Spatial patterns and infestation processes in the horse chestnut leafminer *Cameraria ohridella*: a tale of two cities

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Abstract

Spatial patterns of the horse chestnut leafminer *Cameraria ohridella* Deschka & Dimic (Lepidoptera: Gracillariidae) population density was analysed in the cities of Bern and Brussels in order to explore its spatial population dynamics. The surveys were carried out in Bern in 1998 and 2000 and in Brussels in 2001 to assess population density in relation to local characteristics. In Brussels, population density was also measured using pheromone traps distributed over the city and collected twice per moth generation. A quantitative relationship was found between local population density (measured by pheromone traps and survey observations) and the amount of leaves left on the ground the previous fall. Several other factors were related to observed infestation levels: the occurrence of the pathogen *Guignardia aesculi* was inversely related to infestation by *C. ohridella* in Bern in 1998 and 2000, the number of horse chestnut trees within 800 m distance was positively related to infestation level in Bern in 2000, and the proportion of green areas within 100 m and the number of other horse chestnut trees within 2000 m were positively related to infestation levels in the 2001 Brussels survey. The pattern of infestation levels as a function of distance to potential population reservoirs suggested that *C. ohridella* re-invades areas where overwintering leaves have been cleaned from refuge areas such as parks or urban forests. Our results indicate that the removal of leaves is a feasible first aid control measure to reduce moth population densities. However, leaf removal may not reduce moth densities when done improperly. In places where proper leaf removal is not feasible, other control measures are needed.

Introduction

The horse chestnut leafminer, *Cameraria ohridella*, is an invasive species that has spread rapidly through Central and Western Europe over the last 15 years (Šefrová & Laštuvka, 2001). Damage caused by larval mining in the leaves is spectacular in cities where the main host species, the white-flowering horse chestnut *Aesculus hippocastanum* (Hippocastanaceae), is abundant, and the aesthetic impact of trees already yellowing and browning in streets, parks, and gardens in June raises public concern. All leaves of the trees may eventually be infested throughout the season, and heavily infested trees can lose some of their leaves prematurely in early summer. In addition to damage by *C. ohridella*, infestations of horse chestnut trees by the pathogen *Guignardia aesculi* (Peck) Stewart are frequently observed. The true long-term effect of the leaf damage by *C. ohridella* on host-tree vigour is still unclear (Skuhravý, 1999, but see Salleo et al., 2003; Thalmann et al., 2003) and its social impact still is considered to be the main consequence in cities. The pest is thus mostly an urban problem.

The pupae overwinter in the dead leaves which have fallen to the ground and the removal and destruction of

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these leaves is currently the only practical control method in an urban context where the environmental impact of the use of chemicals must be minimised. Parasitism rates are very low (generally less than 5%) especially in recently invaded areas (Grabenweger & Lethmayer, 1999) and the prospect of introducing exotic natural enemies is still hypothetical, as the true origin of the leafminer is unknown (Holzschuh, 1997). Effective chemical control of the leafminer can be achieved by spraying horse chestnut trees with chemical insecticides (e.g., diflubenzuron; Mertelik, 1999) or the application of systemic insecticides (e.g., imidacloprid; Lohrer et al., 2000), but these pose potential environmental hazards, particularly in urban environments.

No satisfying method has thus yet been found to control the pest to an acceptable level and populations typically rebound despite controlling efforts of leaf removal. This is partly due to the fact that *C. ohridella* has a high growth rate, which allows populations to rapidly rise from a low number of surviving individuals [three generations are usually observed per year (Tomiczek & Krehan, 1998); population growth was estimated approximately as tenfold per generation (Šefrová & Laštuvka, 2001)]. However, this does not explain how populations may rebound in locations such as in streets without ground vegetation where 100% of the leaves are often removed in the winter. Following the initial colonisation of a city, *C. ohridella* appears to colonise most available horse chestnut trees within 1–2 years, which suggests a very high dispersal ability. It is therefore hypothesised that parks, private gardens or urban forest, where leaf removal is technically difficult because of the ground vegetation, may act as population reservoirs from which the moth would colonise the rest of the city by dispersal.

Despite a widespread distribution, local moth population densities vary within cities and the analysis of this spatial variation may provide an insight into the underlying dynamics producing them. Spatial pattern analysis is often the only form of investigation which is possible in the early stages of landscape-scale ecological studies. First, because meaningful experiments are extremely difficult to realize at such spatial scale. Second, because of the multiplicity of factors (habitat, environmental conditions) which cannot be easily incorporated into experiments. For example, if dispersal is predominantly influenced by wind, spatial variation in population density may be more continuous along prevailing wind directions, as observed with spatial distribution in Oxford of the horse chestnut scale, *Pulvinaria regalis* (Speight et al., 1998). Furthermore, if populations disperse from locations where leaves are abundant, such as parks or urban forests (source) into locations where populations are eradicated every year (sink), gradients in population density would be expected

to be observed as subsequent evidence of source-sink dynamics. Spatial pattern analysis may therefore provide evidence for the creation of hypotheses about causality that may subsequently be investigated experimentally.

This study analysed the spatial patterns of *C. ohridella* population densities in Bern (Switzerland) and Brussels (Belgium) in order to draw inference about the colonisation processes. Population abundance was evaluated using pheromone trapping and damage surveys in relation to factors such as the local amount of leaves left on the ground during the winter, site characteristics, and the location of potential population reservoirs.

Materials and methods

Data

In Bern, a total of 175 sites representing an estimated 1530 horse chestnut trees, including all public horse chestnut trees distributed throughout the city area, was surveyed in 1998. In 2000, the survey was extended to include, as far as possible, all horse chestnut sites in Bern by systematically walking through all the streets of the city area and recording all horse chestnut trees (399 sites, 2075 trees). Trees were surveyed from 31 August to 23 September 1998, at a period when mines of all three moth generations were present, and from 7 August to 5 September 2000, when mines of only the first two generations were present. The level of infestation of *C. ohridella* was estimated visually by counting the number of mines at a site discovered within a period of 30 s on one arbitrarily chosen tree per site or small group of trees standing together. In addition, in 2000 the percentage of damaged foliage was estimated in classes of 20%. The mine counts provided a good estimate of moth infestations at low infestation levels. However, at infestation levels higher than about 40% damaged leaf area (in 25 sites out of 175 in 1998 and 75 sites out of 399 in 2000), mine counts levelled off at about 140 mines 30 s^{-1}. Therefore, 2000 data mine counts at high infestation levels were corrected by extrapolating from mine counts at low infestation levels by linear regression of mine counts vs. percentage foliage damaged (in 75 sites out of 399; Corrected Mine Count = 3 × Percentage Foliage Damaged; R^2 = 0.185; n = 281; P < 0.001). The 1998 mine counts, the 2000 corrected mine counts, and the difference between 1998 and 2000 uncorrected mine counts are presented in Figure 1a–c. Several variables were directly assessed during the survey, and one variable was extracted using a Geographical Information System (GIS) (Tables 1 and 2).

In the Brussels 2001 survey, abundance was measured using two different methods: the survey observation of both foliage damage and pheromone traps. Infestations of *C. ohridella* on trees were surveyed in 262 sampling sites
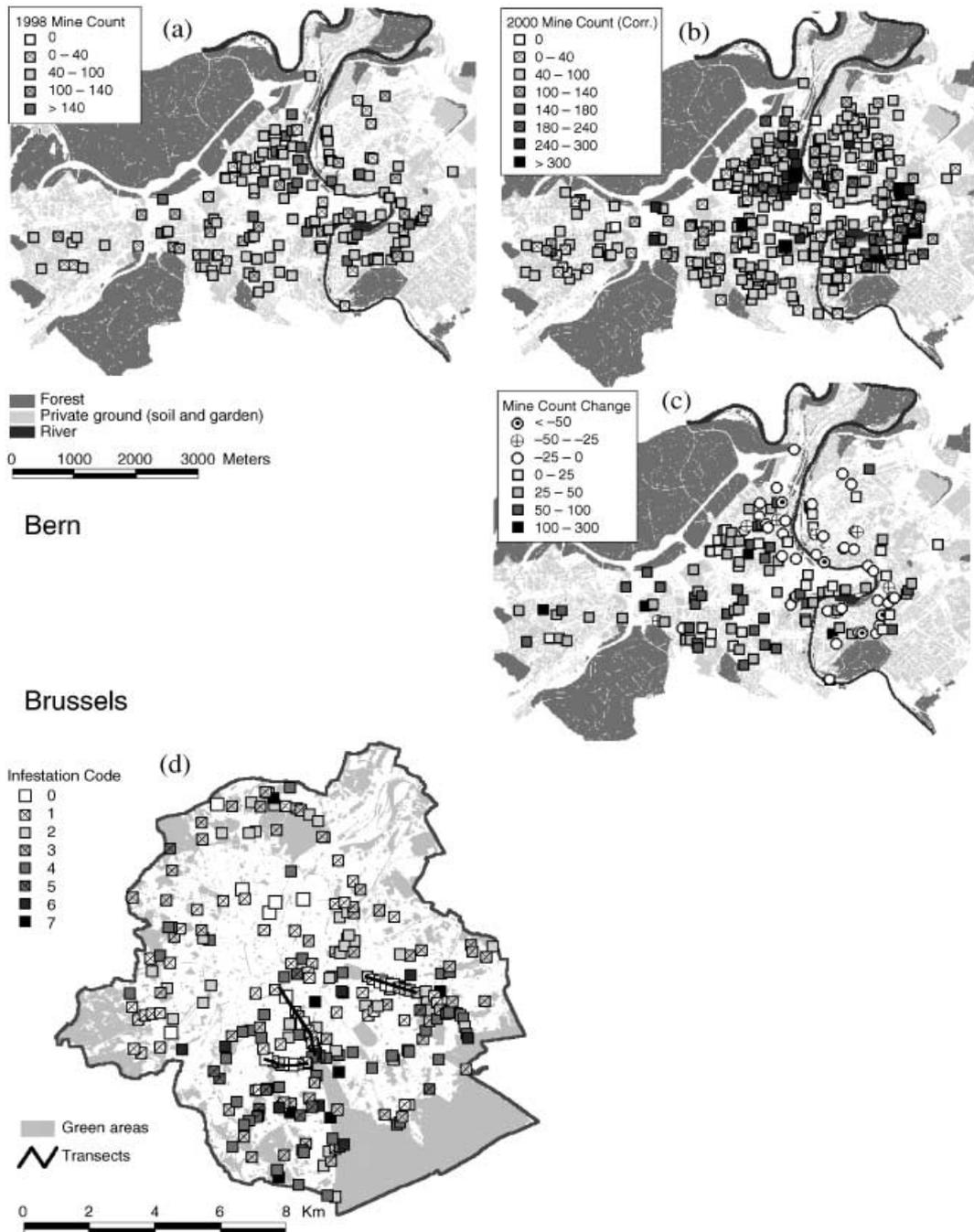
Figure 1 Map of population density estimates as measured by mine counts in Bern 1998 (a), corrected mine counts in 2000 (b) and by Infestation Code in Brussels 2001 (d). The difference between mine count observed in 2000 and 1998 is presented in (c). Legends of the classes were chosen to represent equivalent levels of infestation density across cities and years (e.g., mine count 40–100 corresponds approximately to infestation code 2).

(Figure 1d) during the first two weeks of July 2001 at a period when the flights of the second generation were occurring and when the damage was mostly a consequence of the first generation flights. Infestation levels were estimated visually with the help of pictures of foliage for which percentage of damaged foliage had been estimated using image processing (Gilbert & Grégoire, 2003). This technique allowed us to differentiate eight classes of

Table 1 Explanatory variables for Bern entered into the linear model

Category	Measurement type	Code
Location	GPS XY coordinate	XY
Is located in a street	Yes or No	ISSTR
Is located in a garden	Yes or No	ISGRD
Is located in a park	Yes or No	ISPRK
Is located on the river bank	Yes or No	ISRB
Is located on the embankment	Yes or No	ISEMB
Is a single tree	Yes or No	ISSING
Is a row of trees	Yes or No	ISROW
Is a group of trees	Yes or No	ISGROUF
Number of trees	Absolute	TRNBR
Distance to the nearest site with chestnut trees	Absolute	DIST
Has the ground sealed	Yes or No	ISSEA
Has the ground moderately sealed	Yes or No	ISMOD
Has soil on the ground	Yes or No	ISSOIL
Has litter	Yes or No	HASLI
Has refuges	Yes or No	HASREF
Overwintering leaves index[a]	Score from 0 to 2	OLI
Trunk diameter[a]	Score from 1 to 3	DIAM
Tree height[c]	Score from 1 to 4	TH
Guignardia aesculi code[d]	Score from 0 to 4	GCODE
Estimated number of chestnut trees within X m (X ranging from 100 to 3000 m by 100 m steps)[e]	Absolute	TNAEX

[a]Overwintering leaves index: 0: no leaves; 1: refuges; 2: litter present.
[b]Trunk diameter: 1: 0–40 cm; 2: 40–70 cm; 3: > 70 cm.
[c]Tree height: 1: 0–5 m; 2: 5–8 m; 3: 8–12 m; 4: > 12 m.
[d]Abundance of *Guignardia aesculi*: 0: not present; 1: low; 2: moderate; 3: high; 4: very high.
[e]The number of horse chestnut trees within a given distance was estimated using the GIS database of horse chestnut trees number estimated during the survey.

percentage of damaged foliage: 0%, 0–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75% and 75–100%.

Several habitat variables were assessed during the survey (Table 2), whereas two additional types of variables were extracted from a Geographical Information System. The average proportion of green areas in a given circular neighbourhood was estimated at each sampling site for 30 different radius distances (from 100 to 3000 m in steps of 100 m). This estimate was calculated using a raster GIS data layer of green areas (proportion of green area per 50×50 m pixel) derived from a vector layer estimating the proportion of green area in each city block of houses (IGEAT, 1997). The number of horse chestnut trees was estimated for the same distance neighbourhood intervals using a vector GIS layer of horse chestnut tree locations. This database was built using four sources of data: a database identifying all horse chestnut trees located in the streets administered by the Region of Brussels, a database of all horse chestnut trees located in the streets administered by the 19 city councils, a database of the number of horse chestnut trees found within green areas administered by

the Brussels Institute for the Management of the Environment (BIME), and horse chestnut trees observed during our field survey not recorded in the three other databases. In absence of a systematic census, this combined database was the best measure of the distribution of horse chestnut trees in the city. *Cameraria ohridella* is reported to infest several *Aesculus* spp., but only the *A. hippocastanum*, which are known to be the favoured host for *C. ohridella*, were included in the survey. Sampling was carried out by driving randomly along the city streets and stopping when a horse chestnut tree was seen. A sample point was taken every 200 m in cases of horse chestnut tree alignments along streets. Green areas located along the sampling route were also surveyed by entering them into a search for horse chestnut trees.

Pheromone traps were distributed in 60 locations throughout Brussels during the first two population generations. For logistical reasons, it was not possible to collect the traps at a frequency required to prevent saturation of the sticky traps. Bottle traps allowing insect accumulation and less frequent visits were therefore designed (Figure 2)

Table 2 Explanatory variables for Brussels entered into the linear model

Category	Measurement type	Code
Location	GPS XY coordinate	XY
Overwintering leaves index[a]	Score from 0 to 4	OLI
Tree Height[b]	Score from 0 to 3	TH
Presence of *Guignardia aesculi*[c]	Yes or No	GUI
Is located in a street	Yes or No	ISSTR
Is located in a private garden	Yes or No	ISGRD
Is located in a park	Yes or No	ISPRK
Evidence of ground vegetation	Yes or No	VEG
Proportion of green area within X m distance (X ranging from 100 to 3000 m by 100 m steps)[d]	Absolute	AVGAX
Estimated number of chestnut trees within X m (X ranging from 100 to 3000 m by 100 m steps)[e]	Absolute	TNAEX

[a]Overwintering leaves index: 0: absent (no leaves); 1: rare refuges (it is possible to find at least one intact leave after a thorough search); 2: refuges (intact leaves can be seen from under the tree without having to search); 3: abundant (leaves are abundant on the ground but the litter is not intact); 4: intact litter (the litter does not seem to have been modified).
[b]Tree height was estimated visually in three classes 1: < 5m; 2: 5–10 m; 3: above 10 m.
[c]Presence/absence of the pathogen *Guignardia aesculi* (Peck) assessed visually.
[d]The proportion of green area within a given distance radius was assessed using a Geographical Information System and the geographical database layer of green areas provided by the IBGE.
[e]The number of horse chestnut trees within a given distance was estimated using a GIS and a database combining all sources of information available on the location of horse chestnut trees in Brussels.
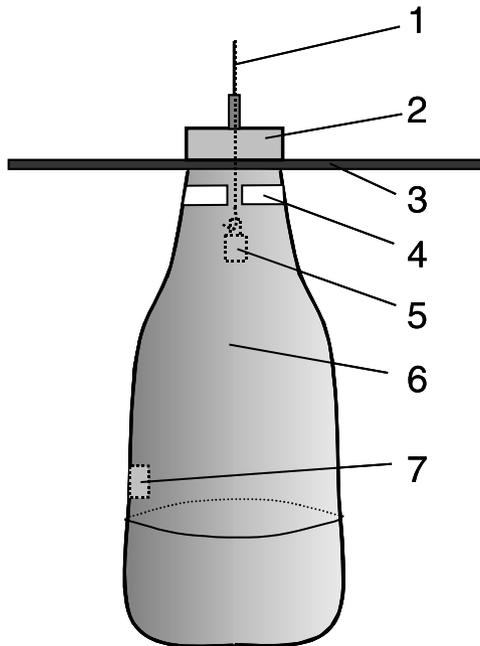

Figure 2 The milk-bottle trap was made from a recycled PET milk bottle container (6) cut into two parts: the bottom part where dead insects accumulate and the top part where a Vapona strip was stapled (7). The milk bottle cap (2) was used to maintain a square hood (3) designed to protect the trap from the rain and to direct the males into the holes (4). The hanging wire (1) was fixed through the cap and held the pheromone dispenser (5).

and used for spatial monitoring. Rubber septa (Thomas Scientific, Swedesboro, NJ, USA, Cat. no. 1780-J07) treated with 500 ng of (8E,10Z)-tetradeca-8,10-dienal (Svatoš et al., 1999) were used as pheromone dispensers in these traps. Attracted males were killed with the insecticide dichlorvos (Vapona strip, 5278 B, NV Sara Lee H&BC Belgium SA). The number of trapped males was counted by hand. A complementary set of ten Delta-traps (Biolatrap delta 155; ZD Chelčice, Czech Republic) with paper sticky inserts (200×80 cm), covered with Lunamelt PS 3199/05 glue (Vetox, Praha, Czech Republic) baited with the same pheromone (100 ng) and observed daily were distributed in five sites throughout the city and used to assess the temporal dynamic of male emergence.

All traps were placed into the canopy of horse chestnut trees (*A. hippocastanum*), 1–3 m above the ground. The Overwintering leaves index (OLI; see Table 2) was recorded at each trapping site. The 60 milk-bottle traps used for spatial monitoring were deployed on the day the first catches were observed in any of the ten Delta-traps, and collected and renewed 15 days later for a second trapping period within the first population generation. The first trapping period was thus from 25/04/2001 to 09/05/2001; the second trapping period was from 09/05/2001 to 23/05/2001. The 09/05/2001 and 23/05/2001 correspond, respectively, to 36% and 96% of the cumulated catches made in the ten Delta-traps during the first generation (1269 moths

caught in total). Following the first trapping campaign results, it was decided to renew and collect all the bottle traps every 3 weeks during the second generation to better target the expected date of 50% of the cumulated catches made during the second generation. The first trapping period was thus from 29/06/2001 to 20/07/2001 and the second trapping period from 20/07/2001 to 10/08/2001. The 20/07/2001 and 10/08/2001 correspond, respectively, to 52% and 99% of the cumulated catches made in the Delta-traps during the second generation (14 541 moths caught in total). Because these traps were in public areas, we had a significant number of traps damaged by vandalism. The number of undamaged traps was thus 43 and 47 for the 1st and 2nd trapping periods of the first generation, and 41 and 37 for the 1st and 2nd trapping periods of the second generation.

Analysis

Insect count data are known to present a strong proportionality between local mean and variance, a highly left-skewed frequency distribution, and tend to be far from normal (Taylor, 1961). This was the case with pheromone trap catches and with the mine counts from the Bern surveys. These data were thus log-transformed [$\log 10(x + 1)$] to reduce the proportionality between mean and variance and to normalise their frequency distributions.

The spatial distribution of population density was analysed using geostatistical tools allowing the quantification of the statistical spatial dependence of sampling points replicated through space (Isaaks & Srivastava, 1989). Statistical spatial dependence is important to the analysis of spatial datasets, first for the insight it provides on the variable under study when subject to interpretation (Rossi et al., 1992) and second because it represents a bias to the assumption of independence among samples that needs to be taken into account in parametric statistical analyses such as linear models (Lennon, 2000). Spatial dependence in population density was analysed by the standardized semivariogram of Bern 1998 and 2000 log-transformed mine counts, infestation code and log-transformed pheromone trap catches observed in Brussels in 2001.

Step-wise multiple regression analyses were carried out to analyse the relationship between measures of infestation density observed in Bern and Brussels and other factors described in Tables 1 and 2. The dependent variable, and most likely explanatory variables, were spatially autocorrelated which represent a violation of the assumption of independence among samples and could have invalidated the level of significance of the linear model and of the individual factors. Spatial autocorrelation in the regression residuals can be accounted for by incorporating a model of covariance among observations into the general linear model framework (Little et al., 1996). However, this method does not account for spatial autocorrelation in the explanatory variables. Here, we used the method described by Clifford et al. (1989) and modified by Dutilleul (1993) to test the significance of the single correlation between the dependent variables and individual factors, which was provided in the result tables as a conservative measure of individual factors of significance.

The decrease in infestation level as a function of distance from potential population reservoirs was tested in both cities using different approaches. In Bern, potential reservoirs were defined in 1998 and 2000 as sites where the population density was high (locations where mine count was >140 in 1998 and locations where >60% foliage was damaged in 2000, respectively) and where the overwintering litter was present. The distance to these potential reservoirs was estimated from all other points, and the residuals of a step-wise multiple regression model including significant site characteristics were plotted as a function of that distance and modelled. Residuals were used in this analysis in an attempt to remove the variability related to site conditions from the relationship between infestation and distance to potential reservoirs.

In Brussels, the survey sampled only a low proportion of the estimated number of horse chestnut trees. Using survey data to identify population reservoirs could thus have been misleading. Furthermore, Brussels has several large green areas located deep in the city centre (Figure 1d) which constitute good population reservoir candidates because they include many horse chestnut trees; therefore leaves are frequently left in place during winter. The decrease in infestation level as a function of distance from these green areas was thus modelled by pooling the observation data from three transect avenues (Figure 1d) connected to these green areas, where all the leaves had been removed during the winter (OLI = 0). Here, transect avenues constituted standardised sites with respect to OLI, allowing us to directly analyse raw measures of infestations in relation to the distance to potential reservoirs.

Two modelling functions were compared, a linear model, and a model similar to a normal distribution function. This choice stemmed from the assumption that insect movement can be described by random Brownian motion, following a simple diffusion model originally suggested by Skellam (Holmes et al., 1994). When it combined with exponential local population growth and when the population is assumed to start from a single point source, Skellam's model translates into the following normal function (Shigesada & Kawasaki, 1997):

$$N(x, t) = \frac{N_{(0,0)}}{4\pi Dt} \exp 10 \left(rt - \frac{x^2}{4Dt} \right)$$

Table 3 Linear model of observed infestation levels observed in Bern 1998, Bern 2000, and Brussels 2001

	R^2	n	P	Effect	Estimate	SE	t	Sig.	Corr. Sig.[g]
Bern 1998	0.49	169	<0.001	OLI[a]	0.251	0.06	3.66	<0.001	<0.001
				GCODE[b]	−0.134	0.05	−2.95	0.004	0.034
				SMODEL[c]	1.000	0.11	10.34	<0.001	0.029
Bern 2000	0.40	392	<0.001	OLI[a]	0.092	0.015	6.07	<0.001	<0.001
				GCODE[b]	−0.084	0.011	−7.33	<0.001	<0.001
				SMODEL[c]	1.000	0.123	8.39	<0.001	<0.001
				NAE800[d]	3.07E−04	1.21 E−04	2.53	0.012	0.021
Brussels 2001	0.62	257	<0.001	OLI[a]	0.975	0.059	16.41	<0.001	<0.001
				AVGA100[e]	0.017	0.003	5.59	<0.001	<0.001
				NAE2000[f]	0.267	0.131	2.05	0.042	0.061

[a]Overwintering leaves index.
[b]*Guignardia aesculi* code.
[c]Spatial model.
[d]Total number of horse chestnut trees in a 800 m neighbourhood.
[e]Proportion of green areas in a 100 m neighbourhood.
[f]Total number of horse chestnut trees in a 2 km neighbourhood.
[g]Significance of the individual correlation between the covariate and the dependent variable, corrected to account for spatial autocorrelation.

where N is population density at spatial coordinates x, D is the diffusion coefficient that measures dispersal rate, r is the rate of population increase, and t is the time. A normal decrease function in the form $Y = A.exp10(–x^2/B)$, where A and B are the function parameters, was thus adjusted to provide the best fit. In the Bern data set, values predicted by the diffusion spatial model (SMODEL) were incorporated as a complementary variable with a fixed factor equal to 1 into the regression analyses.

Results

The distribution of mine counts in Bern (Figure 1a,b) shows that higher moth infestation levels were concentrated in the eastern part of the city around the river, where horse chestnut trees are often located in parks or in large private gardens in diplomatic residential areas. In the eastern part, infestation levels also showed the least change between sampling years (Figure 1c). By contrast, in the south-western parts of Bern almost all the sites increased in their infestation level. In Brussels, the highest infestation levels were observed in the southern part of the city (Figure 1d), i.e., in areas where parks and urban forest were the most abundant, whereas sites located in the city core with very dense building blocks had lower levels of infestation. Population estimates measured in Bern and Brussels showed evidence of a strong spatial dependence up to a distance of 1100 m in Bern 1998, 800 m in Bern 2000, and up to 1900 m in Brussels 2001 (Figure 3). The

spatial dependence was isotropic, i.e., it did not change significantly according to direction.

In Bern, three parameters were found to be significantly correlated with population estimates in both study years (Table 3): the Overwintering leaves index (OLI), the *Guignardia aesculi* code (GCODE), and the spatial model (SMODEL) (Figure 4). In the Bern 2000 data, the number of horse chestnut trees found in an 800 m neighbourhood was also found to be significantly correlated with population log-transformed mine counts. In Brussels, three parameters were found to be significantly correlated to infestation levels in the multiple regression analysis: the OLI, the average proportion of green areas within 100 m, and the total number of horse chestnut trees found in a 2 km neighbourhood (Table 3), although this factor was not individually significantly correlated to infestation level when spatial autocorrelation was accounted for.

Finally, the measure of population estimates as a function of distance to potential population reservoirs showed a decrease in Bern and Brussels (Figure 4). In Bern 1998, both the linear and diffusion models had an equivalent fit to the observed pattern, whereas a better fit of the diffusion model was observed in Bern 2000 and Brussels 2001.

The pheromone trapping of both population generations observed in Brussels showed a clear positive relationship between catches and the amount of overwintering leaves (Figure 5a,b). In the first generation (Figure 5a), the two trapping periods gave similar results, showing a strong relationship between catches and OLI and a very small
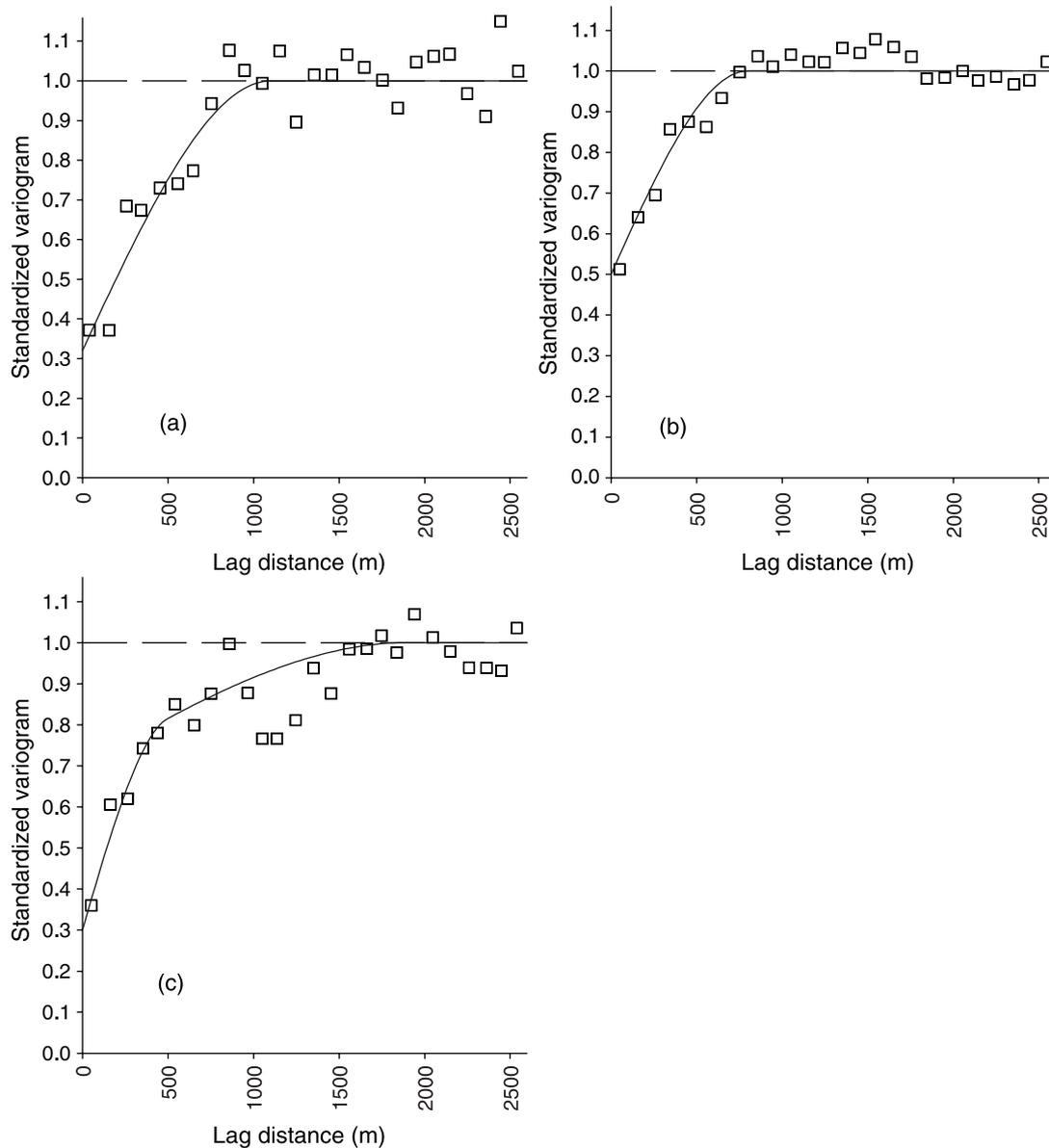
Figure 3 Standardized semivariogram of population levels estimated in Bern 1998 (A: Nugget: 0.32; Spherical Model; Scale: 0.68; Range: 1100 m), Bern 2000 (B: Nugget: 0.5; Spherical Model; Scale: 0.5; Range: 800 m), and Brussels 2001 (C: Nugget: 0.3; Spherical Model 1: Scale: 0.4; Range: 500 m; Spherical Model 2: Scale: 0.3; Range: 1900 m), respectively.

number of catches in places where no leaves were present. However, the second period of the first generation had more catches than the first (one-way ANOVA; n = 84; F = 6.89; P = 0.01). This increase was simply due to the fact that the first trapping period covered 36% of the emergence catches made by the Delta traps whereas the second trapping period covered 60% of the catches (including the peak). In the second generation (Figure 5b), both trapping periods were also very close, but the relationship differed

from the first generation. First, the slope of the linear model was lower, and second, the intercept was about 10-fold higher, and finally the relationship as measured by both R^2 values was much weaker. In addition, the average number of log-transformed catches per trap increased by a much higher factor (5.17) in locations where no overwintering leaves were observed than in other locations (Figure 5c).

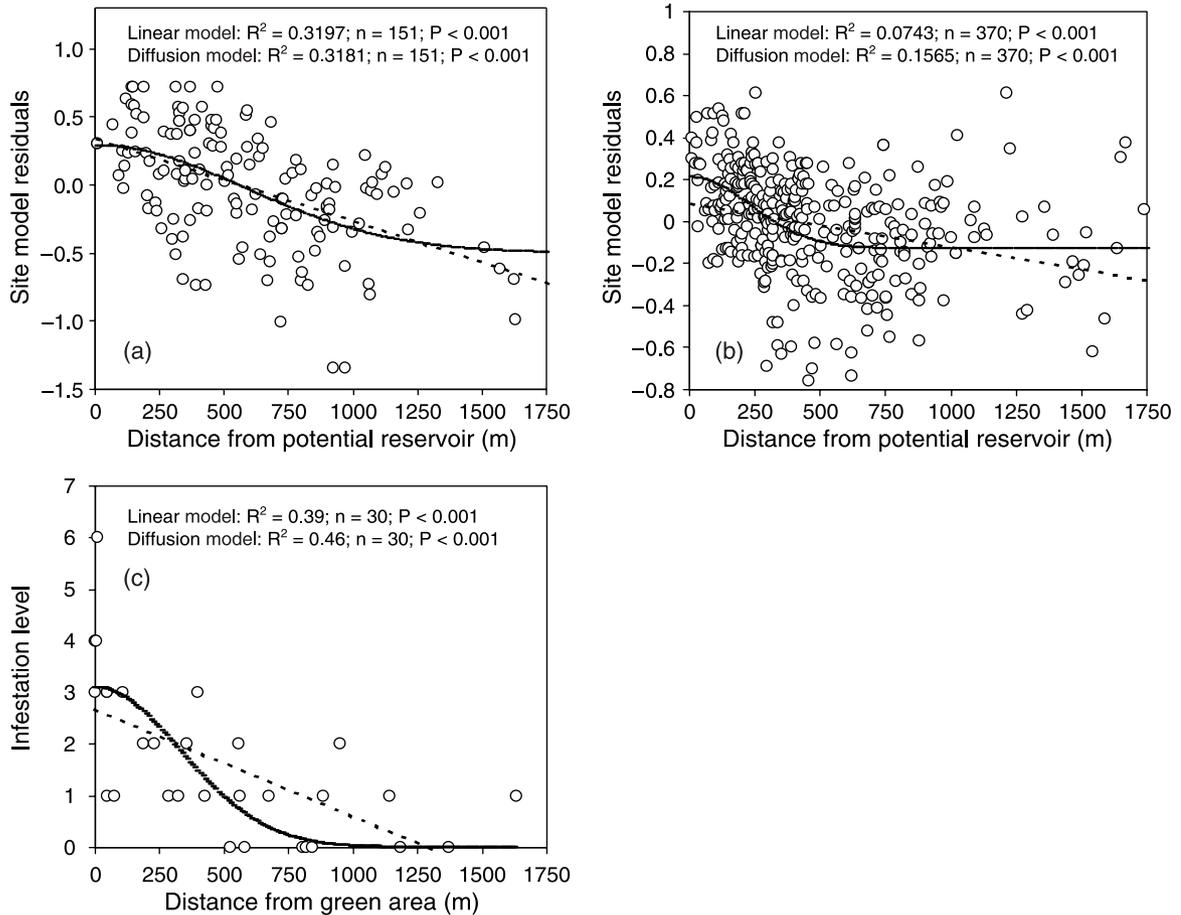The semivariograms of all the trapping periods were flat, showing that the catches were spatially independent

Figure 4 Best-fit model of the decrease in infestation density as a function of the distance from potential reservoirs in all compass directions in Bern 1998 (A) and Bern 2000 (B), and from green areas along three street transects in Brussels (C).

within the scale of this study. A linear relationship between log-transformed pheromone catches of the first generation and subsequent infestations observed during the survey was found to be fairly strong ($Y = 1.8008X + 0.8012$; $R^2 = 0.71$; $P < 0.001$; $n = 46$).

Discussion

Our results quantitatively demonstrate that the amount of overwintering leaves is the main factor explaining variability in infestation density of *C. ohridella* at the site level. It should be noted that the amount of leaf litter left at a site determined moth population densities even late in the season. The overwintering leaves index (OLI) was strongly related to *C. ohridella* population size estimated by pheromone traps in Brussels 2001, and by surveys in Bern 1998, Bern 2000, and Brussels 2001. Furthermore, the relationship between infestation levels and the proportion of green areas within a 100 m neighbourhood

observed in Brussels may be interpreted by the fact that green areas may potentially include more refuges where leaves are difficult to remove than in the dense urban habitat (these more distant leaves are not taken into account in the OLI, which concentrates on the leaves observed under the sampled tree). At the site level, removing the leaves during the winter therefore has a direct effect on the damage that can be quantified using the relationships presented in Table 3. However, the use of this control method in parks and urban forests is not practical. Pheromone trap catches of the second generation observed in sites with refuges (OLI = 1–2) were almost similar to those where overwintering leaves were more abundant (OLI = 3–4), confirming that moth populations were able to rebound from a low number of surviving individuals, and that leaf removal requires the elimination of nearly 100% of the leaves to be effective. Such a ratio cannot be achieved in parks and urban forests. In contrast, removing nearly 100% of the leaves from street

(a) First generation

First period (white / cont. line)
y = 0.3811x + 0.3121
R² = 0.6278; p < 0.001; n = 43

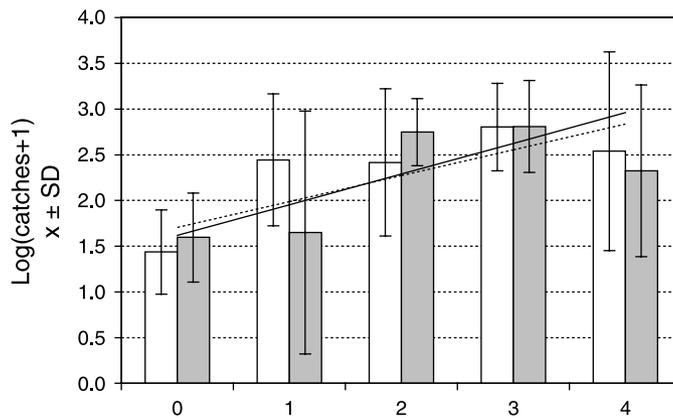Second period (grey / dotted line)
y = 0.5034x + 0.5539
R² = 0.7105; P < 0.001; n = 47
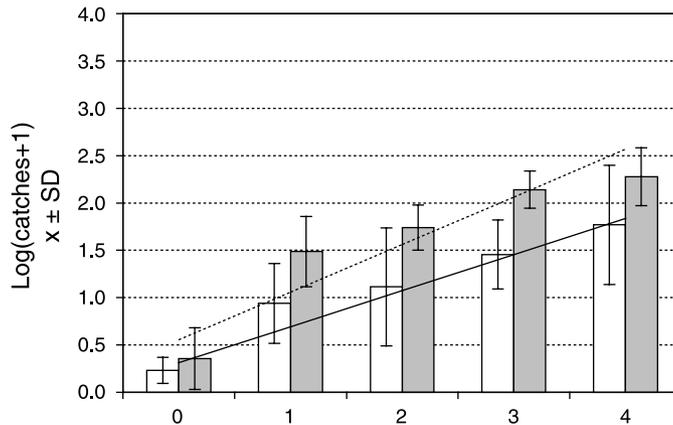
(b) Second generation

First period (white / cont. line)
y = 0.336x + 1.6172
R² = 0.2569; P < 0.001; n = 41

Second period (grey / dotted line)
y = 0.2821x + 1.7056
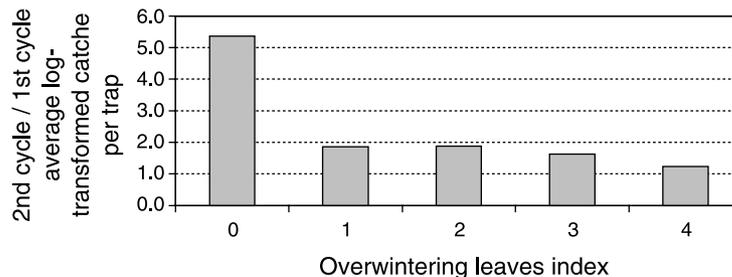R² = 0.2165; P = 0.003; n = 37

(c) 2nd / 1st generation

Figure 5 Relationship between log-transformed pheromone trap catches and Overwintering leaves index (OLI) in Brussels: first population generation (a), second population generation (b), and ratio between the two population generations (c). Results of linear regression of log-transformed catches vs. OLI are presented beside each graph.

trees is a much easier task, and the infestation of street trees may have a higher impact on their health because of their low vigour related to higher pollution and soil compaction (Speight et al., 1998). These trees are thus more important to protect from additional sources of vigour loss caused by *C. ohridella*.

The negative correlation between the leaf pathogen *Guignardia aesculi* and moth infestation levels found in both years in Bern indicates a negative interaction between

the fungus and the leafminer. In Brussels, moth infestation data were collected after the first moth generation at a time when symptoms of pathogen infection were only beginning to develop. Thus, a similar relationship was not observed. Plant pathogens and herbivorous insects often have a mutual negative effect on each other, mostly because both share the same resource and can thus be regarded as competitors (Hatcher, 1995, but see Friedli & Bacher, 2001). A negative interaction between the two horse chestnut

tree parasites suggests that after the exclusion of one pest by effective controls, the other may exploit the released resources, thus nullifying the successful control of its competitor. However, further research is required to clarify the interaction between *C. ohridella* and *G. aesculi*.

The dispersal of individuals from population reservoirs is suggested by the convergent results of separate analyses. Firstly, gradients of decreasing infestation level as a function of distance to potential population reservoirs are observed in the Bern 1998, Bern 2000, and Brussels 2001 survey data. No alternative explanation other than dispersal from potential reservoirs could be found to explain such a pattern. Secondly, moths caught during the first generation at sites with OLI = 0 must have dispersed from sites where the leaf litter was left intact during winter. Comparisons of pheromone trap catches between the generations showed that there was much more population increase between the 1st and 2nd generation in locations where the overwintering leaves had been removed during the winter and this can be interpreted as the effect of insect dispersal coming from areas with refuges towards areas where leaves are absent. An alternative interpretation of these results could be a higher rate of population growth observed on trees with low initial densities because of some form of density dependence (e.g., limited number of 'best leaves' to infest). However, this explanation would not explain why gradients are observed from potential population reservoirs. Thirdly, the effect of dispersal can also be the interpretation of the relationship found between infestation level and the amount of horse chestnut trees found in a 800 m neighbourhood in Bern, 2000 m in Brussels. Indeed, in presence of dispersal, a tree located where OLI = 0 is more likely to be re-colonised if it has many other horse chestnut trees in the neighbourhood than if it is isolated from other trees by the urban habitat. Having the same hypothesis supported by convergent results of separate experiments (pheromone trapping and survey) is a strong argument to suppose that *C. ohridella* disperses in the city from locations with high population reservoirs, i.e., where overwintering leaves were abundant, to locations where leaves were removed during winter. The dynamics of *C. ohridella* population in cities therefore appears as a particular source-sink metapopulation, following the ideas of Pulliam (1988). In these systems, one or more source populations regularly produce an excess of individuals that disperse to less optimal habitat, having population growth rates consistently less than zero. Here, population growth rate in locations where the litter is removed (sink) is forced to a negative value, and high population growth rates where the leaves are left in place (source) annually produces an excess of individuals dispersing into sinks. Our results provide an original observation of such dynamics in urban

ecology, as these source-sink systems are classically applied to islands isolated from the mainland, or to patches of varying size and quality in a fragmented landscape (Stacey et al., 1997). Such source-sink dynamics at the scale of cities would explain why the local eradication of this pest from a site (for example by leaf removal) does not lead to the sustainable control of *C. ohridella*.

The pattern of change of moth infestation in Bern between 1998 and 2000 indicated that the eastern city regions were infested before the western, and that moth populations at the site level were expanding in the west while they had reached densities close to maximum carrying capacity in the east. This implies that while overall population densities may vary between years, there seem to be site-dependent carrying capacities which moth populations reach after some years of growth. Considering only sites in 2000, where we assume the observed infestation density reached values close to the carrying capacity (east of Swiss coordinate 599900) sink sites (litter removed, N = 69) had significantly lower infestation levels than potential source sites (litter present, N = 95; sink: corrected mine counts 68 ± 37, source: 124 ± 73, Tukey HSD, P < 0.001). This indicates that the maximum infestation level that can be attained is considerably lower in a sink site. In other words, at sites where the moth has to invade each year anew by dispersal, *C. ohridella* infestation levels cannot reach the maximal densities permitted by the site conditions. This again emphasizes the effectiveness of consequent leaf removal in reducing moth densities.

It is difficult to infer actual spreading rates on the basis of the survey data because local abundance may be influenced by external factors which were not taken into account in the present study, and because we do not know how well the population estimates used in this study (mine counts and infestation code) relate to actual populations. However, the gradients from potential reservoirs observed in Bern 1998, Bern 2000, and Brussels 2001 provide consistent results: Bern 1998 survey data represent the result of three generations and stabilizes at an approximate distance of 1500–1700 m; the Bern 2000 data survey represents the result from only two generations and stabilizes at a distance of 500–700 m; the Brussels data only represent the results of the first generation and stabilizes at a distance of 750–1000 m. Although this distance (per generation) appeared to be much higher than in Bern, the Brussels gradient was observed along street transects which may facilitate the spread over longer distances by a 'canyon effect' (DePaul & Sheih, 1986; Speight et al., 1998) as compared to Bern gradients observed in all compass directions through the city mosaic. Furthermore, the spatial structure of populations appeared to be slightly different in Bern and Brussels, as shown by the fairly similar semivariograms of 1998

and 2000 Bern survey data, in contrast with the spatial structure observed in Brussels 2001 infestation code. Many factors related to the city's characteristics may explain such variations in the spatial structure of populations, such as the spatial distribution of population reservoirs, the topography, the prevailing wind direction, or the structure of the streets and buildings in contributing to a canyon effect. Pooling the results of the gradients observed in the three data sets, a spread rate (distance between sites with equal population densities in two successive generations) of a few hundred meters appears to be a realistic figure for *C. ohridella* in cities. These results are not contradictory to the much faster long-distance spread observed in *C. ohridella* (estimated as 60 km per year; Šefrová & Laštuvka, 2001), as large-scale invasions are generally associated with long-distance passive transportation translating into stratified dispersal such as that observed in other biological invasions (e.g., Sharov & Liebhold, 1998; Gilbert et al., 2003), and already reported in Gracillariidae (e.g., Nash et al., 1995).

Two conclusions can be drawn from these results in an applied perspective. First, studies on the spatial distribution of related species from the Gracillariidae family using pheromone trapping have not been performed, and our results indicate that pheromone traps respond quantitatively well to local populations, as shown by the relationship with OLI at the first generation and allowed us to predict subsequent infestation levels better than using the single measure of OLI. They can therefore be used efficiently in spatial monitoring. Second, direct experiments could be designed to refine a spatially explicit source–sink metapopulation model. This model would allow us to predict infestation dynamics on city scale according to various control scenarios and to better target spatial areas where leaf removal control effort should be concentrated.

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