state and the states of its neighbours. In contrast to cellular automata, of which they are a generalization, IPSs can account for spatial variation and stochasticity in these transition rules.

## Integration of IPS and SDM

The engine of our combined spread model is an IPS that takes into account spatial variation in transition probabilities by means of a habitat suitability function $H(\boldsymbol{x})$. Each cell $\boldsymbol{x}$ can be in one of two states, as specified by the infestation status function $I(\boldsymbol{x})$, namely either occupied (denoted by 1) or unoccupied (denoted by 0). For each unoccupied cell $\boldsymbol{x}$, the distance to the nearest occupied cell $r(\boldsymbol{x})$ is computed at each time-step. The probability of cell $\boldsymbol{x}$ becoming infested during the respective time-step is then given by

$$P(\boldsymbol{x}) = S(r(\boldsymbol{x}))H(\boldsymbol{x}), \tag{1}$$

which means that, conceptually, it is the product of $S(r(\boldsymbol{x}))$, the distance-dependent probability of colonizers arriving at cell $\boldsymbol{x}$, and $H(\boldsymbol{x})$, the probability that these colonizers find a favourable environment for establishment in cell $\boldsymbol{x}$. These infestation probabilities $P(\boldsymbol{x})$ are then compared to uniformly distributed random numbers in the interval [0,1]. If the random number is smaller than $P(\boldsymbol{x})$, $I(\boldsymbol{x})$ is set to 1; otherwise, the cell is left unoccupied ($I(\boldsymbol{x}) = 0$). Thus, an updated infestation status is generated for use in the next time-step. We modelled $S(r)$ of equation (1) as a two-parameter Gaussian function:

$$S(r) = a \exp(-r^2/2d^2). \tag{2}$$

We henceforth call this function the spread kernel (instead of dispersal kernel), as it refers to the distance-dependent colonization of sites by populations rather than just to the dispersal of individuals or seeds. We used a simple Gaussian instead of a leptokurtic function, although the latter is usually supposed to better capture rare long-distance dispersal (or spread) events (e.g. Kot *et al.*, 1996; Higgins & Richardson, 1999; Gilbert *et al.*, 2004). This was because in our study system (see below) trials with a sum of two Gaussian kernels, one for short- and one for long-distance spread, did not improve the results. However, with smaller grains and/or larger extents of the study system, and a calibration strategy that takes into account distances to all potential seed sources, not only to the nearest occupied cell, a leptokurtic version of $S$ would probably be better. We contrast this integrated model (henceforward called the COMBINED model) with one driven purely by a neighbourhood distance function $S(r(\boldsymbol{x}))$ (SPREAD model), and one accounting only for variation in habitat

suitability patterns $H(\boldsymbol{x})$ (HABITAT model). Thus, the HABITAT model reduces to a simulation with the underlying SDM as the only spatial constraint of the invasion process, whereas the SPREAD model corresponds to a spread simulation on a uniform landscape. Note that the HABITAT model can be considered a special case of the COMBINED model, namely one with parameter $d$ in equation (2) set to infinity. Its spread kernel $S(r(\boldsymbol{x}))$ thus reduces to the parameter $a$ (cf. Table 1).

In the current formulation, our models do not account for possible extinction of the species in cells that have at some point become infested. As *A. artemisiifolia* is an annual species establishing a persistent seed bank (up to 35 years, Brandes & Nitzsche, 2007), we consider this formulation reasonable when modelling a restricted time-span of 15 years.

## CASE STUDY

We compare the performance of the COMBINED, SPREAD and HABITAT models using data from the empirical invasion of *A. artemisiifolia* in Austria between 1990 and 2005. *Ambrosia artemisiifolia* (ragweed) is an annual forb that produces strongly allergenic pollen and is hence causing considerable problems for public health (Taramarcaz *et al.*, 2005). Its native range is restricted to parts of the central USA. The species was introduced to Europe during the 19th century, but started to become invasive only in the mid 20th century (Chauvel *et al.*, 2006; Brandes & Nitzsche, 2007). In Austria, its spread has accelerated considerably since the early 1990s (Dullinger *et al.*, 2009), with new populations infesting mainly ruderal habitats and agricultural fields (Essl *et al.*, 2009).

## Species distribution data

Although our simulations were focused on the range dynamics in Austria, we fitted SDMs with data on the current distribution of *A. artemisiifolia* in both Austria and Germany to account for a wider range of environmental conditions and to estimate the limits of the species more accurately.

**Table 1** Specification of the functions representing habitat- and distance-dependent infestation probabilities in the various models (HABITAT, SPREAD and COMBINED) used to simulate the invasion of *Ambrosia artemisiifolia* in Austria between 1990 and 2005. $H(\boldsymbol{x})$ is the habitat suitability function, defined by either a generalized linear or a generalized additive model, which relates the occurrence of *A. artemisiifolia* to various environmental variables; $a \exp(-r^2/2d^2)$ is a two-parameter Gaussian function for the decrease in colonization probability with distance from the nearest occupied cell $r$ (see Materials and Methods for further details).

|  | Model | | |
| --- | --- | --- | --- |
|  | HABITAT | SPREAD | COMBINED |
| Habitat suitability | $H(\boldsymbol{x})$ | 1 | $H(\boldsymbol{x})$ |
| Spread kernel | $a$ | $a \exp(-r^2/2d^2)$ | $a \exp(-r^2/2d^2)$ |

We collected all available records of ragweed in these two countries up to the year 2005. Data were taken from the databases of the project Floristic Mapping of Central Europe (FMC, cf. Niklfeld, 1971) in Austria (Niklfeld, 1998) and Germany (Schönfelder, 1999). Started in the late 1960s, this project systematically collects and compiles distribution data of all vascular plant species on a regular grid of $3 \times 5$ geographical minutes (*c.* 30 km$^2$). In addition to using the FMC, we searched several public and private herbaria as well as the floristic literature. The locality of each additional record was assigned to a grid cell of the FMC. For Austria, we evaluated the exact date of each record, if not given in the database, by consulting the original source or the relevant botanists. This information did not deliver an exact reconstruction of the annual invasion history, as not all cells of the FMC were searched for ragweed each year. Rather, it represents a mixture of expansion and detection history.

## Fitting SDMs and generating habitat suitabilities

Spatially explicit data on climatic conditions, topography, land use, river- and human-traffic networks (streets and railways) for both Austria and Germany were collected from various sources (see Table 2). All raster GIS data were re-sampled to match the resolution of the FMC grid. For river- and human-traffic networks, the accumulated length of these elements within each FMC grid cell was calculated. The current (= year 2005) distribution of *A. artemisiifolia* in Austria and Germany was then related to the environmental variables by means of both a GLM and a GAM. Non-linear effects of the individual predictors were accounted for by means of second-order polynomials in GLMs and by smoothing splines with four target degrees of freedom in GAMs. Variables included in the final models were selected by means of a combined forward and backward selection procedure based on the Akaike information criterion as implemented in the R-function *step* (R Development Core Team, 2006). Goodness of model fit was evaluated using adjusted $D^2$-values (Guisan & Zimmermann, 2000), and discrimination ability by means of the area under the receiver operating characteristic curve (AUC; e.g. Swets, 1988) calculated after a 10-fold cross-validation of the training dataset (van Houwelingen & Le Cessie, 1990).

Generalized linear models and GAMs fitted with the combined data from Austria and Germany were then used to predict the current probability of occurrence of *A. artemisiifolia* across the 2612 FMC cells in Austria. In biogeographical applications, this probability-scaled output of GLMs, GAMs and similar statistical tools is usually translated into occurrence predictions using a probability threshold that maximizes the correctly predicted percentages of presences and absences (e.g. Pearce & Ferrier, 2000). This can be regarded as the best prediction of the species' actual distribution, or, in the case of an invasive plant, of the infestation status, if only environmental determinants, and no dispersal constraints, are considered. The real invasion process is driven by dispersal events, however, and these dispersal events are influenced by a multitude of factors not explicitly accounted for in our simulations models. A common way to deal with such

**Table 2** Environmental predictor variables used to calibrate the species distribution models of *Ambrosia artemisiifolia* in Austria and Germany for the year 2005.

| Category | Variables | Source | Original scale |
|---|---|---|---|
| Climate – temperature | Mean annual, mean winter, mean summer temperature and mean temperatures of monthly triplets (corresponding to the four seasons winter, spring, summer and autumn) | ATEAM Project (New *et al.*, 2002) | $10' \times 10'$ |
| Climate – precipitation | Mean annual and mean seasonal (monthly triplets) precipitation sums | ATEAM Project (New *et al.*, 2002) | $10' \times 10'$ |
| River network | Length of rivers and channels | Digital Austrian Map (Austrian Mapping Agency BEV); Digital Landscape Model 1000 (Federal Agency for Cartography and Geodesy, BKG) | 1 : 50,000 to 1 : 200,000 |
| Topography | Elevation; standard deviation of curvature | Digital elevation models (Austrian Mapping Agency, BEV; Federal Agency for Cartography and Geodesy, BKG) | 250 m |
| Land cover/habitat quality | Proportional area of suitable land-cover types within a quadrant | CORINE land cover (European Environment Agency, EEA) | 100 m |
| Human traffic | Length of major streets, minor streets and railway tracks | Austria: Tele Atlas N.V. (© 2005); Germany: Digital Basic Landscape Model (Federal Agency for Cartography and Geodesy, BKG) | 1 : 50,000 to 1 : 200,000 |

unknown processes is to introduce stochasticity (e.g. Clark, 2009), as we do here by cell- and year-wise comparison of predicted probabilities to random numbers. Therefore, the presences generated in any single simulation run will deviate from those generated by applying a threshold criterion to SDM predictions, even in the case of the HABITAT model. However, for a simulation run consisting of 15 time-steps, defining the habitat suitability by

$$H(\boldsymbol{x}) = 1 - (1 - h(\boldsymbol{x}))^{1/15} \qquad (3)$$

(where $h(\boldsymbol{x})$ is the prediction of the GLM or GAM, respectively) ensures that, averaged over a large number of simulation runs, the cell-wise occurrence probabilities predicted by the SDM are recovered.

### Model specification and parameter estimation

The three models to compare were calibrated to reconstruct the observed range dynamics of *A. artemisiifolia* in Austria between 1990 and 2005. They are hence operating on the same two-dimensional grid given by the 2612 cells of the FMC in Austria. They also share the discrete annual time-scale (15 time-steps) and the initial state configuration, which is defined by the documented distribution of *A. artemisiifolia* across this grid in 1990.

We used a maximum-likelihood approach to estimate the values of the parameters $a$ and $d$ of equation (2) (or of $a$ only in the case of the HABITAT models) from the observed time series of cell-occupancy patterns between 1990 and 2005 (cf. Etienne *et al.*, 2004; Facon & David, 2006). As our model formulations do not allow for extinctions, there are only two types of relevant transitions, namely an unoccupied cell becoming occupied or remaining unoccupied. The probability or likelihood $P(\boldsymbol{x})$ of a single cell becoming occupied during 1 year is given by equation (1); the likelihood of its remaining unoccupied is its complement, $1 - P(\boldsymbol{x})$. Considering individual cell transitions as independent events, the log likelihood of observing the 15-year time series of occupancy data for the whole Austrian FMC grid is then given by the summed log likelihoods across all transitions of unoccupied cells over all 15 time-steps. The values of parameters $a$ and $d$ that maximize this sum were found by numerical optimization. The fits of the SPREAD, HABITAT and COMBINED models to the data were compared by likelihood ratio tests.

For clarity, we note that for the HABITAT and COMBINED models this method of parameter estimation represents a 'sequential' maximum likelihood approach, as the coefficients of the environmental predictors in the SDM and the parameters $a$ and $d$ were not estimated jointly. Instead, we first calibrated the SDM, and then determined $a$ and $d$, given the fitted SDM. This approach has the advantage that it can in principle be combined with any type of SDM, including those that do not use maximum likelihood for parameter estimation, such as, for example, artificial neural networks (e.g. Pearson *et al.*, 2002).

### Model evaluation

The ability of the various models to reconstruct the recent ragweed invasion in Austria was evaluated by means of the following measures of concordance between the results of 1000 simulations with optimized parameter sets and the observed invasion pattern:

**1.** Averaged final simulation results for 2005 were compared with the documented infestation status in 2005 (excluding the cells already occupied in 1990) by means of the area under the receiver operating characteristic curve (AUC). The AUC is a measure of a model's discrimination ability taking values between 0 and 1, with 0 indicating perfect inverse discrimination, 0.5 random, and 1 perfect correct discrimination. According to conventional rules of thumb, AUC values between 0.7 and 0.8 are considered to indicate fair models, values between 0.8 and 0.9 good models, and values between 0.9 and 1 excellent models (e.g. Swets, 1988; Araújo *et al.*, 2005). Note, however, that the AUC is insensitive to the spatial arrangement of response predictions and hence to spatial autocorrelation in spread patterns.

**2.** Moran's *I*. Spatially restricted spread capacity must result in spatial autocorrelation of the infested cells in the resulting infestation pattern, at least within the width of the spread kernel. As a measure of spatial correlation we use Moran's *I* with 7-km distance classes (which roughly correspond to the extent of one cell of the FMC grid). For each distance class, Moran's *I* was calculated for the observed distribution of *A. artemisiifolia* in 2005 as well as for the final infestation patterns (= year 2005) produced by each of the 1000 simulation runs performed with each model. The observed index values were then standardized by the simulations' means and standard deviations, and the sums of these *z*-scores over the first three distance classes (which correspond approximately to the kernel width of the COMBINED models, cf. Table 3) were compared to a chi square-distribution with three degrees of freedom. This test hence delivers the probability that the observed spatial pattern has been produced by a process adequately captured by the respective simulation model.

## RESULTS

Generalized linear models and GAMs produced very similar results in terms of discrimination capacity (cross-validated AUC = 0.83 and 0.84, respectively), goodness of fit (adjusted $D^2$ = 0.23 and 0.25, respectively) and spatial pattern of predictions (Pearson's *r* among GAM and GLM predictions = 0.97). SDM outputs (Fig. 1) show a concentration of highly suitable cells in the warmer eastern and southern parts of Austria, whereas the territory of the Alps in the central and western parts of the country is largely classified as unsuitable, with the exception of some larger valleys.

Log-likelihood values demonstrate a clear hierarchy among the SPREAD, HABITAT and COMBINED models, with SPREAD being worst at explaining the observed invasion patterns (Table 3). Owing to the lack of habitat information,

**Table 3** Spread kernel parameter estimates for the models (Combined, Habitat and Spread) used to simulate the invasion of *Ambrosia artemisiifolia* in Austria between 1990 and 2005. Kernel height (*a*) is the dimensionless pre-factor of the kernel (cf. Table 1). Kernel width (in kilometres) is defined as the square root of the variance per dimension of the Gaussian kernel and equals parameter *d* in equation (2) and Table 1. Model comparison is based on likelihood ratio tests with degrees of freedom (d.f.) equal to the differences in the number of estimated parameters (including coefficients of the species distribution models for comparisons involving Spread). ln(*L*): log likelihood of the parameterized models. *P*-values < 0.05 are given in bold.

| Model | Kernel height (*a*) | Kernel width (*d*; km) | ln(*L*) | Test | d.f. | *P*-value |
|---|---|---|---|---|---|---|
| 1. Combined$_{GLM}$ | 0.659 | 23.43 | −998.00 | 1 vs. 2 | 1 | **0.0075** |
| 2. Habitat$_{GLM}$ | 0.579 | Inf | −1001.57 | | | |
| 3. Combined$_{GAM}$ | 0.628 | 26.05 | −995.74 | 3 vs. 4 | 1 | **0.0309** |
| 4. Habitat$_{GAM}$ | 0.567 | Inf | −998.13 | | | |
| 5. Spread | 0.011 | 12.58 | −1092.17 | 1 vs. 5 | 21 | **<0.0001** in all cases |
| | | | | 2 vs. 5 | 22 | |
| | | | | 3 vs. 5 | 67 | |
| | | | | 4 vs. 5 | 66 | |

Spread-based simulations frequently predicted the infestation of unsuitable cells (Fig. 2), resulting in a low AUC (Table 4). Moreover, despite a much narrower kernel width (Fig. 3), Spread captured the spatial structure of the invasion process poorly, and consistently and significantly under-predicted the autocorrelation in infestation patterns (Table 4, Fig. 3).

Taking account of habitat suitability information considerably, and highly significantly, improved models of the observed invasion (Table 3). The Habitat models predicted infestation patterns closely following the distribution of suitable cells (Fig. 2), and their AUC values were hence much higher than the one derived from Spread simulations (Table 4). Spatial autocorrelation in habitat suitability (cf. Fig. 1), together with the rather small extent of the study system, obviously constrained the distances of random spread simulations. Hence, despite an unrestricted kernel, both GLM- and GAM-based Habitat models also reproduced the spatial structure of the invasion significantly better than did Spread (Table 4).

Restricting dispersal distances by introducing a finite parameter *d* (i.e. switching from Habitat to Combined) again significantly improved model fits to the data for both GLM- and GAM-based model formulations (Table 3). However, the increase in explained deviance was much lower than when replacing Spread by Habitat. As a consequence, simulated invasion patterns were visually similar (Fig. 2) and produced more or less identical AUC values (Table 4). The superiority of the Combined models hence rests largely upon their capacity to better capture the spatial autocorrelation in invasion patterns (Table 4), a consequence of the now spatially restricted spread kernels (Fig. 3).

## DISCUSSION

### Advantages and limitations of the modelling approach

Empirical studies usually demonstrate that habitat configuration and dispersal processes interact in determining the spatial
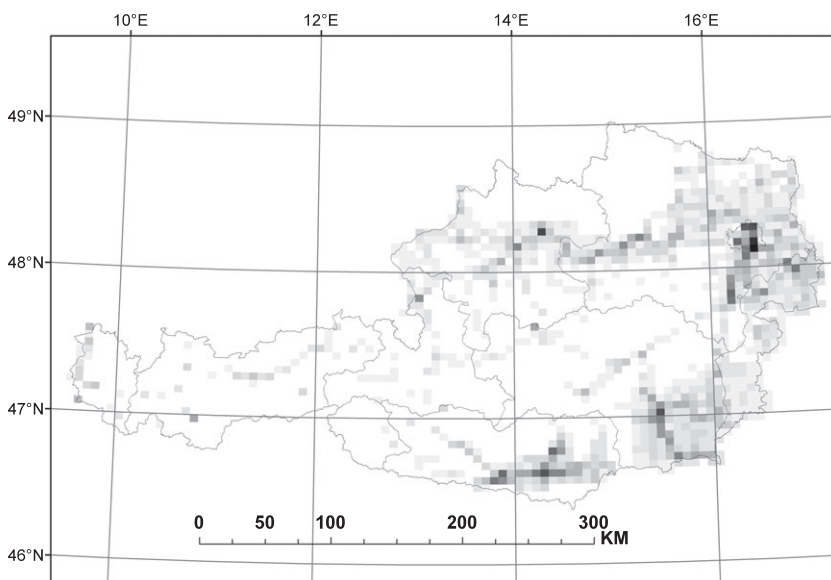


**Figure 1** Rescaled habitat suitability map for *Ambrosia artemisiifolia* in Austria based on a generalized linear model calibrated with the distribution of the species in Austria and Germany observed until the year 2005. The squares represent the cells of the 3 × 5 min grid of the Floristic Mapping of Central Europe. Suitability increases from white to black. Generalized additive model predictions deliver a nearly identical pattern. Projection: Lambert Conformical Conic.
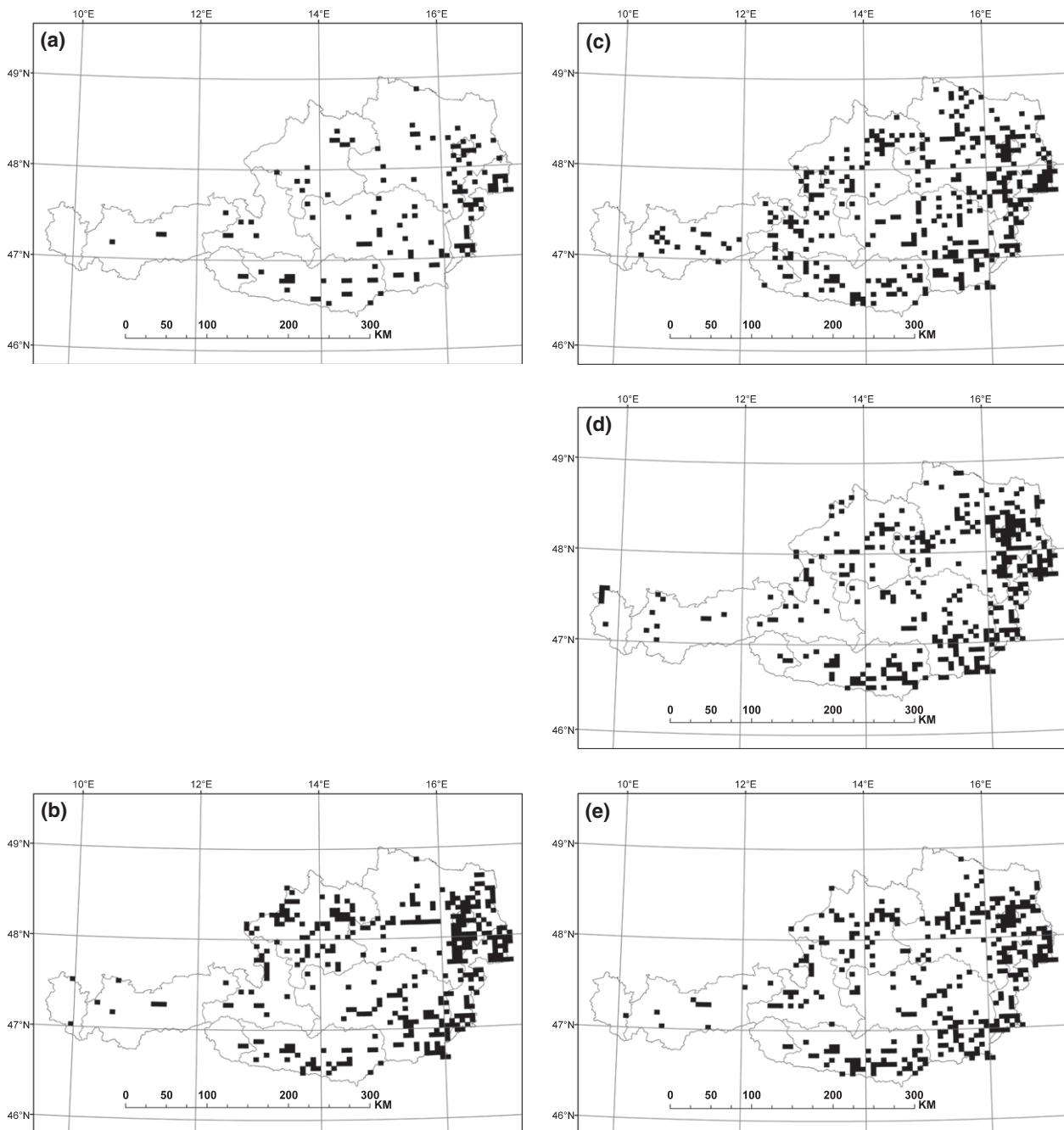
**Figure 2** Distribution of *Ambrosia artemisiifolia* across the 3 × 5 min grid of the Floristic Mapping of Central Europe. (a) Observed distribution in 1990 = initial-state configuration of the simulation runs; (b) observed distribution in 2005; (c–e) distribution in 2005 as predicted by simulation runs of the SPREAD, HABITAT$_{GLM}$ and COMBINED$_{GLM}$ models, respectively (see Materials and Methods for further details). Predictions of the HABITAT$_{GAM}$ and COMBINED$_{GAM}$ models are visually hardly distinguishable from those of HABITAT$_{GLM}$ and COMBINED$_{GLM}$. Black squares indicate infested cells. Projection: Lambert Conformical Conic.

pattern and rate of invasive spread (Havel *et al.*, 2002; Rouget & Richardson, 2003; Foxcroft *et al.*, 2004; Meentemeyer *et al.*, 2008). The results of our model comparison confirm this combined effect of habitat and dispersal constraints. They demonstrate that neglecting habitat suitability results in predictions of ragweed spread into regions that are in fact unsuitable for the species, and that hence actually represent barriers to its further migration. Taking habitat suitability into account, but assuming that spread is spatially unrestricted, entailed simulations that correctly predicted prevalent infestation of susceptible areas but reproduced the spatially auto-correlated invasion process less adequately than the COMBINED approach, although the improvement upon the HABITAT models was less pronounced than expected. However, we suppose that for larger regions, with less strongly auto-correlated habitat patterns, the spatial spread restrictions

**Table 4** Evaluation statistics for the models (Combined, Habitat and Spread) used to simulate the invasion of *Ambrosia artemisiifolia* in Austria between 1990 and 2005. AUC values are areas under the receiver operating characteristic curve. SSSE (sum of squared scaled errors) values are sums of squared differences between simulated and real Moran's *I* values in the first three distance classes (<7 km, 7–14 km, 14–21 km) divided by the respective standard deviations of 1000 simulations with optimized parameter sets (cf. Table 3). *P*-values are based on comparing these differences to a chi square-distribution with three degrees of freedom.  *P*-values < 0.05 are given in bold.

| Model | AUC | SSSE | *P*-value |
|---|---|---|---|
| 1. Combined$_{GLM}$ | 0.83 | 3.24 | 0.357 |
| 2. Habitat$_{GLM}$ | 0.82 | 12.56 | **0.006** |
| 3. Combined$_{GAM}$ | 0.83 | 2.68 | 0.443 |
| 4. Habitat$_{GAM}$ | 0.83 | 8.23 | **0.042** |
| 5. Spread | 0.60 | 118.05 | **<0.0001** |

implemented in Combined will considerably increase its superiority over a purely habitat-driven simulation.

Besides increasing the accuracy of predictions under stable environmental conditions, an important further advantage of our Combined modelling approach is that scenarios of environmental change can be incorporated consistently. Human-land use and land-use changes are well known to affect alien plant invasions (Hobbs & Huenneke, 1992), and other components of global change may also interact with invasive spread (Dukes & Mooney, 1999). Climate warming in particular is likely to alter the spatial pattern of habitats for both native and alien plants. Using SDMs calibrated with current distribution data to predict the expected new distribution of potential habitats under scenarios of environmental change is common practice, especially to forecast the ecological consequences of climate change (e.g. Thuiller *et al.*, 2005b). In the context of invasion modelling, this approach can be used within our combined modelling framework to simulate the spread of alien plants through changing environments by updating spatial suitability layers, and hence habitat-dependent infestation probabilities, with each time-step (e.g. Midgley *et al.*, 2006). In central Europe, for example, this may be relevant as the spread of many alien plants is thought to be currently limited or at least slowed by climatic constraints (Walther, 2002, 2003). The strong effect of temperature on the current distribution of *A. artemisiifolia* in Austria suggests that ragweed is among these climatically limited invaders (Essl *et al.*, 2009), and that a substantially warmer climate will probably trigger and accelerate its spread into areas as-yet uncolonized (M. Leitner *et al.*, in preparation).

Although generally we consider the integration of IPSs and SDMs to provide a powerful framework with which to simulate alien invasions, the particular Combined model for ragweed invasion in Austria has some limitations. First, the power of an SDM to capture the ecological niche of a species appropriately rests on the assumption that the species' current distribution is in equilibrium with its environment (Peterson *et al.*, 1999; Guisan & Thuiller, 2005). This assumption is, by definition, violated for invasive species in the adventive range if they have not yet colonized all suitable terrain. The bias thus introduced in habitat suitability
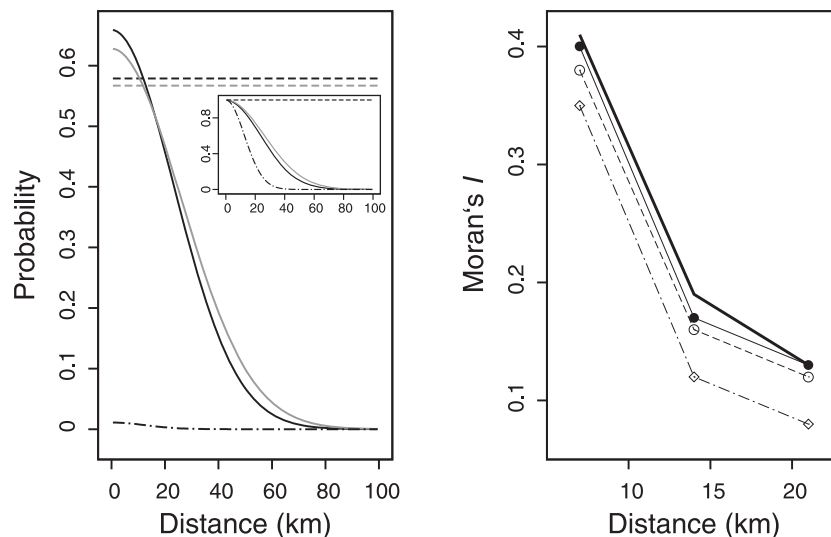


**Figure 3** Left panel: Optimized spread kernels *S*(*r*) for the models used to simulate the invasion of *Ambrosia artemisiifolia* in Austria between 1990 and 2005. Solid black line, Combined$_{GLM}$; solid grey line, Combined$_{GAM}$; dashed black line, Habitat$_{GLM}$; dashed grey line, Habitat$_{GAM}$; dashed–dotted line, Spread. The inset panel gives kernel widths only, that is, it ignores parameters *a* of *S*(*r*) (cf. Table 3). Right panel: Autocorrelograms illustrating the spatial autocorrelation in real (thick solid line) and simulated invasion patterns within the first three distance classes around each newly infested cell (<7 km, 7–14 km, 14–21 km). Combined$_{GLM}$ is represented by a thin solid line and filled circles, Habitat$_{GLM}$ by a dashed line and open circles, and Spread by a dashed–dotted line and open diamonds. Combined$_{GAM}$ and Habitat$_{GAM}$ are very close to Combined$_{GLM}$ and Habitat$_{GLM}$, respectively, and are not drawn for clarity.

estimates will depend on how representatively the species has sampled all relevant environmental gradients. In the case of *A. artemisiifolia* in Austria, this bias should be fairly low: a recent review has shown that the distribution of records closely follows climatic gradients and land-use patterns (Dullinger *et al.*, 2009; Essl *et al.*, 2009), and that, since the 1970s, all suitable regions have been colonized by at least some scattered and isolated populations. If they are easily available, however, it might generally be useful to parameterize SDMs with distribution data from the native range (e.g. Weber, 2001; Kriticos *et al.*, 2003), especially if the invasion is still in an early stage. Nevertheless, the cross-continental transfer of SDMs may also be problematic, as realized niches may vary among native and introduced ranges (Broennimann *et al.*, 2007). A combination of native and adventive range data seems hence most promising. A Bayesian framework, which has already been applied to the problem of invasive spread (e.g. Wikle, 2003), might be especially useful in this respect. In such a framework, the likelihood function for the available spread data might be formulated such that it integrates the coefficients of the habitat variables (instead of fitting the habitat model beforehand as we did here), and prior distributions on these coefficients might be specified on the basis of fitting SDMs to native distribution data.

Second, spread probabilities for ragweed were derived from patterns of empirical data on a purely phenomenological basis (cf. Havel *et al.*, 2002; Gilbert *et al.*, 2004; Meentemeyer *et al.*, 2008). Although the parameter estimates provide a reasonable fit to this individual phase of the invasion history of *A. artemisiifolia* in Austria, their generic validity is of course questionable. More mechanistic approaches to dispersal kernel parameterization (e.g. Katul *et al.*, 2005; Will & Tackenberg, 2008) may help to provide more generally valid estimates, or to modify estimates according to available information on spatial or temporal variation of dispersal vector properties (e.g. von der Lippe & Kowarik, 2007; Nathan *et al.*, 2008). Such region- or time-specific variation in dispersal kernel parameters could easily be implemented in the proposed modelling framework.

Third, local population growth, which, together with dispersal kernels, determines spread rates (e.g. Kot *et al.*, 1996), is not explicitly represented but is implicit to phenomenological spread kernel parameter estimates. This greatly simplifies parameter estimation and modelling if appropriate time series of distribution data are available, but may mask regional differences in invasion speed owing to variation in demographic parameters (Caswell *et al.*, 2003; Keith *et al.*, 2008). We think, however, that most of this variation will be captured by differences in habitat suitability estimates. As infestation probability depends on habitat suitability, less suitable cells will, on average, need more time-steps to become occupied at a given level of propagule pressure (= distance-dependent infestation probability). This delay in a cell becoming occupied, and hence a propagule source, should indicate the slower build-up of a local population able to contribute emigrants to the next generation.

## Comparison with other spatially explicit modelling frameworks

Metapopulation models have recently been proposed as a novel approach to combine habitat and dispersal information in models of invasive spread (Facon & David, 2006). However, plants rarely seem to be organized as metapopulations (Freckleton & Watkinson, 2002). In particular, the binary distinction between suitable habitat and unsuitable matrix does not seem to be appropriate for many of them (Murphy & Lovett-Doust, 2004). In contrast to such binary habitat representations, integrating a SDM into a spread model offers a tool for the spatial prediction of continuous gradients in suitability. Along such continuous gradients, trade-offs between habitat quality and propagule pressure in promoting successful colonizations can be captured more appropriately (Havel *et al.*, 2002; Rouget & Richardson, 2003; Meentemeyer *et al.*, 2008), as, for example, less suitable sites may occasionally function as stepping stones of migration when propagule input is high. The dynamic part of such a hybrid model does not necessarily have to be an IPS, however. Extensions of traditional metapopulation models that incorporate variation in patch quality (e.g. Etienne *et al.*, 2004) represent an adequate alternative framework. In particular, making colonization (and extinction) probabilities in stochastic patch occupancy models (Ovaskainen & Hanski, 2004) dependent on SDM predictions would be conceptually similar to the Combined model presented here. Such hybrids between SDMs and metapopulation models should hence be similarly useful to predict invasive spread, especially in fragmented landscapes where the delineation of a non-suitable matrix is adequate.

## Management implications

The significant economic costs of *A. artemisiifolia* invasion (Reinhardt *et al.*, 2003) and the rapid and ongoing expansion of the species in Austria call for a management response. Total eradication is clearly unfeasible, but halting further ragweed invasion will still bear significant gains for public health. The superiority of the Combined model suggests spatial restrictions on the species' annual spread, which are not only due to spatial autocorrelation of suitable habitats. Reducing the rate of unintentional human transport, its main dispersal pathway in Austria (Essl *et al.*, 2009), for example by strengthening regulations on seed contamination, should hence be a first and important step to decreasing the rate of its further expansion. Moreover, these spatial constraints suggest concentrating eradication measures on peripheral and isolated populations, as these will contribute the most to expansion into regions currently not, or only sparsely, colonized. Clearly, models always simplify reality, and care has to be taken when basing management decisions on their results. Nevertheless, using the Combined model for predictions to the near future may indicate where new marginal or peripheral populations might be expected first and where a prospective monitoring of

susceptible habitat types, such as agricultural fields, road and railway verges, or ruderal sites (Essl *et al.*, 2009), would hence be most helpful for cost-effective early eradication and impeding further spread. The effects of such region-specific management activities on the further spread of the species might be incorporated into model simulations by additionally weighting infestation probabilities by some spatially varied indicator of management intensity or efficiency. Owing to ragweed's sensitivity to climatic gradients in Austria (Essl *et al.*, 2009), however, such simulations should urgently consider appropriate climate warming scenarios in order to make useful predictions.

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## BIOSKETCH

**Manfred G. Smolik** is a physicist at the University of Vienna with a special interest in modelling diffusion processes in various physical systems and applying these methods to other fields. This interdisciplinary interest led him to collaborate with ecologists on the question of invasive plant spread. This paper is part of his Master's thesis.

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