

Forecasting *Cameraria ohridella* invasion dynamics in recently invaded countries: from validation to prediction

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Summary

1. Biological invasions have an anthropogenic origin, and although many species are able to spread on their own within the newly invaded area, long-distance dispersal events shown to accelerate rates of spread are frequently associated with human activities. In a previous study, the performances of several invasion models of the spread of the horse chestnut leafminer *Cameraria ohridella* in Germany were compared, demonstrating that the best model in qualitative and quantitative terms was a stratified dispersal model taking into account the effect of human population density on the probability of long-distance dispersal events.
2. Similar data were collected in France over 4 years (2000–2004, 5274 observation points). These data were used to assess the performance of the best-fit models from Germany using the original parameters and to model the spread of the leafminer in France.
3. The stratified dispersal model accounting for variations in human population density developed in Germany, predicted the invasion of France with a similar level of predictive power as in the area where it was developed. This suggests that an equivalent level of predictability can be expected in a newly invaded country with similar environmental conditions.
4. We applied the model to forecast the future invasion dynamics in the UK from 2005 to 2008, based on the first observations of *Cameraria* in the country in 2002–2004. Predictions are discussed in the light of different prevailing environmental conditions.
5. *Synthesis and application.* The model and predictions developed in this study provide one of the few examples of an a priori model of invasion in a newly invaded country, and provide a simple modelling framework that can be used to explore the spread of other invading organisms. In the case of *Cameraria*, little can be done to prevent or slow its spread but our model, by predicting changes in distribution and rates of spread, provides fore-warning of where and when damaging pest populations are likely to appear.

Key-words: biological invasion, leafminer, long-distance dispersal, spatial model, stratified dispersal

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Introduction

Predicting patterns of spread is a general challenge for invasion ecology (Sakai *et al.* 2001), and an extensive theoretical literature has developed to model invasion

dynamics (Shigesada & Kawasaki 1997). Several approaches have been used to model invasion patterns (Higgins & Richardson 1996; Muirhead & MacIsaac 2005) but particularly useful have been spatially realistic simulation modelling techniques used recently to identify associations between landscape characteristics and invasive dynamics for insects (Sharov, Liebhold & Roberts 1997; Sharov & Liebhold 1998; Gilbert *et al.* 2004), plants (Wadsworth *et al.* 2000; Higgins, Richardson & Cowling 2001; Volin *et al.* 2004) and diseases (Keeling *et al.* 2001;

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Smith *et al.* 2002; Gilbert *et al.* 2005). However, few of these models have been subject to validation using an independent data set (Wadsworth *et al.* 2000) and then applied to forecast invasion in a recently invaded area (but see Russell *et al.* 2004).

The horse chestnut leafminer *Cameraria ohridella* Deschka & Dimič (Lepidoptera, Gracillariidae) is an invasive species of uncertain origin (Grabenweger & Grill 2000), first observed and identified in Macedonia in 1984 (Deschka & Dimič 1986). The species has subsequently invaded much of central and western Europe over the last 20 years at an approximate rate of 60 km year⁻¹ (Šefrová & Lastuvka 2001). This rate of spread is higher than generally observed in other invasive leafminers (e.g. 10 km year⁻¹ for *Phyllonorycter* spp.; Csoka 2001; Šefrová 2001), other lepidoptera (0.1–21 km year⁻¹; Liebhold, Halverson & Elmes 1992; Agassiz 1996) and other invasive tree-dwelling species, such as oak gall wasps (20–40 km year⁻¹; Walker, Leather & Crawley 2002).

Cameraria ohridella (*Cameraria* hereafter) has been reported recently from Spain (Villalva & Del Estal 2003), UK (Straw & Bellett-Travers 2004), Denmark (Karsholt & Kristensen 2003), Ukraine (Akimov *et al.* 2003) and Sweden (O. Anderbrand, personal communication). It appears to have a low impact on the vigour of its host-tree (Salleo *et al.* 2003; Thalmann *et al.* 2003) but damage is particularly spectacular in cities, where the main host-species, the white-flowering horse chestnut *Aesculus hippocastanum* L. (Hippocastanaceae), is abundant. Larval development has been observed on other *Aesculus* species, such as *A. turbinata*, *A. flava* and *A. pavia*, but these species are infrequent in Europe and are minor hosts compared with *A. hippocastanum* (Freise, Heitland & Sturm 2004). Some infestations have also been recorded on *Acer platanoides* and *Acer pseudoplatanus*, but these appear to be opportunistic infestations adjacent to heavily infested horse chestnut trees. Once detected in a location, *Cameraria* rarely goes extinct (< 2% extinctions; Gilbert *et al.* 2004) but quickly reaches epidemic levels that cause severe damage. The considerable establishment success relates to three main factors: (i) no natural enemy appears to exert significant pressure on its population (typically < 5% parasitism rate; Freise, Heitland & Tosevski 2002); (ii) the moth shows 3–5 generations year⁻¹ with a high growth rate (approximately 1 : 10 generation⁻¹; Šefrová & Lastuvka 2001); (iii) population patterns in cities suggest a source–sink dynamic that allows populations to rebuild rapidly even after significant control efforts (Gilbert *et al.* 2003). Pupae overwinter on the ground in fallen leaves, and although leaves are swept from around trees lining streets this is not the case for trees in parks and gardens. In the spring, populations from parks and gardens disperse toward trees located along streets and this allows populations to re-establish quickly.

In a previous study (Gilbert *et al.* 2004), the invasion pattern in Germany was analysed using stochastic simulation models, and the best description of the observed spread was obtained using a stratified dispersal model

that combined short-distance and long-distance dispersal events, with the probability of long-distance establishment varying according to human population density. Two non-exclusive hypotheses were proposed to account for the association with human population: the higher probability of establishment relating to a higher density of horse chestnut trees in cities, and the higher risk of passive transportation of adults or infested leaves by cars and other vehicles between highly populated locations.

The aim of the present study was to test the predictive power of the models developed in Germany using an independent data set, i.e. the invasion in France, and to apply the model to forecast the spread of the leafminer in a newly invaded country, the UK, where *Cameraria* was first observed in 2002.

Materials and methods

Cameraria distribution data for France were collected through surveys carried out in August in 2000 ($n = 41$ locations), 2001 ($n = 1062$), 2002 ($n = 1433$), 2003 ($n = 1290$) and 2004 ($n = 1448$). Surveys were distributed to match the expected spread of the moth, and were concentrated in the eastern part of France in the earlier years and in the western part of France in later years (Fig. 1). The large majority of the sampling points were visited only once, especially if *Cameraria* was found to be present, except in an area in north-western France where points were visited throughout 2001–03 (Augustin *et al.* 2004). Sites were visited at the end of the season, when leaf damage represented the accumulated effect of the three annual generations.

Population density was estimated visually at each location by assigning leaves a damage score (0–7) based on the overall proportion of leaf area damaged by the moth (0, 0%; 1, 0–2%; 2, 2–5%; 3, 5–10%; 4, 10–25%; 5, 25–50%; 6, 50–75%; 7, 75–100%). This damage score was linearly related to log-transformed [$\log_{10}(x + 1)$] mine numbers per leaf arising from the first generation (Gilbert & Grégoire 2003). This population assessment method has been compared previously with pheromone trap catch data for monitoring the regional spread of *Cameraria* in north-eastern France (Augustin *et al.* 2004). This study showed that pheromone trap data were suitable for monitoring fluctuations in *Cameraria* populations over time, but that visual observations of damage had a higher sensitivity to low population levels, were cheaper and faster to implement and were more suitable for large-scale monitoring of *Cameraria* populations.

Cameraria rarely goes extinct after it has been detected at a newly invaded site (a group of trees), and takes 2–3 years to reach maximum population densities (Gilbert *et al.* 2004). This pattern allows rules to be built to derive past or future status according to observations of damage score, and to transform population data to derive presence–absence status at each location in each year (Gilbert *et al.* 2004). The low probability of extinction allows the assumption that a location in year n is

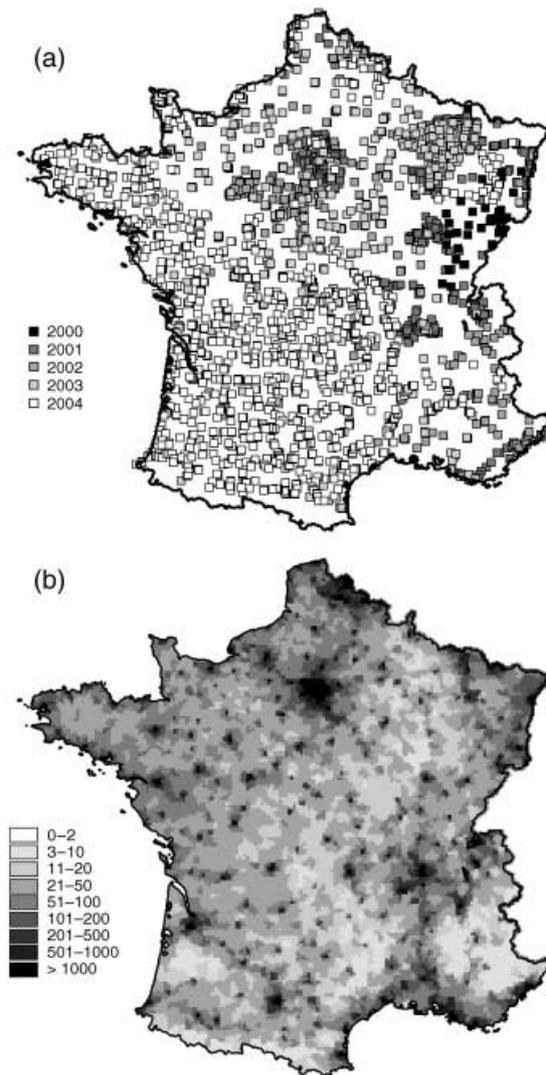


Fig. 1. (a) Distribution of *Cameraria* observation points in France in 2000–04. (b) Distribution of human population density in France (people km⁻²).

infested if it was infested in any previous year and, conversely, that a location in year n is uninfested if it was observed to be uninfested in any following year. There is a clear relationship between infestation status in a location in year n and infestation level in year n_{+1} and n_{+2} , respectively, because recently infested sites generally have a lower level of infestation than sites infested for a longer period. Using a training set of locations observed in 2001, 2002 and 2003 in northern France (Augustin *et al.* 2004), we used logistic regressions to predict the infestation probability in year n as a function of damage score in year n_{+1} and n_{+2} , respectively. The model relating infestation probability P_{inf} to year n_{+1} damage score D_S was as follows:

$$\text{Logit}(P_{\text{inf}}) = 2.589D_S - 3.536 \quad (\% \text{ correct} = 93.9; \\ P < 0.001)$$

Whereas the model relating P_{inf} to year n_{+2} damage score was:

$$\text{Logit}(P_{\text{inf}}) = 1.485D_S - 4.511 \quad (\% \text{ correct} = 80.7; \\ P < 0.001)$$

The threshold value of 0.5 was used to derive presence of an infestation (0/1) from the estimated probability of the logistic model. On occasion, infestation status could not be inferred, i.e. the status in a location in year n was unknown if *Cameraria* was absent in any previous years and if a damage score was observed in years n_{+3} or n_{+4} .

Ordinary kriging was used to interpolate the presence–absence data for display purposes, and to delineate the most likely area of initial infestations, i.e. the area where the 2000 interpolated infestation probability was higher than 0.9. In order to match as closely as possible with the definition of the area of initial infestation used in the study in Germany, we used a similar interpolation model for all years, i.e. a spherical model with a nugget of 0.43, a scale parameter of 0.6 and a range parameter of 79 km.

Data on human population densities were obtained from the Gridded Population of the World (GPW) Version 2 (Center for International Earth Science Information Network (CIESIN) *et al.* 2000), resampled at the 2.5-km resolution.

Data on the distribution of *Cameraria* in the UK were obtained in a less systematic way than in France, and relied on site visits and limited surveys around the area of initial infestation in 2002 and 2003, and collation of records of infestation received from individuals, local authorities and other organizations. Despite the unstructured collection of data, the presence–absence data for locations in the UK were considered accurate, because of the large numbers of people and organizations interested in the spread of the moth and submitting records. The threats posed by *Cameraria* were well publicized in advance of its arrival, and repeated requests and reminders were made for information on infestation, especially in south-east England.

The simulation model was developed in R (R Development Core Team 2004) at a resolution of 2.5 km cell⁻¹. The model was similar in all aspects to the one developed for Germany (Gilbert *et al.* 2004) but details of its formulation are repeated here. We assumed 3 generations year⁻¹ over the 5 years (as generally observed in France; Augustin *et al.* 2004) and the algorithm we used to simulate the spread over 1 generation involved four steps. First, the distance of each cell to the nearest occupied cell in the previous time step was calculated. Secondly, the infestation probability of each cell was estimated as a function of that distance and, in the last model, also as a function of the local human population density. 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 starts with the initial distribution (set as the area where interpolated infestation probability in 2000 is > 0.9) and iterates until the 15th

Table 1. The three models used to predict the invasion pattern of *Cameraria* in France, and their parameters from the analysis of the invasion in Germany

| Model | Parameters | SSE | R ² |
|---|---|--------|----------------|
| Diffusion | $\alpha = 1.58 \cdot 10^{-9}$ | 2256.0 | 0.016 |
| Stratified dispersal | $\alpha = 2.5 \cdot 10^{-8}, \beta = -7.0, \gamma = 4.0 \cdot 10^{-11}$ | 2734.0 | < 0 |
| Stratified dispersal and human population | $\alpha = 2.5 \cdot 10^{-8}, \beta = -6.7, \gamma = 4.2 \cdot 10^{-11}, \phi = 2.1$ | 1364.0 | 0.405 |

generation (i.e. for 5 years). *Cameraria* was present in Belgium, Germany, Switzerland and Italy before it appeared in France, and populations in these countries may have contributed to the invasion of France. However, the distribution of *Cameraria* within these countries in 2000 was unknown, and it was considered hazardous to assume that they were fully invaded and to include their populations in the starting distribution for the model.

The functions used to estimate infestation probability vary according to the model used (Fig. 2). In the first

model, infestation probability decreases as a function of distance following a normal curve (Fig. 2a). The second model is a stratified dispersal implementation and assumes that propagules disperse by two independent dispersal processes occurring at different spatial scales, each one having dispersal distance normally distributed (Fig. 2b). Infestation probability is estimated by the probabilities of short-distance dispersal (P_1) and long-distance dispersal (P_2) combined with an ‘or’ statement. In the third model, it is assumed that long-distance dispersal probability is a function of the distance to the nearest infested cell (P_2) combined with a function of human population density (P_3) and an ‘and’ statement (Fig. 2c). To estimate P_3 , a logistic function was set to have a maximum probability when human population is maximum, a minimum probability when human population is minimum and a probability equal to 0.5 when $\ln(\text{human population density})$ is equal to the observed median $\ln(\text{human population density})$. P_3 was estimated as:

$$P_3 = \frac{e^{(h-h_m) \times \phi}}{1 + e^{(h-h_m) \times \phi}}$$

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 run using the best-fit parameters from the analysis carried out in Germany (Table 1). The quantitative adjustment was evaluated as follows. We set $I_{i,t}$ as the observed infestation status at location i in year t . Each simulation generated 15 layers of occupied (1) and unoccupied (0) cells (5×3 generations). The 3rd, 6th, 9th, 12th and 15th iteration layers were used as predictions for the years 2000, 2001, 2002, 2003 and 2004, respectively. For each parameter set, 100 runs were performed and the average infestation status of the 3rd, 6th, 9th, 12th and 15th 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 models’ R^2 values were estimated as a complementary measure of model fitness, as $1 - \text{SSE}/\text{SST}$, with $\text{SST} = \sum_{i,t} (I_{i,t} - \hat{I}_t)^2$, where \hat{I}_t is the average of $I_{i,t}$. The fit was evaluated over the whole time series, or for each year, and the models’ SSE and the observed distribution SST were plotted as a function of years to compare the performances of the models over time.

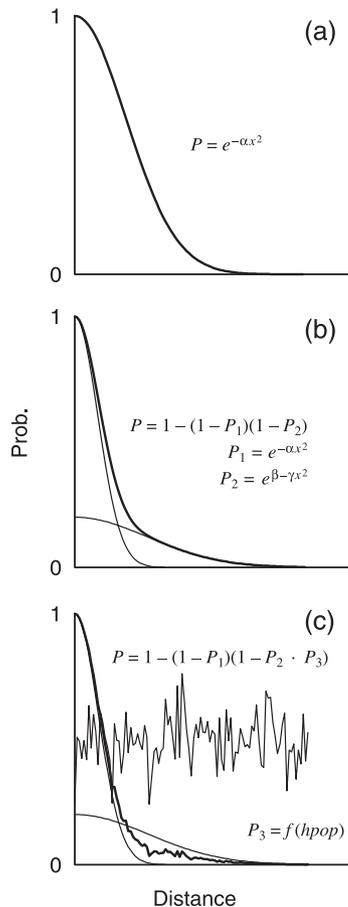


Fig. 2. Functions used to predict infestation probability (Prob.) as a function of distance to the nearest infested cell in the three tested models: (a) diffusion model; (b) stratified dispersal model (thicker line) combining a short-scale and large-scale diffusion model; (c) stratified dispersal model 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, $hpop$ is the human population density, and α , β and γ are model parameters. The figures illustrate the shape of the different functions and the way they are combined, but do not correspond to actual distance or human population density units.

Finally, the model with the best fit to the observed pattern of spread in France was run for the UK at a similar resolution to predict the distribution of *Cameraria* in 2005–08, taking as the initial distribution the 2.5-km cells where *Cameraria* had been observed in 2002–04.

Results

Our results indicated that a reasonable prediction of the *Cameraria* invasion of France was obtained when the stratified dispersal model incorporated human population density (Fig. 3). The predicted pattern of invasion provided by this model was similar to the observed invasion, even though the model used parameters derived from the invasion of Germany. The model even predicted some specific details of the observed invasion of France

(Fig. 3). In 2001, the model indicated a higher probability of infestation in the urbanized areas of Paris and Lyon. In 2002, the model captured the strong establishment of *Cameraria* in the eastern part of France and the probability of some long-distance establishment events in the western and southern parts of the country. Deviations were observed in 2003 and more particularly in 2004, when the model predicted a higher probability of presence in the Massif Central and Brittany than was actually observed.

The stratified dispersal model that ignored the effect of human population density predicted a much more rapid invasion than was actually observed, with the western part of France having a high probability of colonization by 2002 and most of France becoming infested by 2003 (Fig. 3). The quantitative assessment presented in Table 1

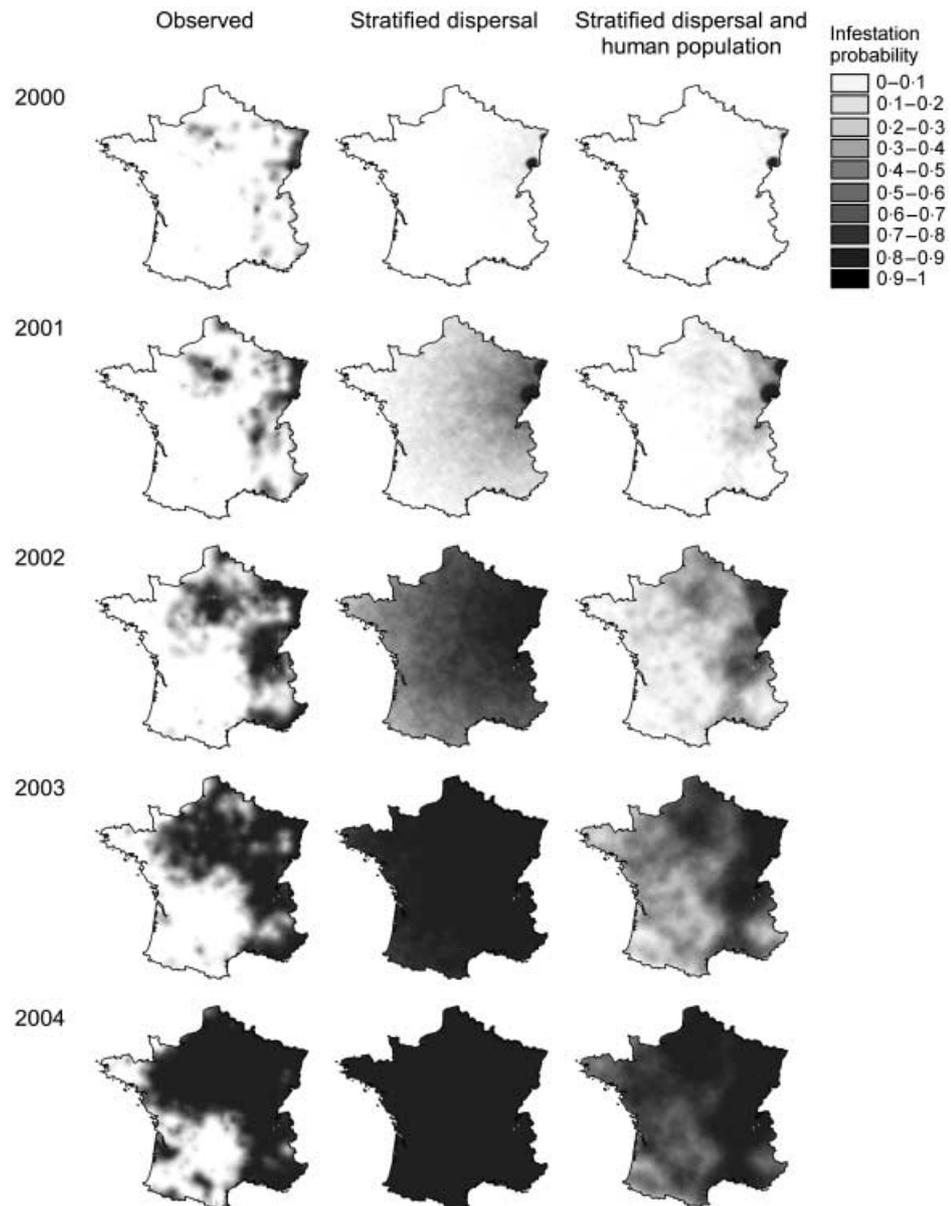


Fig. 3. The observed distribution of *Cameraria* infestation in France during 2000–04 (derived from the spatial interpolation of infestation status) compared with the predicted distribution of infestation probabilities provided by the two stratified dispersal models.

confirmed these visual interpretations from the maps of predicted probabilities. The stratified dispersal model that included human population density clearly outperformed the two other models. Looking at the annual fit of the three models (Fig. 4), we saw that the diffusion model never showed a better predictive power than using the overall proportion of occupied sites as a predictor in all locations. The two stratified dispersal models did slightly better than the average observed proportion of occupied sites until 2001, but then the model that ignored human population density clearly deviated from the observed pattern of invasion. In contrast, the model accounting for human population density showed its highest level of predictive power in 2002 and 2003, and was still better than the mean in 2004.

The stratified dispersal model accounting for human population density predicted that most southern and central parts of the UK should be colonized by 2006–07, and northern areas should be reached around 2008 (Fig. 5).

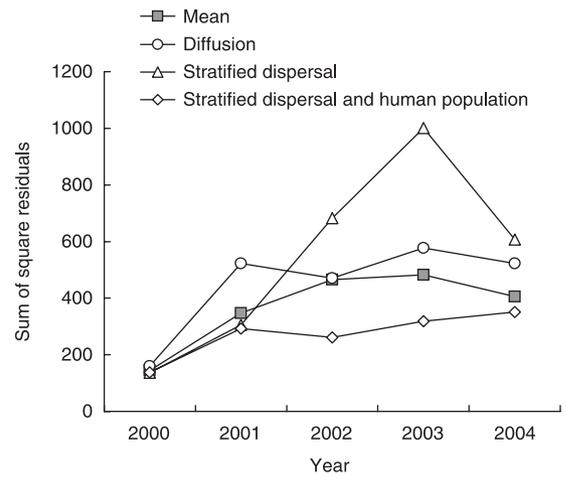


Fig. 4. Sum of squared residuals of the three model predictions (diffusion, stratified dispersal, stratified dispersal and human population density) from 2000 to 2004, compared with the sum of squared observed differences to the mean (mean), showing the best fit in each year of the stratified dispersal model with the effect of human population density included.

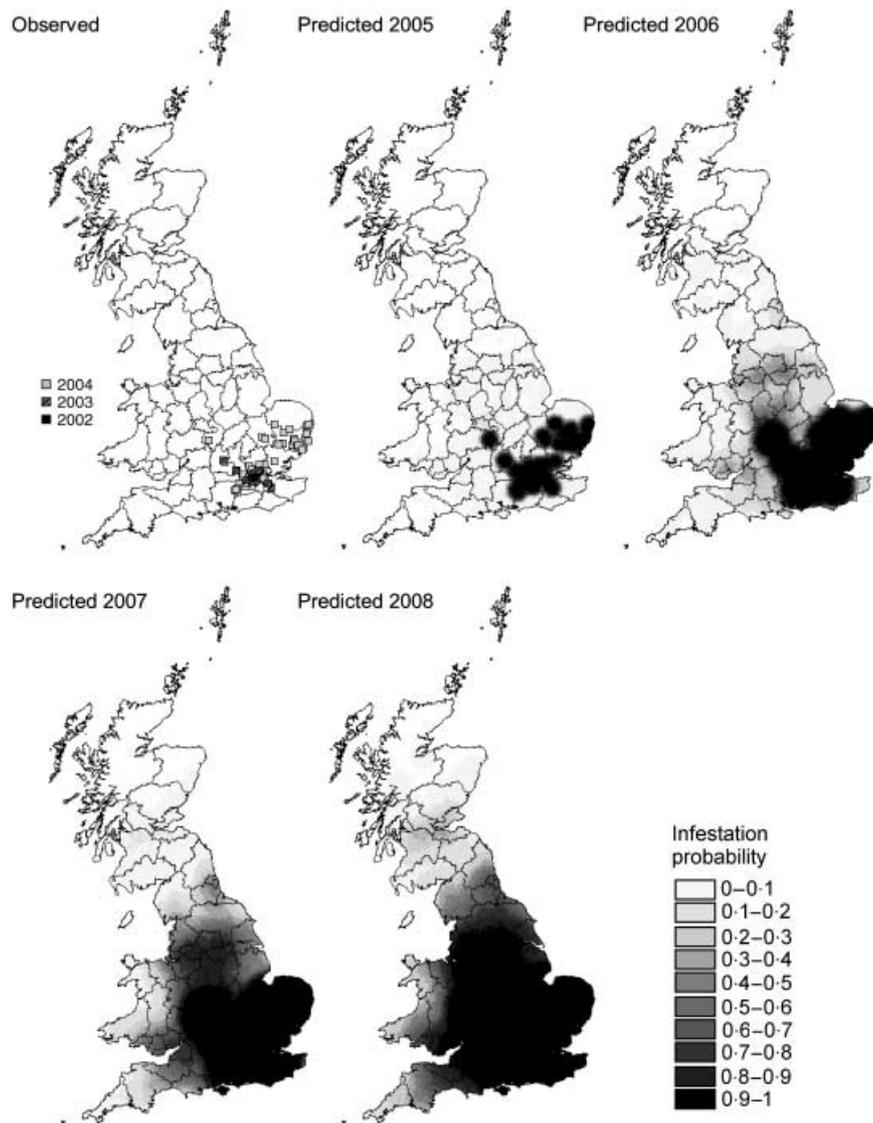


Fig. 5. Distribution of *Cameraria* infestation probabilities in the UK for the years 2005–08, as predicted by the stratified dispersal model that includes the effect of human population density.

Discussion

A stratified model of spread accounting for variations in human population density developed in Germany can thus be applied effectively to predict invasive patterns in another country (with an $R^2 = 0.405$, the predictions in France are almost as good as in Germany, where R^2 was 0.458), suggesting that the model can also be applied to forecast where and when the species is likely to be observed in a recently invaded country, as long as environmental and landscape conditions are similar.

As previously discussed in Gilbert *et al.* (2004), the role of human population density may relate to two major factors: flow of vehicles and density of horse chestnut trees. There is an obvious association between the size of cities and the flow of vehicles and trains, and possibly also in the trade of nursery material, which may transport adult moths or infested leaf fragments over long distances. The more rapid infestation of big cities was even more obvious in France than it was in Germany (Fig. 3). The cities of Paris, Lyon and Marseilles were first colonized in 2000–01, and the cities of Toulouse and Bordeaux were the first locations to be colonized in western France in 2002–03. The second factor, a higher concentration of host-plants in highly populated areas, may result in a higher probability of interception of insects arriving in a given location, either by means of transportation or brought by wind over long distances.

The main mechanism responsible for spreading the moth over long distances is still a matter of debate, and there is evidence for both wind and vehicles being important. In an unpublished experiment, we trapped some *Cameraria* individuals in pheromone traps in an underground car park, whereas none was captured on the street above, suggesting that the individuals in the car park had been brought in with the cars. Conversely, some infested trees have been observed several hundreds metres away from any road. Inadvertent long-distance transport of *Cameraria* in infested nursery stock has also been reported, for example the first reports of *Cameraria* near Paris (Augustin & Reynaud 2000) and near Madrid. It has been argued that wind is more likely to be the main method of long-distance dispersal, because new infestations have never been observed very far (> 1000 km) from existing infested towns (Šefrová & Lastuvka 2001). However, *Cameraria* mines are small and the species is hard to detect during the initial stages of infestation. Each visit to a city or location usually involves surveying only a small number of trees, and it is very easy to miss a few mines distributed in the canopy of a horse chestnut tree. The fact that very little extinction is observed in survey data indicates only that extinction is rare when population density lies above the detection level, not that extinctions never occur. Therefore, inadvertent introduction of low numbers of individuals in or on vehicles may not necessarily lead to successful establishment, and an Allee effect may lead to local extinction without the species ever being detected. Successful

establishment might thus require frequent reintroduction up to a density above a population threshold that guarantees establishment, explaining why no foci have yet been observed over very long distances. None of the suggested pathways, anthropogenic transport or wind, can be excluded from causing the long-range dispersal of *Cameraria*, but a clear understanding of their relative contribution is yet to be achieved.

Human population density also forms a good surrogate variable for the distribution of areas unsuitable for *Cameraria*, such as large continuous agricultural and forests areas and mountains. For example, the model accounts for geographical barriers such as the French Massif Central and the Southern Alps because of their low human population density. Similarly, the observed invasion starting on the eastern border of France took a while to reach Paris, and this was also captured by the model because of the large continuous and less populated agricultural plains in north-eastern France.

Given that the model is validated by the overall good fit to the observed pattern of spread, one can explore the model deviation to identify other factors responsible for favouring or preventing spread. First, our model ignored the possible invasion from neighbouring countries where *Cameraria* was reported prior to 2000, and this may account for some of the observed deviations. For example, the south-western coast of France was invaded earlier than predicted by the best model, most probably because the model ignored the very probable invasion along the coast from Italy. A second factor that is ignored is the unknown distribution of horse chestnut tree density. Although no comprehensive census exists on the host-plant's distribution in France, we noticed that horse chestnut trees are scarce in the western part of Brittany and in the Massif Central, as it was difficult to find locations in these areas for surveys. This missing variable may explain the most significant deviations from the observed distribution in the Massif Central and Brittany, where the model clearly overestimates the presence of the insect in 2003 and 2004. Thirdly, other variables not considered in this analysis could also explain the deviations, such as climatic factors, in particular rainfall and wind. Rain is a very important mortality factor at the time of adult emergence (Heitland & Metzger 1997), and Brittany and the Massif Central are areas with some of the highest rainfall in France (areas with annual precipitation > 1300 mm year⁻¹ occur in the Alps, the Massif Central, the Pyrenean mountains and Brittany; Météo France 2004). Also, the dominant wind direction during the main flight periods may slow down or favour spread in certain directions. Both variables are routinely recorded nation-wide and could be used in the future to explore the association between their geographical distribution at the most important periods of flight (2nd generation in June–July) and the geographical distribution of the model residuals.

Despite these sources of variation, the model presents a reasonably good fit to the observed data in France,

which suggests that an equivalent predictive power could be expected in the forecast of the invasion of the UK. Horse chestnut trees are also found abundantly in cities in the UK, and the distribution map of presence–absence of horse chestnut trees shows that it is present almost everywhere except in some northern parts of Scotland (Preston, Pearman & Dines 2002). Some mountains in the north may be an obstacle to invasion, but these are clearly accounted for by the low human population density in the predicted pattern of spread (Fig. 5). However, Germany and the eastern part of France (where most of the spread took place) share a more continental climate than the UK, which has a primarily oceanic climate resulting in cooler summers and often milder, more unpredictable winters. The difference in climate might be expected to result in a different rate and pattern of spread. As previously mentioned, heavy rains are thought to have a substantial impact on *Cameraria* populations if they occur during the flight period. Rainfall has much less effect if it occurs between generations, i.e. when most individuals are inside the leaves. Therefore any attempt to use climatic data would require knowing precisely the time of emergence in the year of interest, and these dates were unknown in our data set, which only includes the presence or absence of the moth in a given location in a given year. Temperature would also be expected to influence population dynamics, as *Cameraria* is reported to complete up to five generations in mediterranean countries but no more than three generations in northern countries. Unpublished data suggest that the higher number of generations in the south, observed for example in Italy, has more to do with earlier emergence and a longer period of activity than faster generation cycles (P. Radeghieri, personal communication). Preliminary observations in the UK indicate that *Cameraria* is going through three generations just as it does in northern France. This was very evident in 2003 and 2004 in London, where the first generation was established in May, second generation adults were active in July, and from then on all life stages were present right through to late September and October. The second and third generations clearly overlapped, but there was a strong third generation present. Published quantitative data on the effect of temperature on *Cameraria* populations are still missing, and would be required to account for temperature in population models. Given that precipitation and temperature both have an effect on *Cameraria* population dynamics, and that these conditions in the UK differ from Germany and France where the model was trained and validated, the prediction with regards to the UK should be interpreted cautiously.

The modelling approach used in this study could be applied to the establishment and spread of *Cameraria* in other countries in Europe, or on other continents such as North America. Several cities where *Cameraria* is now present are important ports, exporting goods in containers to other continents (e.g. Hamburg and Bremen). The presence of *Cameraria* in these cities,

over-wintering as pupae in dead leaves (Freise & Heitland 2001), means that there is a high risk of transportation of the species during the winter season to other continents where suitable host-plants are present.

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