



Understanding flying insect dispersion: Multiscale analyses of fragmented landscapes

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ABSTRACT

A multiscale model was developed to simulate the rate of landing of a winged insect, the grain aphid, *Sitobion avenae* F. At a large scale (kilometric scale), it is convenient to use a deterministic model of their dispersion, based upon diffusion–advection–reaction partial derivative equations. At a small scale (hectometric scale), the process of site selection ('landing') is only partially understood, but is known to include the perception of field colour and landscape characteristics. Several hypotheses on aphids' behaviour were tested to simulate the rate of landing: the simulation was done by a cellular automata submodel under five different hypotheses on the precise organisation of the landing behaviour. We found a strong interaction between the effect of the proportion of wheat crops in the landscape and their spatial organisation. The spatial correlation between the places occupied by wheat crops appears crucial to determine the global rate of landing of the aerial insect stock. The shape of the response surface of landing rate against the proportion of surface occupied by wheat, and the spatial autocorrelation of wheat plots, appears very regular and relatively simple to model by ad hoc mathematical functions. Large scale simulations using the results of the small scale model in a diffusion–reaction equation solved numerically, showed that, on a real landscape extracted from a GIS on the whole Brittany region (western France), the spatial pattern of the aphid landing is sensitive to the hypothesis tested on their landing behaviour. This hierarchical modelling combining two different approaches at two different scales (mathematical deterministic equations on a large multi-kilometric scale, and partly stochastic cellular automata on a small hectometric scale), requires methods to validate its results in the field, in the framework of a decision support system. Such a multiscale model has a wide field of application including not only plant protection but also management and conservancy of animal species dispersing by flight.

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1. Introduction

Multiscale analysis in ecology is often viewed as reflecting a natural hierarchy of ecological scales (Kent et al., 2011; Singh et al., 2011). It may also reflect merely a convenient nesting of modelling scales based on different knowledge of the ecological processes at different scales. We give here an example of such a nesting and of its use.

At large scale, the aerial spread of flying insects is well described by mathematically explicit diffusion–advection–reaction equations. The reaction–diffusion equations were introduced by Fisher (1937) and Kolmogorov et al. (1937) with homogenous coefficients and are now commonly employed to describe spatially explicit biological invasions e.g. Berestycki and Rossi (2008), Murray (2003), Okubo (1980), Shigesada and Kawasaki (1997). Diffusion is suitable to describe the free flight of small insects in a weak or null wind. Advection is convenient when the wind is stronger and trails the insects in its direction. The reaction term represents the local population dynamics

which is strongly influenced by emigration and immigration resulting from take-off and landing of the aerial stock of insects.

These latter are behavioural events which are themselves determined at a local scale (i.e. field site selection), typically ranged between some decametres and some hectometres. Landing, especially, is known to be governed by two mechanisms: a phototaxis (Moericke, 1955) and/or an optomotor reflex (Kennedy and Booth, 1963). Aphids are primarily attracted by surfaces reflecting a large proportion of long-wave energy (e.g. green or yellowing fields), and secondly by colour contrasts in the landscape due to field edges and alternation of different crops.

This scale mis-match problem is associated with the emergence of a macroscopic pattern (the rate of landing of a stock of winged aphids), from individual behaviours (the landing decisions). The multiscale modelling approaches cited above (Kent et al., 2011; Melbourne-Thomas et al., 2011; Singh et al., 2011) are increasingly used to address such issues. We therefore tried to find the rate of landing function through a microscale algorithmic subpopulation model.

Here we focused on the grain aphid *Sitobion avenae*, a major agricultural pest in Europe (Dixon, 1987; Fiévet et al., 2007; Pierre and Dedryver, 1984) causing substantial damage to wheat by sap feeding in spring. Aphids reproduce parthenogenetically from spring to

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autumn. During this period they produce alternatively wingless and winged adult morphs. Wingless ones are mainly adapted to the exploitation of host plants in situ when winged ones are adapted for dispersion of the species. Transition from wingless to winged morphs is due to damaging environmental conditions like resource decrease or overcrowding (Dixon, 1987). Aphids can disperse over short or medium distances (several kilometres) by active flight (diffusion) (Llewellyn and Loxdale, 2003; Loxdale et al., 1993) and/or over long distances by passive flight, born by wind streams (advection) (Hardie, 1993; Loxdale et al., 1985; Simon et al., 1999).

The core aim of the work described in this paper was to develop a multi-scale model of the landing rate of the grain aphid using diffusion–reaction for large scale and cellular automata (Banks, 1970; Codd, 1968; Von Neumann and Burks, 1966) for small scale.

2. Methods

Aphid migration and multiplication at the country scale, were represented by a two-dimensional diffusion–reaction system of equations. Advection by strong winds was not modelled in this initial work.

A discretisation of this macroscale model was undertaken. The macroscale unit (5 km × 5 km) was divided in 20 × 20 microscale cells. The rules for landing rate were defined for each unit using a microscale system. The solution of this microscale system was carried out with cellular automata (Banks, 1970; Codd, 1968; Von Neumann and Burks, 1966). Cellular automata are open and flexible discrete dynamic models, consisting in a grid divided into many ‘cells’ which can have different status. The status of the cells is updated simultaneously using a rule which represents relationships between each cell and its neighbourhood. By repeating this procedure, it is possible to simulate many kinds of complex behaviours.

Ad hoc mathematical equations derived from the simulation results were used to link the microscale and the macroscale models. The coefficients of the macroscale system were then defined and a comparison between the different landing rules undertaken.

2.1. The macroscale model

In this system, state variables are, A , the wingless aphids density at field level and, C , the aerial winged aphids density (Eq. (1)), in the two dimensional spatial domain Ω :

$$\begin{cases} \frac{\partial A}{\partial t} = r[\alpha_1 C + A(1-\alpha_2)] \\ \frac{\partial C}{\partial t} = D\nabla_x^2 C + C(1-\alpha_1) + A\alpha_2 \end{cases} \quad (1)$$

where:

- $A(t, x)$ and $C(t, x)$ correspond to the population density of wingless and winged aphids at time t and at position $x = (x_1, x_2)$
- $\alpha_1(t, x)$ is the aphids landing rate with $0 \leq \alpha_1 \leq 1$
- $\alpha_2(t, x)$ is the aphids take-off rate with $0 \leq \alpha_2 \leq 1$
- $r(t, x)$ is the observed growth rate, with $-1 \leq r \leq 1$.
- $D(t, x)$ is the diffusion and $\nabla_x^2 = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2}$.

For initial and boundary conditions (Eq. (2)):

$$\begin{cases} C(0, x) = C_0(x) \\ A(0, x) = A_0(x) \\ C(t, x) = 0 \quad \forall (t, x) \in \Gamma_1 \\ A(t, x) = 0 \quad \forall (t, x) \in \Gamma_1 \\ D\nabla C(t, x) \cdot \nu = l \quad \forall (t, x) \in \Gamma_2 \\ \nabla A(t, x) \cdot \nu = l \quad \forall (t, x) \in \Gamma_2 \end{cases} \quad (2)$$

where:

- $C_0(x)$ and $A_0(x)$ are initial conditions of $C(t, x)$ and $A(t, x)$ with $C_0(x) \geq 0$ and $A_0(x) \geq 0$ on Ω .

- Γ_1 represents marine borders and uncrossable mountains
- Γ_2 represents land frontiers and crossable mountains
- $\Gamma_1 \cup \Gamma_2 = \Gamma$, $\Gamma_1 \cap \Gamma_2 = \emptyset$, where Γ is the boundary domain
- ν is the unit outward normal to Γ_2 on Ω .

In this paper we focused on the landscape properties of the north-western French region of Brittany which has a prominent polyculture and fields of varied sizes. We used field data from 2009 derived from the European Common Agricultural Policy (CAP) to provide the arrangement of cereals in the fields. We solved partial differential equations using a numerical scheme, having a discretisation in time and space (macroscale unit). For computational issues, discretisation of the macroscale system leads to a space step K equal to 5 km and a time step H equal to 24 h. For each unit, p was the proportion of cereals $p \in [0, 1]$.

All the coefficients of our model were obtained deterministically using field data except the landing rate α_1 . The shape of this coefficient is linked to the nature of the aphid landing phase that can only be represented at a very small scale (a group of fields). In order to model the mechanism of aphid landing, we defined a microscale system corresponding to the description of aphid population dynamics in one macroscale unit.

2.2. The microscale model

Each unit of the macroscale system, named B , was divided into 400 cells b_i^j , i and j representing the position of a cell in the unit. Hence the microscale space step is k , with $k = 0.25$ km; and b_i^j was considered binary with $b_i^j = 1$ if it contained cereals and $b_i^j = 0$ otherwise. At this small scale, we considered two subspaces: an aerial compartment containing winged aphids and a field compartment containing wingless aphids. The time step of the macroscale system H was divided in many microscale time steps h . In a given unit, initial conditions (A_0 and C_0), growth rate r , take-off rate α_2 and diffusion D were constant and homogenous; and at the initial time h_0 , we considered A_0 as null.

During an aphid flying period, there are in average seven repetitive flights lasting more than 1 min (Kennedy and Booth, 1963). However, the first uninterrupted flight lasts about 75% of the total time spent flying (Johnson, 1969). According to the literature, long-term landing is unlikely to happen after the first flight. Hence, we considered that this first flight is a transit flight between cells and is not to be included in our microscale model. For that reason, we only modelled the six last subsequent flights.

We applied the formula given by Shigesada and Kawasaki (1997) to estimate precisely the diffusion coefficient D , generally used for approximation of the diffusion coefficient (for example by Robinet, 2006 and Roques, 2004):

$$D = \frac{d^2}{\Pi h} = \frac{v_{\max}^2 h}{\Pi} \quad (3)$$

where d is the mean displacement by an individual's ‘random walk’ during time h . The speed of aphid movements was set to be the aphid flight speed estimated to be 0.9 m/s (3.24 km/h) (Compton, 2002) which leads to the diffusion coefficient equaling 0.223 km²/h².

According to estimation from Johnson (1969), the microscale time step h equals 4 min. During h , the growth rate and the take-off rate are negligible and are set to 0. For each macroscale unit, we needed to define the disposition of cereals linked to their proportion of the cropping area. There are several kinds of indices to define correlation between different patches (Gardner et al., 1987; Keitt, 2000; and Roques and Stoica, 2007). We utilised an index of correlation between two different patches (developed by

Suzuki and Sasaki, 2011), denoted as η , which varies between -1 and 1 :

$$\eta = \frac{\text{Cov}(b_i^j, b_i^j)}{\sqrt{\text{Var}(b_i^j)\text{Var}(b_i^j)}} = \frac{x_{ss}(0) - (1-p)}{p(1-p)} \quad (4)$$

where $x_{ss}(0)$ is the probability of two cereal cells to be adjacent in a Von Neumann neighbourhood. Spatially correlated configurations for a non zero η were generated by a Metropolis Hastings algorithm by optimizing η (Suzuki and Sasaki, 2011).

The link between aerial and field domains is established with five hypothetical landing rules for β_1 . We also specified a criterion of landing quality which is defined as the proportion of landing aphids over the whole simulation:

$$\beta_{1i}^j = \frac{\sum_{k=h_0}^{h_{final}} A_k}{\sum_{k=h_0}^{h_{final}} A_k + \sum_{k=h_0}^{h_{final}} C_k} \quad (5)$$

We supposed 5 hypothetical rules for β_1 :

- β_1^1 : aphids land once they have perceived a cereal field, independently of η
- β_1^2 : the landing rate is linked to landscape discontinuances (e.g. field edges). If flying aphids are over a cell b_i^j with cereals ($b_i^j = 1$) then the landing probability increases with the number of b_i^j neighbour cells without wheat. For example, if b_i^j has only one neighbour cell without wheat then β_1^2 equals $1/4$, $\beta_1^2 = 1/2$ if there are 2 neighbour cells without wheat, and so on... If wheat constitutes 100% of the unit ($p = 1$), there is no aphid landing ($\beta_1^2 = 0$ for all cells of the unit).
- β_1^3 : in opposite of β_1^2 , the landing rate is inversely linked to landscape discontinuances. If an aphid flies over the cell b_i^j with cereals ($b_i^j = 1$) and there is only one neighbour cell without wheat then they land with a probability of $3/4$, $1/2$ if there are 2 neighbour cells without cereals, and so on...
- β_1^4 : if $p \leq 0.5$ the landing rule considered is item 2: β_1^2 and else if $p \geq 0.5$ the landing rule considers the item 1: β_1^1 .
- β_1^5 : if $p \leq 0.5$ the landing rule considered is item 3: β_1^3 and else if $p \geq 0.5$ the landing rule considers the item 1: β_1^1 .

In order to determine the effect of the landing rule on the criterion of landing quality, numerical experiments are undertaken for the microscale model, and the five β_1 rules implemented.

The experimental design incorporated a uniform contrast step variation of the proportion of cereals p and the coefficient of correlation η : $p \in [0,1]$ per 0.1 step and $\eta \in [-1,1]$ per 0.1 step. The resolution of the microscale system was carried out with cellular automata (Banks, 1970; Codd, 1968; Von Neumann and Burks, 1966) using Netlogo software program (Wilensky, 1999).

2.3. The link between the macroscale model and the microscale model

From the macroscale model to the microscale model, the landing rate α_1 is defined as the response function of the criterion of landing quality depending on p , η and β_1^j , $j \in \{1,2,\dots,5\}$, rule. In order to explore the relationship between the response (α_1) and the explanatory variables (p and η), Generalized Additive Models (GAM, Hastie and Tibshirani, 1990) have been used. These are statistical models for blending properties of Generalized Linear Models (GLM, McCullagh and Nelder, 1989) with additive terms. They have the advantage of being able to deal with linear, highly non-linear and non-monotonic relationships between the response and the set of explanatory variables using smoothing functions (Zuur et al., 2009).

After exploring the shape of the relation between α_1^j , β_1^j , p and η , we constructed an ad-hoc non-linear model. The regression model had the form $\beta_1^j = f(p_i, \eta_i, Q) + \varepsilon_i$ for $i \in [1, n]$, where β_1^j are responses corresponding to the landing rule, f is a known function, p_i the proportion of cereals, η_i the autocorrelation term, Q the parameter vector and ε_i are random errors. The unknown parameter vector Q was estimated from the data by non-linear least squares.

3. Results

From each landing scenario within the microscale simulation, a clear bivariate function emerged. Despite the random arrangement of wheat fields in the macroscale units, the resulting landing rate, as a function of spatial autocorrelation and wheat proportion, was rather smooth. The points obtained were easily approached by ad hoc functions with very high determination coefficients. All landing rules but one (β_1^2), resulted in a monotonic relation between wheat proportion and landing rate. In three cases the rate of landing reached or almost reached 1 when $p = 1$ (rules β_1^1 , β_1^3 , β_1^4) while, in two cases it stayed lower than 1 (β_1^2 , β_1^5). The landing rate was also sensitive to the autocorrelation coefficient and its response was sigmoidal and approached by an arc-tangent function. The inflexion point is obtained for zero correlation. Practically, the effect of the autocorrelation coefficient was to group wheat units in large areas ($\eta \approx 1$), randomly on the domain ($\eta \approx 0$) or in a quasi regular arrangement ($\eta \approx -1$). This simulates different farming structures: very large fields in intensive wheat production areas at one end, and dispersed small fields in polycultural systems at the other.

3.1. Relationship between the response variable, the proportion of wheat, and spatial autocorrelation

In order to study the landing rate, 5 models were defined, one for each landing rule β_1^j . For each rule, we generated artificial landscapes with a variation of two parameters: the proportion of wheat p and the spatial autocorrelation index η ; p from 0 to 1 by a step of 0.1 and η from -1 to 1 by a step of 0.1.

$$\text{Model 1 } \alpha_1^1 = \log(a_1 + a(-p^2 + p) \text{atan}(k\eta) + a_2 p)$$

$$\text{Model 2 } \alpha_1^2 = \frac{a_4 \exp(p) + a_5 \log(1 + p)}{1 - a_1 \text{atan}(k\eta) + \exp(a_2(p - a_3))}$$

$$\text{Model 3 } \alpha_1^3 = \log(a_2 + a_1(p - p^2) \text{atan}(k\eta)) + a_3 p$$

$$\text{Model 4 } \alpha_1^4 = \log(a_2 + a_1(p - p^2) \text{atan}(k\eta) + a_3 p)$$

$$\text{Model 5 } \alpha_1^5 = \begin{cases} \log(a_2 + a_1(p - p^2) \text{atan}(-k\eta) + a_3 p) & \text{if } p < 0.5 \\ \log(a_2 + a_1(p - p^2) \text{atan}(k\eta) + a_3 p) & \text{if } p \geq 0.5 \end{cases}$$

where p = the proportion of wheat, η = the spatial arrangement of wheat and a_1, a_2, a_3, a_4 and k are the coefficients; $\log(\cdot)$ is the logarithmic function and $\text{atan}(\cdot)$ is the arctangent function. All these models explained a large proportion of variance with a goodness of fit r^2 greater than 95% (Table 1). See also Figure S1 in the supplementary material.

3.2. Landing rate in the macroscale model

We observed a heterogeneous distribution of the wheat fields in Brittany: the main landing fields are located in the mid southeast and mid northern parts of Brittany. The different models above resulted in different spatial distributions of the landing rate. The

Table 1
Model fits for $\alpha_j^i, j = \{1, \dots, 5\}$.

Model	df	AIC	BIC	LogLik	r^2
α_1^1	4	-988.2113	-971.7198	499.1057	0.9949
α_2^2	6	-708.8230	-685.7348	361.4115	0.9976
α_3^3	4	-677.5959	-661.1043	343.7979	0.9823
α_4^4	4	-953.0862	-936.5946	481.5431	0.9895
α_1^5 if $p < 0.5$	4	-360.5057	-348.5956	185.2529	0.9496
α_1^5 if $p \geq 0.5$	4	-598.0683	-584.1308	304.0341	0.9695

final result was thus sensitive to the chosen landing rule. Roughly speaking, the spatial distributions obtained could be classified in three categories (see also Figure S2 in the supplementary material):

1. With the function α_2^2 the landing distribution is very similar to the proportion of wheat.
2. With functions α_1^1 and α_4^4 the landing rate is slightly higher than the proportion of wheat. This was due to the negative convexity of both functions which favours landing for medium ranges of p .
3. With functions α_3^3 and α_5^5 the landing rate was clearly lower than the wheat proportion. This is mainly due to the convexity of the two functions, especially in the range of negative spatial correlations. As a consequence, the landing concentrates only on areas of Brittany where the proportion of wheat was both the highest and the more aggregated.

To summarise, the result of these resolutions of the macroscale model depends strongly on the sign of the convexity of the response functions.

4. Discussion

The fitting by empirical functions was sufficient to achieve the goals of the present modelling, although the case where $p > 0.5$ is very unlikely in Europe where crop rotations are at least biennial and where the largest size of a field seldom exceeds 1 km². A strong decrease of landing for high wheat proportions as described by the rule β_2^2 seems also biologically unlikely.

We found in this study, a well-known effect of transfer functions: the key effect arises from their convexity (a classic effect of Jensen's inequality). When considering the shape of the fitted functions, α_1^1 , α_2^2 and α_4^4 were always negatively convex with respect to p , for all values of η . Function α_3^3 was positively convex, whatever η in the range $0 \leq p \leq 0.5 \cap -1 \leq \eta \leq 0$, and negatively convex outside this range.

The sensitivity of the macroscale model to the convexity of the landing rate function provides a guide for further investigations attempting to validate such large scale models. Obviously, we have to study the shape of this function. Although the task is awkward, we have some tools which can be used later to achieve it. Since 2001, we have at hand (Plantegenest et al., 2001) a comprehensive deterministic model able to estimate the maximum rate of increase of the aphids in the fields, and by difference, the rate of local immigration. We also have at hand a database associating aerial aphid catches (Hullé et al., 1987) and field population dynamics of aphids (Ciss et al., 2011). We can therefore study the relationship between aerial captures and the estimated immigration. Moreover, the fields under study were easily characterised by their local environment in a 5×5 km². Information on proportion and distribution of wheat fields at such a spatial resolution is readily available, for example from low level satellite images, which should allow us to determine p and η for our model. Contrasted replications of the observations in different geographic contexts, would further help to determine the adequate function.

These results clearly showed that aphid landing rates at a regional scale could strongly differ in function of the biological hypotheses made on their landing behaviour at field scale. Aphid landing

behaviour is very difficult to study and available results are scarce and sometimes contradictory (Irwin et al., 2007). The two main hypotheses on the causes of aphid alighting are attraction by long-wave light from the crops, and optomotor reaction due to perception of wave-length changes linked to alternation of plant and soil or fields and edges. However, since the work of Kennedy and Booth (1963), there is a consensus for considering that these two hypotheses are not antagonistic and refer to successive steps of the same complex phenomenon. If this is true, α_2^2 and α_4^4 are probably closer to biological reality than the other responses, particularly α_3^3 and α_5^5 .

In the past, some authors opposed formally defined mathematical models and numerical algorithmic models. This opposition took a special strength with the development of the Individual Based Models (IBM), whose advocates insisted on their bottom-up feature as compared to the top-down approach of the mathematical population models (DeAngelis et al., 1994; Grimm, 1999). In this study, we combined both, exploiting an algorithm to describe a semi-complex ecological behaviour and replacing its results in a mathematical model susceptible of numerical resolution and mathematical analysis. This was done at two different ecological scales, a nesting increasingly required in the analysis of complex systems.

The present work is part of research on modelling the dispersion of grain aphid *S. avenae* in relation to temperature, host plant phenology and global warming. Ultimately, we plan to use this global model, by integration with long term national survey on winged and wingless aphids (Agraphid network of France and neighbourhood), in order to estimate the validity of all its parameters, including the landing rate.

In a more general context, aerial dispersal, i.e. the movements of winged organisms away from their parental source (Nathan, 2001), has widespread consequences on the spatial ecology of many animal species, especially those inhabiting ephemeral habitats, whose success strongly depends on their ability to colonize new patches and to subsequently multiply. As a consequence, taking into account dispersal processes is necessary for species management and their conservancy (e.g. birds and beneficial insects), as well as for crop protection against plant feeders. However, dispersal often remains a 'black box' in our knowledge of many animal species, due to its difficulty of direct assessment. In the above study, we exemplify how mathematical modelling of one dispersal step (landing) may provide an alternation for studying of insect dispersal in the absence of direct observation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecoinf.2012.11.004>.

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