

Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*

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Summary

1. After its initial discovery in Macedonia in 1985, during the last 19 years the leaf-miner moth *Cameraria ohridella* has invaded most of Central and Western Europe. The species, which causes aesthetic damage to horse chestnuts, is generally observed first in highly populated locations before colonizing the countryside. This pattern is consistent with a stratified dispersal process combining long-distance movements and local diffusion.
2. Using large-scale spatial data on damage caused by *Cameraria ohridella* in Germany, three stochastic spatial models of spread are compared: a diffusion model, a leptokurtic dispersal model and a stratified dispersal model that assumes a two-scale dispersal process. In addition, the association between human population and moth invasion is tested in this last model by linking long-distance infestation probability to human population density. Finally, these spatial models constructed with data from Germany are tested at the European scale and compared to historical records of first occurrence.
3. The fat-tailed dispersal kernel models (leptokurtic and stratified dispersal models) allowing for long-distance dispersal provide better predictions than the diffusion model. Among these models, the stratified dispersal model incorporating the effect of human population density provides the best description of the spread of *Cameraria ohridella* in Germany in predictive (lowest sum of squared errors) and qualitative (similar fractal dimension) terms.
4. The roles of short-distance and long-distance dispersal in *Cameraria ohridella* invasion ecology in relation to human population are discussed, together with the models' scale-dependence and limitations.

Key-words: biological invasion, Gracillariidae, spatial model, stratified dispersal.

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Introduction

Understanding the spatial dynamics of invasive species is critical in any attempt at predicting their spread to new areas and represents a challenge in the application of theoretical models of invasive spread (Sakai *et al.* 2001). The expansion phase of invading organisms is generally described by the change in range distance as a function of time (Shigesada & Kawasaki 1997). The approaches adopted most widely to model these expansions employ diffusion models (Skellam 1951), strati-

fied diffusion models (Shigesada, Kawasaki & Takeda 1995) and integrodifference models (Kot, Lewis & van den Driessche 1996). However, these approaches have been directed largely at constructing hypothetical invasions that fit the global features of spread such as the type of range-distance vs. time relationship, rather than capturing the details of the spatial patterns of spread on the basis of large spatial data set. In particular, although stratified dispersal that assumes a two-scale dispersal process is now accepted widely in invasion ecology (Shigesada & Kawasaki 1997), very few models have used this concept to explore detailed spatial patterns of spread. In insect ecology, the only case to our knowledge where a stochastic stratified dispersal model was used is the assessment by Sharov & Liebhold (1998) of the effect of an integrated pest management strategy on the

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spread of the invasive forest defoliator *Lymantria dispar* (Lepidoptera: Lymantriidae).

The invasive horse chestnut leafminer *Cameraria ohridella* Deschka & Dimic (Lepidoptera, Gracillariidae) was found and described first in Macedonia, and has spread rapidly through Central and Western Europe over the last 19 years (Sefrova & Lastuvka 2001 and references therein). The origin of the pest remains unknown (Grabenweger & Grill 2000). It was reported recently in the United Kingdom (United Kingdom Parliament 2002), Denmark (Karsholt & Kristensen 2003) and Ukraine (Akimov *et al.* 2003). Damage caused by larval mining in the leaves is spectacular in cities where the main host species, the white-flowering horse chestnut *Aesculus hippocastanum* L. (Hippocastanaceae), is abundant. The quantitative geographical distribution of white-flowering horse chestnut in Europe is unknown, but it has been planted intensively in almost every country. In Germany it is found in high abundance in cities, but it can also be observed in small villages or in the countryside. Every leaf on a tree may eventually be infested within a season, which may cause premature abscission in early summer. The true long-term effect of leaf damage by *C. ohridella* on host-tree vigour is still unclear (Thalman *et al.* 2003). Parasitism rates are very low (generally lower than 5%), especially in recently invaded areas (Freise, Heitland & Tosevski 2002), and are thus assumed to have no effect on the invasion dynamics. Three generations are usually observed per year (Tomiczek & Krehan 1998) and population growth is estimated approximately as 10-fold per generation (Sefrova & Lastuvka 2001). The spread of the leafminer was estimated as approximately 60 km per year on the basis of first observation dates in European countries (Sefrova & Lastuvka 2001), which is higher than rates of spread observed generally in other invasive Lepidoptera [e.g. *Lymantria dispar*: 9.45–20.78 km/year (Liebhold, Halverson & Elmes 1992); invading lepidoptera in the United Kingdom: 0.06–10.3 km/year (Agassiz 1996)], but seems comparable to rates of spread observed in other invasive leafminers (Agassiz 2002). Within cities, the moth is assumed to disperse by flight, and indirect observations suggest a rate of spread of a few hundred metres per generation (Gilbert *et al.* 2003a). Over larger distances, *C. ohridella* is presumably dispersed passively by wind or inadvertently by cars, lorries or trains, as first establishment has been observed frequently near car parks (Heitland *et al.* 1999).

Two hypotheses are explored here. First, the biological invasion by *C. ohridella* follows a stratified dispersal pattern (Hengeveld 1989) allowing long-distance dispersal (wind, human transportation) as well as short-distance diffusion by flight. This type of dispersal is now considered as the norm in invasive organisms and has been described in other invasive insects [e.g. *Lymantria dispar* Sharov & Liebhold (1998); *Dendroctonus micans* (Coleoptera: Scolytidae); Gilbert *et al.* 2003b] and in other Gracillariidae [*Phyllonorycter leucographella* Nash *et al.* (1995)]. Our second hypothesis is that local

human density population correlates with long-distance dispersal, because traffic is more intense in highly populated areas and because higher human densities are associated generally with higher densities of the host-plant *A. hippocastanum*.

To test these hypotheses, we used a database of spatio-temporal observations of damage by *C. ohridella* in Germany to compare four spatially explicit stochastic models of spread differing in the shape of their dispersal kernel: a diffusion model, a leptokurtic dispersal model and a stratified dispersal model that assumes a two-scale dispersal process corresponding to short- and long-distance dispersal events. The fourth model tests the association between long-distance dispersal and human population by allowing long-distance infestation probability to vary according to human population density. The four models with their best-fit parameters are tested at the European scale by comparing their prediction to historical records of first observations.

Materials and methods

DATA

Data on the distribution of *C. ohridella* were compiled from questionnaires collected in 1997 and 1998 and from visual surveys that we carried out between 1998 and 2000 in Germany. In 1997, data were compiled from questionnaires and concern Bavaria and a few isolated spots further north ($n = 203$). In 1998, data were compiled from surveys carried out in Bavaria and other parts of Germany ($n = 1480$), questionnaires ($n = 224$) and additional visual observations ($n = 31$). In 1999, surveys were extended to Nordrhein-Westfalen ($n = 1308$) in addition to Bavaria ($n = 955$). In 2000, only the northern part of Germany was surveyed ($n = 676$). Leaf damage scores were used in surveys and questionnaires (0%; 0–10%; 10–25%; 25–50%; 50–75%; > 75%). These scores were estimated in the field by recording the maximum score observed at each sampling location. These data were grouped by city code by using the highest score. The numbers of surveyed city codes were thus 146, 855, 933 and 331 in 1997, 1998, 1999 and 2000, respectively (Fig. 1). Preliminary data treatment consisted of establishing annual presence/absence distribution through the 1996–99 periods. Only 276 of 1962 sampled city codes were surveyed more than once, and it was necessary to estimate infestation status (presence/absence) in years when no observations had been made. Locations surveyed more than once were thus used as a training set to derive prediction rules on past or future infestation status. Extinctions from one year to the next were very rare (1.16%), and the first rule assumed therefore that year n was infested if any previous year was infested, and conversely, that year n was uninfested if any following year was uninfested (Table 1; rows 1 and 2). Moreover, there was a clear relationship between infestation status in year n and infestation level in year n_{+1} and n_{+2} , respectively, because very recently infested sites

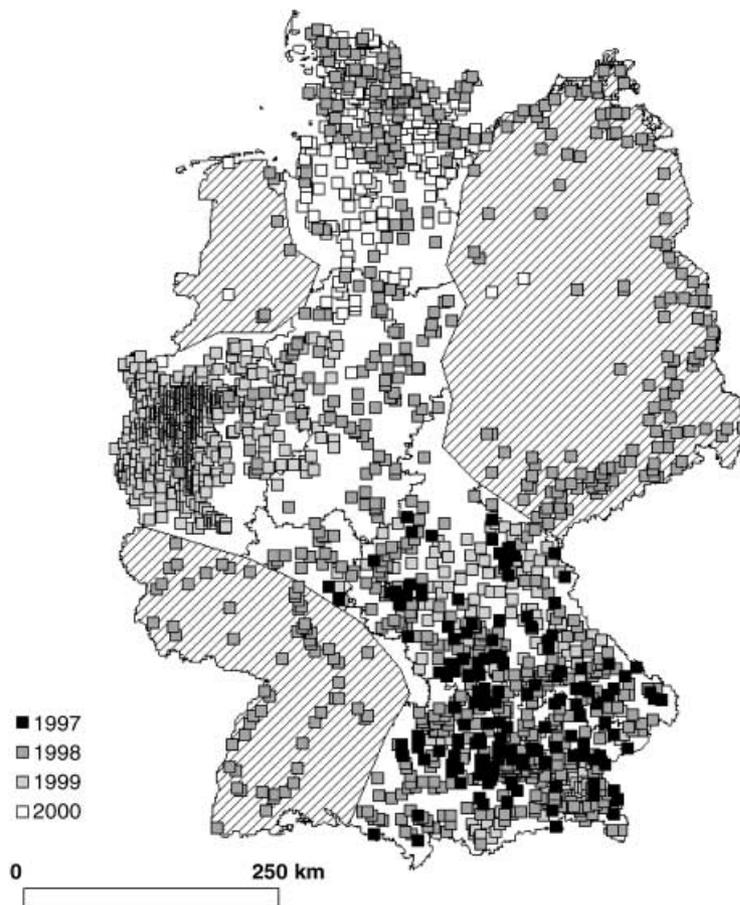


Fig. 1. Distribution of *C. ohridella* damage observations in Germany summarized per city code in 1997 ($n = 146$), 1998 ($n = 855$), 1999 ($n = 933$) and 2000 ($n = 331$) throughout Germany. The greyed shading corresponds to areas with low spatial or temporal sampling density excluded from the analysis.

Table 1. Rules used to predict past/future infestation status

Observed past/future status	Predicted status in year n	Infestation probability	Case no.
Year $n_{-1,2,3}$ infested	Infested	$P = 0.984$	457
Year $n_{+1,2,3}$ uninfested	Uninfested	$P = 0.016$	1932
Year n_{+1} infested	Logistic model (% correct = 90.9; $P < 0.001$)	Logit (P) 1.388 Inf* -0.541	1246
Year n_{+2} infested	Logistic model (% correct = 83.1; $P < 0.001$)	Logit (P) 1.743 Inf** -3.742	1101
Year n_{+3} infested	Unknown	—	—
Year $n_{-1,2,3}$ uninfested	Unknown	—	—

*Infestation level at Year n_{+1} ; **infestation level at Year n_{+2} .

generally have lower levels of infestation than sites infested from a longer period. The second and third rules were thus based upon logistic regression models built to predict the infestation probability in year n as a function of infestation score in year n_{+1} and n_{+2} , respectively (Table 1; rows 3 and 4). The cut-off value of 0.5 was used to predict infestation status (0/1) as a function of the logistic models estimated probability. Finally, predictions were not made when a site was observed to be uninfested in years $n_{-1,2,3}$ or infested only in year n_{+3} (Table 1; rows 5 and 6). At the end of this process, the number of points with observed or predicted infestation status was 1233, 1877, 1928 and 1632 in 1996, 1997, 1998 and 1999, respectively, of which 4736 (71%) were

derived from the rules summarized in Table 1. Areas with low spatial and temporal sampling intensity were excluded from further analyses.

These enhanced observations for infestation status were then interpolated using ordinary kriging (Isaaks & Srivastava 1989) to estimate infestation probabilities in unsampled locations. The global trend was modelled as a linear function of the spatial coordinates, and the residuals of the linear models were used to create a model of semivariance used for ordinary kriging. The results of the ordinary kriging were then added to the trend model (see Table 2 for trend models and ordinary kriging parameters). Global trend functions, standardized semivariograms and ordinary kriging estimates

Table 2. Global trend model and kriging model parameters used to interpolate infestation status. R^2 quantify the relationship between semivariance spherical models used for ordinary kriging and experimental standardized semivariograms

Year	Global trend model	Nugget	Sill	Range (km)	r^2
1996	$Z = -1.27 \cdot 10^{-18} X - 2.21 \cdot 10^{-18} Y + 1.41 \cdot 10^{-11}$	0.54	0.49	104	0.969
1997	$Z = -1.27 \cdot 10^{-18} X - 2.96 \cdot 10^{-18} Y + 1.88 \cdot 10^{-11}$	0.56	0.46	68	0.963
1998	$Z = -2.24 \cdot 10^{-18} X - 5.22 \cdot 10^{-18} Y + 3.32 \cdot 10^{-11}$	0.29	0.75	75	0.946
1999	$Z = -1.97 \cdot 10^{-18} X - 2.90 \cdot 10^{-18} Y + 1.83 \cdot 10^{-11}$	0.34	0.70	69	0.977

were calculated using the software Surfer 8 (Golden Software Inc., Golden, USA). The interpolated distribution of infestation probabilities was used for mapping, and to delineate the most probable area of initial infestations, i.e. area where the 1996 interpolated infestation probability was higher than 0.9.

Data on human population densities were obtained from the Gridded Population of the World (GPW), Version 2 (CIESIN 2000), resampled at the 2.5 km resolution.

ANALYSIS

A spatially explicit model was built to explore simulated spread according to different dispersal assumptions. This model was carried out using data resampled at a 2.5-km resolution using the maximum summarizing function if more than one observation was found in a 2.5-km cell. The model was developed within the Arcview GIS 3.2 platform (ESRI, Redlands, CA, USA), using the Spatial Analyst and Avenue programming language. We assumed three generations per year over the 4 years

(as generally observed in Germany; Freise & Heitland 2001), and the algorithm we used to simulate the spread over one generation involved four steps. First, the distance of each cell to the nearest occupied cell in the previous time step (cells with value equal to 1) was calculated. Secondly, the infestation probability of each cell was estimated as a function of that distance, and as a function of the local human population density in the last model. Thirdly, a layer of random numbers was generated and cells with a random number lower than their infestation probability were set as occupied. Fourthly, each cell's infestation status was updated and the algorithm re-iterated. The algorithm started with the initial distribution (set as the area where interpolated infestation probability in 1996 is > 0.9) and iterated until the 12th generation (i.e. for three years).

The functions used to estimate infestation probability varied according to the model used (Fig. 2). In the first model, termed 'diffusion', infestation probability decreased as a function of distance following a normal curve (Fig. 2a). This type of model, used for half a century

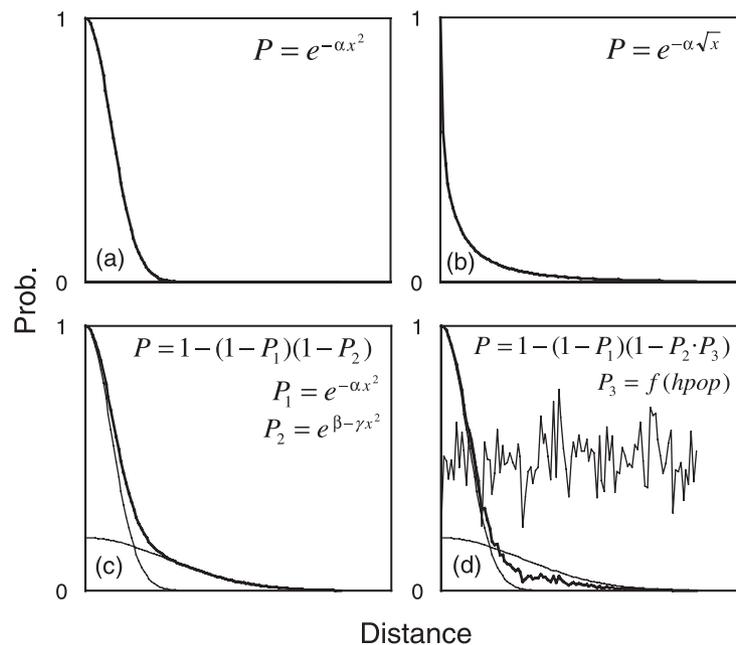


Fig. 2. Function used to predict infestation probability as a function of distance to the shortest infested cell in the four models: (a) diffusion model; (b) leptokurtic dispersal model; (c) stratified dispersal model (in bold) combining a short-scale and large-scale diffusion model; and (d) stratified dispersal model combined with the effect of human population density. P (bold lines), P_1 , P_2 and P_3 (thin lines) are probabilities, x is the distance to the nearest infested cell, and α , β and γ are model parameters. The figure illustrates the shape of the different functions and the way they are combined and does not correspond to actual distance or human population density units.

to model biological invasions, is expected to produce a travelling wave of constant velocity (Shigesada & Kawasaki 1997). Dispersal distance distributions are frequently leptokurtic, i.e. with more propagules near the centre and in the tail than in the normal distribution and this can have a substantial impact on spread predictions (Jeltsch *et al.* 1997). The second model (Fig. 2b), termed 'leptokurtic dispersal', used a leptokurtic function that was shown to generate accelerating travelling waves (Kot *et al.* 1996) observed in some invasions. The third model, termed 'stratified dispersal', assumed that propagules disperse by two independent dispersal processes occurring at different spatial scales, each one having dispersal distance distributed normally (Fig. 2c). Infestation probability was estimated by the probabilities of short-distance dispersal (P_1) and long-distance dispersal (P_2) combined with an 'OR' statement. In the fourth model, it was assumed that long-distance dispersal probability was a function of the distance to the nearest infested cell (P_2) combined with a function of human population density (P_3) by an 'AND' statement (Fig. 2d). P_3 was estimated using a logistic function such as to have a maximum probability when human population was maximum, a minimum probability when human population was minimum and a probability equal to 0.5 when $\ln(\text{human population density})$ was equal to the observed median. P_3 was estimated as

$$P_3 = \frac{e^{(h-h_m) \cdot \phi}}{1 + e^{(h-h_m) \cdot \phi}} \quad \text{eqn 1}$$

where h is $\ln(\text{human population density})$, h_m is the observed median $\ln(\text{human population density})$ and ϕ is a scaling factor. Each model was fitted using a stochastic optimization procedure. We set $I_{i,t}$ the observed infestation status at location i in year t . Each simulation generated 12 layers of occupied (1) and unoccupied (0) cells (4×3 generations). The 3rd, 6th, 9th and 12th iteration layers were used as predictions for the years 1996, 1997, 1998 and 1999, respectively. For each parameter set, 500 runs were performed and the average infestation status of the 3rd, 6th, 9th and 12th iteration layers calculated. This average layer constituted the set of $S_{i,t}$ simulated values. The set of observations $I_{i,t}$ (0 or 1) comprised the raw data against which the set of simulations $S_{i,t}$ (decimal values ranging from 0 to 1) could be evaluated by estimating the sum of the squared difference between observed and simulated values [$\text{SSE} = \sum_{i,t} (I_{i,t} - S_{i,t})^2$]. The r^2 models were estimated as a complementary measure of model fitness as $1 - \text{SSE}/\text{SST}$ with $\text{SST} = \sum_{i,t} (I_{i,t} - \bar{I}_t)^2$ where \bar{I}_t is the average of $I_{i,t}$. For each model, we identified the parameter values that minimized the SSE. In the fourth model, the short-scale diffusion terms α from the best-fitted stratified dispersal model was used because we assumed that human population density should not affect short-term dispersal.

In addition to the least-squares approach used to compare the predictive power of the spatial models, we wanted to compare the spatial geometry of their predicted

distribution. The fractal dimension has been shown to be a useful way to characterize the geometry of a number of patchy spatial patterns (Li 2000 and references therein), especially when patterns exhibit self-similarity at multiple scales. The fractal dimension D of the distribution of *C. ohridella* over 1996–99 in Germany was estimated and compared to the fractal dimension of each best-fitting spatial model. D was determined using the semi-variogram method (Burrough 1983). The semivariogram is defined as:

$$\gamma(h) = \frac{\sum_{i=1}^{N(h)} (z_i - z_{i+h})^2}{2N(h)} \quad \text{eqn 2}$$

where $N(h)$ is the number of pairs of data points separated by distance h , z_i and z_{i+h} are the infestation status at location i and $i+h$, respectively (Rossi *et al.* 1992). D can be calculated from the slope m of the double logarithmic plot of $\gamma(h)$ vs. h by $D = (4 - m)/2$ (Burrough 1983). The fractal dimension standard error was calculated as the standard error of the regression slope divided by 2. A fractal dimension of 1 implies strict spatial dependence, i.e. homogeneity, and a dimension of 2 implies complete spatial randomness. We wanted a single measure of fractal dimension that would characterize the distribution over the 1996–99 periods. The slope m was thus estimated on a log-log plot of $\gamma(h)$ vs. h by pooling the semivariogram values from the 4 years in the observed distribution, and from 4 years \times 100 runs in the simulated distributions. All semivariograms were estimated with the software Surfer 8 (Golden Software Inc, Golden USA) up to a distance of 200 km with a distance interval of 5 km.

Finally, spatial models with their best-fitting parameters were run at the European scale at the same resolution (2.5 km) by forcing the initial foci to the first observation location in lake Ohrid in 1985, such as to compare our models to the European spread reviewed in Sefrova & Lastuvka (2001). The model was run by assuming three generations per year over 1985–2002 through the following countries: Albania, Austria, Belgium, Bosnia Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, France, Germany, Greece, Hungary, Italy, Luxembourg, Montenegro, Netherlands, Poland, Romania, Serbia, Slovakia, Slovenia and Switzerland. Each model was run 500 times and the date of first occurrence in each country over all simulations constituted our set of simulated observations.

Results

Exploratory descriptive analysis indicated that the pattern of spread showed evidence of stratified dispersal with an increasing rate of spread, and that high human population density was related to a higher probability of infestation. The decrease in the proportion of infested sites as a function of distance to the initial foci changed radically from one year to another (Fig. 3). Some

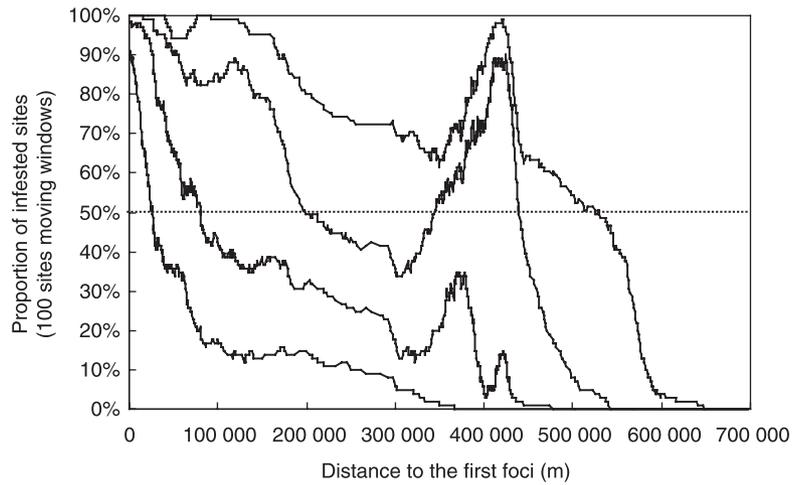


Fig. 3. Proportion of infested sites measured in a 100-sites moving window as a function of the distance to the initial foci. The first intercept between profiles and the 50% level are 26 km, 80 km, 198 km and 528 km for 1996, 1997, 1998 and 1999, respectively.

Table 3. Logistic regression model relating infestation status to the distance to the nearest infested site in the previous year (d) and to the human population density (h)

χ^2	ddl	P	Effect	Estimate	SE	Wald	ddl	Sign.
1402	2	< 0.001	d	-1.002E-05	1.003E-06	394.30	1	< 0.001
			h	6.374E-04	9.40E-05	45.93	1	< 0.001
			cst.	3.187E-01	6.539E-02	23.76	1	< 0.001

Table 4. The four models used to predict the invasion pattern of *C. ohridella* in Germany. The observed distribution had a fractal dimension of 1.806 ± 0.0075 . SSE is the sum of the square difference between the observed infestation status and the simulations predictions

Model	Parameters	SSE	r^2	Fractal dimension
Diffusion	$\alpha = 1.58 \cdot 10^{-9}$	956.6	0.218	1.540 ± 0.0243
Leptokurtic dispersal	$\alpha = 0.0229$	761.2	0.378	1.953 ± 0.0074
Stratified dispersal	$\alpha = 2.5 \cdot 10^{-8}, \beta = -7.0, \gamma = 4.0 \cdot 10^{-11}$	760.1	0.379	1.806 ± 0.0122
Stratified dispersa and H. pop.	$\alpha = 2.5 \cdot 10^{-8}, \beta = 6.7, \gamma = 4.2 \cdot 10^{-11}, \phi = 2.1$	663.5	0.458	1.771 ± 0.0118

subpopulations in 1997 were located far from the main population fringe. These subpopulations eventually grew in 1998 and became part of the main population fringe in 1999. The rate of spread, measured by the increase of the distance at which the profile intercepted the rate of 50% infested sites, increased as a function of time: 54 km from 1996 to 1997, 118 km from 1997 to 1998, and 330 km from 1998 to 1999. A logistic model indicated that infestation probability was related negatively to the distance to the nearest infested site in the previous year (which justifies the use of distance-related models), and related positively to local human population density (Table 3).

A preliminary look at the spatial models distribution in Fig. 4 suggested that the stratified dispersal models (Fig. 4d,e) outperformed the diffusion and leptokurtic dispersal models (Figs 4b,c), because the patterns they produced appeared more similar to the observed distributions. The quantitative comparison indicated slightly different results (Table 4). In predictive terms, there was

a clear increase in predictability from the diffusion model to the fat-tailed models (leptokurtic and stratified dispersal models), with the SSE decreasing by more than 20%. The leptokurtic dispersal model and the stratified dispersal model presented an equivalent fit in predictive terms. The fit improved appreciably when human population density was incorporated (SSE decreased by almost 13%). The fractal dimension of both stratified dispersal models were very close to that of the observed distribution, which confirmed the visual impression that although the predictive power of the leptokurtic dispersal model was close to the stratified dispersal models, the latter produced more realistic simulated distributions.

All models except the diffusion model behaved poorly when run at the European scale (Fig. 5) and underestimated the date of first observation (overestimated the rate of spread), especially in locations infested after 1991. For example, the leptokurtic and stratified dispersal

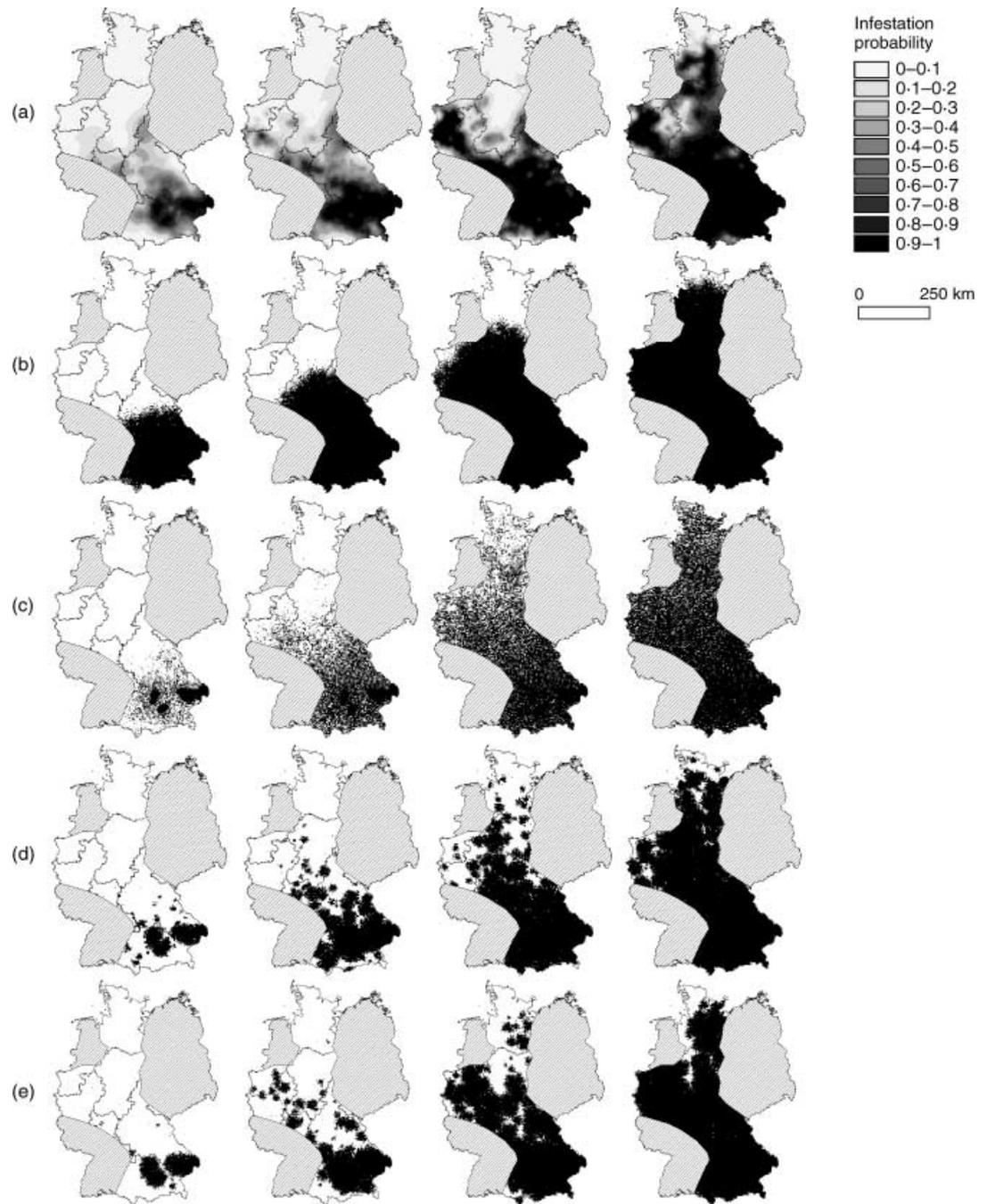


Fig. 4. Distribution of *C. ohridella* infestation probability in Germany over 1996–99 compared to one realization of each spatial model: (a) observed (interpolated infestation probability); (b) diffusion model; (c) leptokurtic dispersal model; (d) stratified dispersal model; and (e) stratified dispersal model combined with the effect of human population density.

model predicted that Germany, Czech Republic, Slovakia, Hungary, Romania and Croatia would have been infested initially between 1986 and 1989, whereas the first infestation in these countries were reported in 1993. The diffusion model performed better, as indicated by the steeper slope of the observed vs. predicted dates regression line, and the predicted year of first infestation in United Kingdom was 1997, which comes closer to the actual date (2002). The stratified dispersal that incorporated the effect of human population density provided intermediate predictions.

Discussion

All fat-tailed dispersal kernels (leptokurtic and stratified dispersal models) provided much better predictions than the thin-tailed Gaussian dispersal kernel, supporting the idea that long-distance dispersal is an essential characteristic of *C. ohridella* invasion dynamics. Long-distance dispersal events have been shown recently to have major consequences on the invasion and metapopulation ecology of plants (Cain, Milligan & Strand 2000) or insects (Wilson & Thomas 2002), as shown in theoretical (Kot

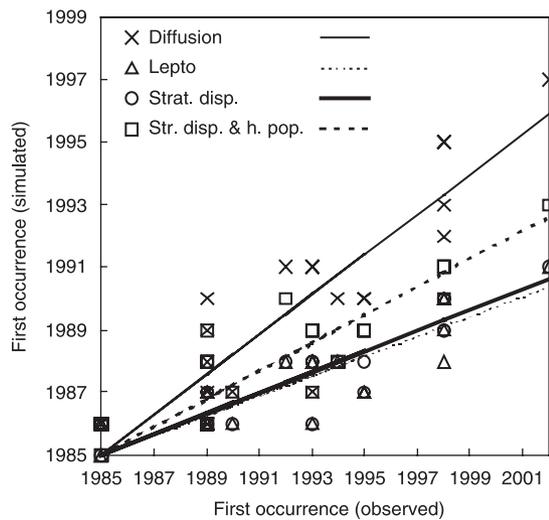


Fig. 5. Date of first occurrence per country as observed in historical records vs. simulated date of first occurrence predicted by the diffusion model [$y = 0.642(1985 - X) + 1985$; $R^2 = 0.813$], the leptokurtic model [$y = 0.316(1985 - X) + 1985$; $R^2 = 0.735$], the stratified dispersal model [$y = 0.333(1985 - X) + 1985$; $R^2 = 0.757$] and the stratified dispersal model combined with the effect of human population density [$y = 0.447(1985 - X) + 1985$; $R^2 = 0.779$].

et al. 1996; Doebeli & Ruxton 1998) and empirical studies (Bullock et al. 2002), but few results demonstrated their importance in predicting the detailed distribution pattern of invasions. Furthermore, determining the shape of the dispersal curve at long distances by direct experiments is made difficult by the scarcity of long-distance dispersal events (Greene & Calogeropoulos 2002). Although inference from genetic data appears to be a useful tool to study long-distance dispersal (Spong & Creel 2001), our results support that in this respect pattern analysis also has much to offer (see also Havel, Shurin & Jones 2002), provided that distribution data are available at sufficiently large spatial and temporal scales. Among the fat-tailed dispersal kernels tested here, the stratified dispersal kernel generated much more realistic distribution patterns than the leptokurtic dispersal model. This result demonstrates that invasion models sharing close quantitative global features (e.g. range-distance vs. time relationship) may produce highly contrasted patterns that need to be confronted with actual distribution data in order to be differentiated.

The short-scale component of the best-fitting stratified dispersal best-fitting model corresponded to a rate of spread of approximately 3 km/generation. Because of its small size, it is unlikely that *C. ohridella* adults may reach this distance by active flight, but they may certainly fly long enough to be wind-blown with such a spread rate such as observed commonly in small flying insects (Compton 2002).

The long-distance component of the stratified dispersal best-fitting model had a probability of establishment equal to $4.0 \cdot 10^{-4}$ at a distance of 143 km, which

corresponds approximately to the limit above which no distant establishment was observed in the simulations. The improvement we found when incorporating the effect of human population density in the long-distance dispersal establishment probability allows understanding of these long-distance dispersal events as two non-exclusive hypotheses. First, horse chestnut trees are generally abundant in cities and this higher density of host plants could translate into a higher probability of interception of wind-blown insects over long distances. Secondly, highly populated areas generally exchange higher flows of people, cars, trains or trucks and hence could be infested more probably by insects transported passively by these means. In contrast to what is stated in Sefrova & Lastuvka (2001), the distribution pattern of *C. ohridella* in Germany results in irregularly distributed dispersal centres, and the hypothesis that anthropogenic transportation contributes largely to long-distance dispersal thus cannot be dismissed, as did these authors. On the contrary, the fact that the best-fitting model displays such a break between short- and long-distance dispersal suggests that these two functions are unlikely to reflect the same mechanism, i.e. passive transport by wind. This is somewhat speculative, as it is difficult to differentiate dispersal mechanisms over long distances from such pattern analyses.

The poor results we observed at the European scale for the leptokurtic and stratified dispersal models are caused probably by the models' scale dependence in time and space. First, leptokurtic and stratified dispersal models are characterized by non-linear range-distance vs. time relationships. In other words, the spread rate they produce at the end of 24 iterations (corresponding to 8 years of spread) is higher than the spread rate observed within the time-scale of 1–4 years (3–12 iterations) for which their best-fitting parameters were found (for example, a run of the best-fitting stratified dispersal model on the European scale has a radial increase of 21.16 km at the 3rd iteration and 36.06 km at the 15th). Secondly, spatial factors important on the German scale are not necessarily the same at the European level. Areas where climatic conditions are particularly unsuitable to dispersal, such as the Alps or the Carpathians, represent barriers that are clearly not taken into account by the models based on German data: it took 4 years to invade 550 km through Germany from the South to the North in a barrier-free landscape, whereas it took 5 years to cover 300 km through the Alps between western Austria and western Switzerland. In addition, if the hypothesis of human-mediated passive transport is verified, the relationships between human population density and flows of cars, trucks and trains are probably different in Germany and central Europe. Despite these limitations at the European scale, the stratified dispersal models including the effect of human population density could be used with the parameters from Germany to derive relevant predictions for other countries not yet fully colonized. However, such predictions should be carried out at the country scale, over a relatively

short period of time (1–2 years), and are expected to provide better results in countries having similar landscape as Germany in term of absence of large-scale geographical barriers, human population density and transportation network (e.g. southern United Kingdom, Denmark or western France).

The models presented here implied several simplifications: (i) population density was ignored, (ii) occupied cells were assumed to be able to send dispersers equally at any given time step (generation) following the first infestation, without taking into account the local population dynamics or the size of the patch to which the cell belonged, (iii) infestation probability at any given cell depended only on the location of the nearest foci, i.e. it ignored the contribution of other surrounding foci and (iv) several factors presumably important to *C. ohridella* dispersal were ignored, such as climate (t° , wind speed and direction), landscape structure (open countryside landscape vs. cities), host-tree distribution or more detailed variables on car, trucks or train flows. However, this approach presents a useful trade-off between simplicity and realism and supports the concept of stratified dispersal as an important modelling framework to understand the spread of invading organisms.

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