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Abstract

The horse-chestnut leafminer *Cameraria ohridella* is an invasive lepidoptera (Gracillariidae) which has spread throughout Europe over the last two decades. The species can be detected easily because of its noticeable damage to horse-chestnut trees leaves, which allows the easy collection of large-scale monitoring data. It is therefore an interesting model species to study invasion processes, and this review summarizes recent progresses in that regard. The date reported here result from monitoring of *C. ohridella* population based on pheromone traps and visual observation of damage carried out in Belgium, France, Germany, Switzerland and the UK. The patterns of spread measured using these different monitoring method, and the key factors associated with short-distance dispersal (within cities), and large-scale dispersal (across landscapes) are presented and discussed.

Introduction

Considerable research has been conducted on the spread of non-indigenous species (Okubo 1980; Andow et al. 1990; Lewis and Kareiva 1993). Understanding the spatial dynamics of invasive species and predicting dispersal patterns is a challenge for invasion ecology (Sakai et al. 2001). Extensive theoretical literature has been produced to model invasion dynamics (Shigesada and Kawasaki 1997).

Several approaches have been used to model invasion patterns (Higgins and Richardson 1996), but spatially realistic simulation modelling techniques used recently to identify associations between landscape characteristics and invasive dynamics have been particularly useful for insects (Sharov et al. 1997; Sharov and Liebhold 1998; Gilbert et al. 2004), plants (Wadsworth et al. 2000; Higgins et al. 2001; Volin et al. 2004) and diseases (Keeling et al. 2001; Smith et al. 2002). However, few of these models have been validated by an independent data set (Wadsworth et al. 2000) and then used to forecast the pattern of invasion in a newly colonized area (Russell et al. 2004).

Over the last two decades *Cameraria ohridella* Deschka and Dimić has spread rapidly throughout Central and Western Europe (Šefrová and Lastuvka 2001). It was reported in France in 2000 (Augustin and Reynaud 2000), in Spain (Villalva and Del Estal 2003), UK (Straw and Bellett-Travers 2004), Denmark (Karsholt and Kristensen 2003), Sweden (Svensson 2004), Lithuania (Ivinskis 2004) and the Ukraine (Akimov et al. 2003) in 2002, on the southern coast of Finland (J. Pöyry, pers. comm.) in 2006. It is expected to spread up to the northern limit of its host-tree distribution in Scandinavian countries, where it can produce at least one generation per year due to climatic conditions.

Once detected in a location, *C. ohridella* reaches outbreak densities in cities and villages where its main host species, the ornamental white-flowering horse chestnut, *Aesculus hippocastanum* L., is abundant. Although the damage inflicted by the horse-chestnut leaf-miner can be spectacular, causing premature abscission in early summer, it appears to have little impact on the vigour of the host tree (Salleo et al. 2003; Thalmann et al. 2003). *Cameraria ohridella* is occasionally found on other *Aesculus* species, such as *A. turbinata* Blume, *A. flava* Sol., or *A. pavia* L, but not on the red horse-chestnut *A. × carnea* Hayne (Freise et al. 2004). It has also been recorded on *Acer platanoides* and *Acer pseudoplatanus*, but these appear to be opportunistic infestations adjacent to heavily infested horse-chestnut trees.

The high invasive potential of this species is mainly attributed to its high population growth resulting from: (i) multivoltinism with 2–4 generations per year [the mean realized fecundity is 34–82 eggs by female and the net reproductive rate is 4–11 in non-overwintering populations (Girardoz et al. 2007a)], (ii) low rates of predation and parasitism that have little effect on the *Cameraria*-population [predation rates are lower than 4% (Grabenweger et al. 2005a) and parasitism rates are usually 10–25% in South Eastern Europe but are generally lower than 10% in recently invaded countries of Central and Western Europe (Freise et al. 2002; Grabenweger 2003; Grabenweger et al. 2005b,b; Volter and Kenis 2006; Girardoz et al. 2007b)], (iii) the absence of inter-specific competition (Freise and Heitland 2004) with other phytophagous insects on its main host, *A. hippocastanum*, resulting in populations limited only by intra-specific competition, (iv) population patterns in cities indicating a source-sink dynamic allowing populations to rebuild in cities despite significant control efforts (Gilbert et al. 2003a), and (v) a relatively high passive dispersal capacity over long-distances (discussed in this paper). Pupae overwinter on the ground inside fallen leaves, and although exhaustive sweeping of leaves in the streets may be realistic, it is not in parks and gardens. In spring, populations from parks and gardens disperse toward trees located along streets and this allows populations to re-establish quickly.

The large-scale dispersal rate of *C. ohridella* in Central and Western Europe was broadly estimated on the basis of first observation dates in European countries (Šefrová and Lastuvka 2001) to be 60 km/year, seemingly faster than other invasive Lepidoptera [e.g. *Lymantria dispar*: 9.45–20.78 km/year

(Liebhold et al. 1992); invading lepidoptera in the UK: 0.06–10.3 km/year (Agassiz 1996)], or invasive tree-dwelling species, such as oak gall wasps (20–40 km/year; Walker et al. 2002) but in fact comparable to rates of spread observed in other invasive leaf-miners (Agassiz 2002).

Both patterns and rates of dispersal are important for understanding and managing invasive species but rely on early detection and extensive monitoring. When our research on *C. ohridella* within the framework of the EU project Controcam started in 2000, the species had only been recently detected in France, and our primary aim was to develop detection and monitoring methods in order to model and understand the dispersal patterns on different spatial scales. The aim of this paper is to present and discuss the various studies undertaken to describe, understand, and predict *C. ohridella* dispersal on large and small spatial scales.

Detection and Monitoring Methods

Pheromone trapping has previously been used to monitor invasions by several Lepidoptera. Sharov et al. (1996), for example, collected pheromone trap data and compared them with two further methods of census (i.e. egg mass counts and defoliation records) to measure the rate of spread of the gypsy moth *Lymantria dispar* (L.) in the northeastern United States. All three census methods have been shown to be suitable tools for measuring dispersal rates of the gypsy moth.

For *C. ohridella*, the suitability of pheromone trapping (Kalinová et al. 2003; Svatos et al. 2008) to measure damage levels and subsequent population densities was evaluated in two studies; one covered the city of Brussels (Gilbert et al. 2003a) and the other, a rural area that included small towns and villages of eastern France (Augustin et al. 2004), respectively. Infestation levels were estimated using two methods: surveying foliage damage through observation and counting the number of males captured in pheromone traps baited with the sex pheromone of *C. ohridella*. For the observational data, a damage score was derived from the visual assessment of the overall proportion of leaves damaged by the moth. Damage (%) was assessed on a scale of 0 to 7 as follows: 0: 0%, 1: 0–2%, 2: 2–5%, 3: 5–10%, 4: 10–25%, 5: 25–50%, 6: 50–75%, 7: 75–100%, which was previously shown to be linearly related to log-transformed [Log 10(x + 1)] mine numbers at the leaf-level (Gilbert and Grégoire 2003), and which allows population estimates.

The pheromone traps described by Gilbert et al. (2003a) and Augustin et al. (2004) were baited with the sex pheromone of *C. ohridella*, (8E,10Z)-tetra-deca-8,10-dienal (Svatos et al. 1999). In Brussels trees were surveyed for the first generation of *C. ohridella* on 262 sites in 2001. In eastern France infestation levels were estimated in 2001 on a network of 69 sites (5–15 km apart) which was extended to 125 locations in 2002. Thus, the population density of *C. ohridella* on horse-chestnut trees was estimated independently from observations both of foliage damage and pheromone trap catch data. In eastern France damage assessment was made for each generation per year between 2001 and 2003. In addition, pheromone traps were also set up at each sampling location during two pheromone trap catch periods (flight of second and third generation) in 2001 and 2002 (Augustin et al. 2004).

In Brussels 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 ($R^2 = 0.71$; $P < 0.001$; Gilbert et al. 2003a). In France, correlations between the damage scores and the log-transformed data from pheromone traps were significant for all generations with a tendency toward a reduction in correlation between observations separated by increasing time-lag. The correlation between trap catch data and damage score estimates was weaker than that expected on the basis of other studies (Gilbert et al. 2003a). This was attributed to the use of the delta-traps whose sticky inserts tended to saturate when the population density was high and thus did not allow for new catches unless renewed frequently. In contrast, the trap models used in the study in Brussels (recycled PET milk bottles with Vapona strips) were able to catch much higher numbers (up to 5000 individuals) and thus did not tend to saturate during trapping periods longer than one to two days in high population sites. However, the sensitivity of visual estimates at low population levels was higher than estimates from pheromone trap data: the frequency of cases with zero catches and non-zero damage scores was higher than that of cases with zero damage scores and positive catches.

Estimates made from damage assessments correlated with log-transformed estimates from pheromone trap catches, suggesting that both techniques can be used to monitor the spread of this pest. However, results indicate that the monitoring of within-year population dynamics would be better evaluated by the use of a network of pheromone traps that permit a high number of catches per trap.

Conversely, it was found more cost efficient to use damage-scale observations for analyses of population dynamics spanning several years and large spatial scales, because the only costs associated with this method are those caused by travel, and these are incurred for pheromone trap placement anyway.

Patterns of Dispersal at Different Spatial Scales

Local patterns within cities

Local patterns of *C. ohridella* within cities were studied in Bern and Brussels (Gilbert et al. 2003a). In Bern, a total of 175 sites and 399 sites, respectively, were surveyed in 1998 and 2000. Moth infestations were 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 1998. 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. Therefore, the data of mine counts at high infestation levels were corrected by extrapolating from mine counts at low infestation levels using linear regression of mine counts vs. the percentage of foliage damaged in 2000.

In Brussels in 2001 trees were surveyed at 262 sites. Infestation levels were estimated using two different methods: the survey observation of both foliage damage and pheromone traps. In both cities, several habitat variables were assessed during the survey; additional variables were extracted using a geographical information system such as the average proportion of green areas in a given circular neighbourhood around each sampling site for different radius distances. The spatial structure of population density was analysed using geostatistical tools allowing the quantification of their statistical spatial dependence (Isaaks and Srivastava 1989).

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 results suggested a dispersal rate of a few hundred meters for *C. ohridella* in cities.

The pattern of infestation levels as a function of distance to potential population reservoirs suggested that *C. ohridella* re-invaded areas where overwintering leaves had been cleaned from refuge areas such as parks or urban forests. The dynamics of *C. ohridella* population in cities therefore appeared as a particular source-sink metapopulation *sensus* Pulliam (1988). In those systems, one or more source populations regularly produce an excess of individuals that disperse to less optimal habitats that have population growth rates consistently less than zero. The source-sink dynamics at the scale of cities would explain why the local eradication of this pest from a site (e.g. by leaf removal) does not lead to a sustainable control of *C. ohridella*.

Regional-scale pattern in rural areas

In rural areas examined in eastern France, spatial patterns in population densities estimated by damage assessment and pheromone trapping were analysed using estimates of the spatial correlogram function (Augustin et al. 2004). Damage scores were interpolated by ordinary kriging (Isaaks and Srivastava 1989), using the best-fit spherical model. Distribution of population estimates from the damage assessment and from pheromone trap catches illustrated that most of the areas studied in 2001 were already infested by *C. ohridella*, and the studied areas in 2002 were quickly overtaken by the spread of the leafminer. Most of the spread occurred from one year to the next (e.g. from generation 1 to 4, and 4 to 7), with no spread or even a decrease (particularly in 2001) in the distribution area, taking place within years. In addition to this trend, a population focus appeared in generation 4 (2002) in the southwest of the study area. These two population foci had merged by the end of 2003.

Two methods were used to measure the rate of spread from 2001 to 2003 with these data (first generation to the ninth): radial distance vs. time and average distance vs. time. The rate of spread measured by the increase in radial distance resulted in average spread rates ranging from 7.9 ± 3.3 to 12.6 ± 4.0 km per generation, whereas these ranged from 5.7 ± 2.4 to 9.2 ± 1.7 km per generation when estimates were based on the average distance from the initial focus. From 2001 to 2003, the spread rate ranged from 17.0 to 37.9 km/year, depending on the population threshold and method used.

National scale pattern in France and Germany

Within cities, the moth is assumed to disperse through the leaves displaced by winds and by active 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 initial locations are frequently observed near car parks (Heitland et al. 1999) and fortuitously with infested seedling through nurseries (Augustin and Reynaud 2000; Villalva and Del Estal 2003). Two hypotheses were explored using monitoring data on the national level from Germany and France. First, the biological invasion by *C. ohridella* was hypothesized to follow 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 the norm for most invasive organisms and has been described in other invasive insects [e.g. *Lymantria dispar* Sharov and Liebhold 1998; *Dendroctonus micans* Kugel. (Coleopera: Scolytidae); Gilbert et al. 2003b;] and in other Gracillariidae [*Phyllonorycter leucographella* (Zeller); Nash et al. 1995;]. Second, the local human density population was hypothesized to correlate with long-distance dispersal, because traffic is more intense between highly populated areas and because higher human densities are generally associated with higher densities of the host-plant *A. hippocastanum*. To test these hypotheses, three spatially explicit stochastic models of spread differing in the shape of their dispersal kernel were compared using spatio-temporal observations of damage by *C. ohridella* carried out in 1997–2000 in Germany: a diffusion model, a leptokurtic dispersal model, and a stratified dispersal model that assumed a two-scale dispersal process corresponding to short-distance and long-distance dispersal events (Gilbert et al. 2004). A fourth model tested 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 were tested on French observations carried out in 2001–2004 (Gilbert et al. 2005).

The best model fitting the spread of *C. ohridella* in Germany was the stratified dispersal model, which took into account the human population density (Gilbert et al. 2004). It outperformed the Gaussian, leptokurtic and stratified dispersal model in terms of its predictive power and spatial configuration of the invaded areas. These models, with their parameters estimated from the invasion in Germany, were used

to predict similar outcomes in France, and were similarly accurate, in particular the stratified dispersal model accounting for human population density.

Interestingly, the stratified dispersal model, which ignores the effect of human population density, predicted a much more rapid invasion than was observed in France. The improvement of the stratified model when incorporating the human population clearly enhanced the model and may be interpreted in different ways. First, in cities, horse-chestnut trees are generally abundant and the likelihood they will intercept insects arriving either on moving vehicles, or brought by wind from long-distances as part of the aerial plankton, is higher. Second, highly populated areas have higher flows of people, cars, trains or truck, contributing to the passive transport of insects. Thirdly, mountainous areas like the Massif Central, clearly less suitable for the dispersion, are also less populated. Several factors presumably important to *C. ohridella* dispersal were ignored in those two studies such as climate (temperature, rainfall, wind speed and direction), landscape structure (open countryside landscape vs. cities), host-tree distribution, or more detailed variables concerning the transportation network. However, the approach presented a clear trade-off between simplicity and realism. The validation of the model developed in Germany using the data from France suggested that an equivalent level of predictability could be expected in the forecast of the invasion of the UK (Gilbert et al. 2005) or in a newly invaded country with similar environmental conditions. The predicted distributions based on 2002-2004 observations for 2005–2007 invasion patterns matches the observed invasion (fig. 1). In term of rates of spread, the short-distance component of the stratified dispersal model was estimated as ~10 km/year, but combined with long-distance dispersal the overall spread rate was estimated as ~30 km/year, which matches the regional-scale study estimates (Augustin et al. 2004).

Dispersal Patterns at Different Spatial Scales

The main apparent discrepancy between these different results is the high spread rate of *C. ohridella* on the regional scale – estimated as between 18 and 37 km/year that suggests a very high dispersal ability – and the fact that spatial heterogeneities in population densities tend to be maintained within cities. Indeed, if dispersal was so high, one would expect that all horse-chestnut trees to be equally damaged at the end of the season, yet the results from the

Bern and Brussels studies (Gilbert et al. 2003a) suggest relatively short-distance population gradients over a few hundred meters. This apparent contradiction can be easily resolved if one considers that only a few individuals are necessary to invade a new area, while visible gradients in damage involves several thousands of individuals. Assuming that individuals do not disperse much, that upon emergence most members of the population fly to the tree above the ground, or in the upper leaves in the second and third cycle emergences. A minor fraction of the population could fly away from that tree especially if the density and intra-specific competition are high, and would probably land on the nearest tree with sufficiently undamaged leaves. This would produce exactly the pattern of short-distance gradients that was observed within cities. If one assumes that those individuals which disperse were blown away by upper-lifting winds, or entered vehicles about to travel over long distances, this would result in rare long-distance dispersal events. Even if on average the frequency of those dispersal events is higher at short and medium distances than at long distances (because for example, more cars travel short distances than long ones), the pattern of dispersal would remain the same because the few individuals brought away by these mechanisms would need a few generations until the damages started being visible. Therefore, even a large-distance spread within cities would remain unnoticed until at least the following year. In addition, even if a higher fraction of the population was involved in those long-distance dispersal events, the dilution resulting from the wind or from being spread by cars would be such that only a very small number of individuals could spread over very long distances. This combination of low-dispersal for a high fraction of the population, and long-distance dispersal for a small number of colonizers may resolve the apparent contradiction between a fast rate of spread and population damage heterogeneity within cities. It also matches the observation that cities were very quickly invaded, with usually less than 2–3 years between the first observation of *C. ohridella* and its widespread distribution on all available hosts, and the observation that most long-distance spread is observed between years, and not within-years.

Dispersal Mechanisms

The question of the dispersal mechanisms involved in long-distance dispersal events remains unresolved. The main mechanisms being proposed in the
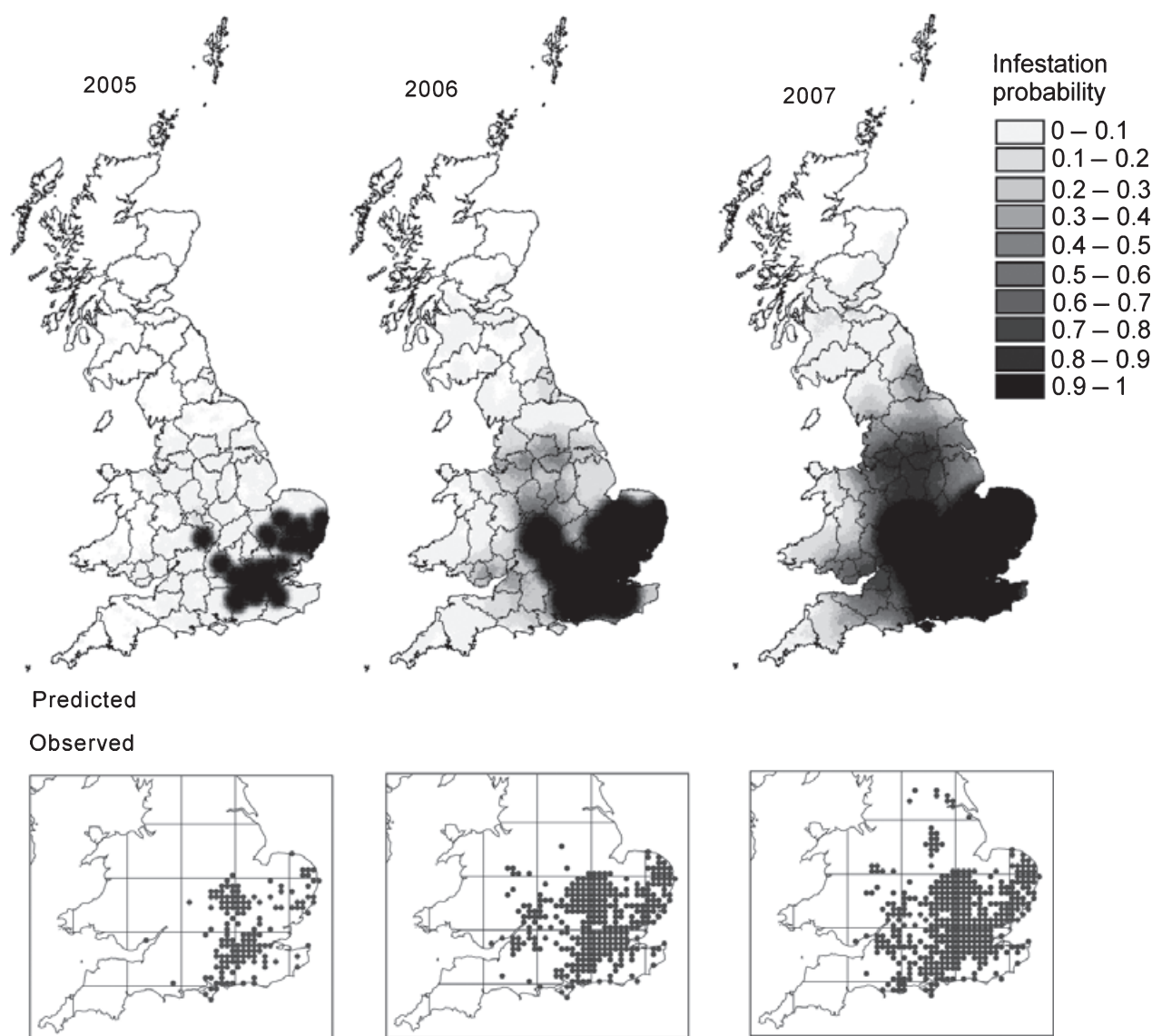
Fig. 1 The observed distribution of *C. ohridella* infestation in the UK during 2005–2007 (Straw, pers. comm.) compared with the distribution of infestation predicted by the stratified dispersal model that takes human population density into account (Gilbert et al. 2005).

literature are the spread through vehicles (car, trucks and trains) and by wind (Gilbert et al. 2005). To disentangle these two effects is difficult: there is anecdotal evidence for both. *Cameraria ohridella* is often found first around parking places or train stations, and was initially observed in the UK in a parking lot at Wimbledon where many foreign visitors had parked cars from abroad. *Cameraria ohridella* was trapped in an underground car parking garage, while a similar trap placed on the surface did not catch any individuals (Gilbert, unpublished data). Conversely, *C. ohridella* has been found infesting very isolated trees, far from any roads or transport

infrastructures. It would be possible to explore the quantitative effect of wind on *C. ohridella* dispersal by analysing the patterns from large-scale invasions in France, Germany and the UK in relation to wind models that use archive meteorological wind records. This approach, which has been used to model the spread of other wind-borne insects that transmit diseases, was apparently successful in explaining large-distance dispersal patterns (Ducheyne et al. 2007). It would allow us to quantify the observed large-scale pattern of dispersal and see if these match the pattern that would be expected if wind was the main dispersal mechanism.

The main dispersal features highlighted in this paper are particularly relevant to other species with similar life-history and dispersal behaviour, in particular other invading gracillariidae (e.g. *Phyllonorycter leucographella, Parectopa robiniella, Phyllonorycter platani*) on other exotic plants. Although *C. ohridella* shows a particularly high growth rate causing spectacular damage compared to these other species, their dispersal may show similar patterns, as they also overwinter in the leaves of their host plant, and can therefore be transported over long-distance (as dead leave, or within living plants). Hence their pattern of dispersal may have much common features with that of *C. ohridella*. Our results also demonstrated that pheromone trapping could be performed as a suitable tool for monitoring and measuring dispersal rates of the species at the city or regional level (Augustin et al. 2004), which could also apply to other Gracillariidae species, provided that sex-pheromones are identified.

In addition, several results highlighted in this review can be generalized to many invasive organisms. In particular, the stratified dispersal pattern of *C. ohridella* where human-mediated long-distance spread combines with local dispersal is becoming considered as a norm in invasion ecology and characterizes the spread of many other invasive insects (Liebhold and Tobin 2008). Another generalizable result is the relationship we found between the probability of long-distance dispersal events and human population density. Since the world explorations of the 15th century, humanity became the dominant vector of invading species. Some introductions are deliberate (Baker 1986), sometimes first for biological control (Simberloff and Stiling 1996), but most are accidental (Baker 1986; Ruiz et al. 2000). Since the intense development of large volumes of commercial exchanges on a worldwide scale in the 1980s, the probability of invasion has considerably increased. Human populated areas and their suburb areas concentrate many of those commercial activities and therefore form potential points of entry and redistribution for many invasive alien species. In addition, the susceptibility of ecosystems to biological invasions is generally higher in human-disturbed ecosystems (Sakai et al. 2001), which also results in a general correlation between human population density and the probability of establishment.

Acknowledgements

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