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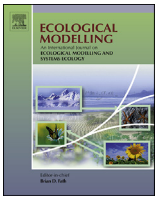

Perception-based foraging for competing resources: Assessing pest population dynamics at the landscape scale from heterogeneous resource distribution

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ABSTRACT

Resource distribution, through its effects on individual foraging and survival, drives population dynamics across the landscape. In an agricultural context, resource distribution is therefore a key information in assessing whether or not a pest population may invade and persist in a given environment. Addressing this issue by means of numerical exploration requires a population model with a sound dependence on the landscape. In this paper, we demonstrate that this dependence is effectively secured by a multi-scale description of the population. We derived a reaction–diffusion population model accounting for two individual-scale processes determining resource utilisation: (1) resource perception as a determinant of mobility and (2) energy supply management as a determinant of survival. In this model, the distribution of two competing resources (feeding and laying sites) affects the spatial population dynamics of a dipteran pest through a heterogeneous dispersion of the individuals and a metabolic currency. We conducted a global sensitivity analysis to evaluate the impact of both individual-scale processes on the population dynamics. This exploration demonstrated the biological relevance of the model according to field observations and theoretical expectations. Our key finding is that resource perception and energy supply management appear as significant as the demographic component regarding the resulting dynamics of the pest. Building on its acute multi-scale landscape dependence, this model may be particularly useful for investigating the putative relationships between agricultural landscape features and pest outbreaks.

1. Introduction

Following the agroecological advances on ecological intensification, segments of agriculture are slowly considering the switch towards alternative crop protection strategies, less reliant on chemical inputs (Wezel et al., 2014; Spiertz, 2014). In this context, understanding ecological services and disservices is a key component of crop protection and yield preservation. Regarding pest management, developing such alternative methods requires extensive knowledge of pest colonisation processes and persistence strategies, as well as determining relevant spatial scales for action. Because insect pest populations are known to be greatly influenced by landscape features (see *e.g.* Jonsen and Fahrig, 1997), experimenting crop protection strategies carries the ecological engineering endeavours at the agro-ecosystem scale. At this scale, levers for action consist in landscape modifications concerning *e.g.* crop rotation patterns, fields size and geometry or semi-natural habitat networks. In the field, such modifications would obviously come at great expenses for scarce repetitions. Ecological modelling can remove those hindrances by using coupled approaches of landscape and population models (as did Papaix et al., 2014; Le Ber et al., 2009; Retho et al., 2008). Such approaches enable one to test *in silico* the modifications of the landscape structure and composition in order to assess its putative relationship with the population dynamics it hosts. The critical point lies in ensuring the population dynamics model a sound landscape dependence.

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From a theoretical point of view, we consider pest distribution across the agricultural mosaic as an emerging pattern resulting from interactions between the pest and landscape features. Some of these interactions take place at the population scale and result in landscape dependent growth and death rates, carrying capacities or migration rates, *i.e.* variables typically encountered in continuous population models (see Shigesada and Kawasaki, 1997; Okubo, 1980). Still, other interactions such as resource perception, energy allocation, spatial memory or optimal foraging strategies, inherently occur at the individual scale and can be determinant of the pest population distribution. Including them in population models is one way to provide an additional landscape responsiveness. Nevertheless, combining individual and population scales is not straightforward and often strains the classical modelling frameworks. Individual scale processes usually conform best to Lagrangian models of which the focal unit is particular and exhibit stochastic behaviours. However, regarding insect pest management we are generally looking for patterns of space-use resulting from more ‘place-based’ models. These Eulerian models can be spatialised through partial differential equations (Skellam, 1951; Okubo, 1980) but usually do not account for lower-scale (*e.g.* individual scale) processes because of their stiff mathematical descriptions. Recently, mechanistic models (see for example Potts et al., 2014; McKenzie et al., 2012; Moorcroft and Lewis, 2006) provided significant advances filling the gap between animal movements and population distributions through space-use patterns. As they focus on ecological equilibria such as home-range patterns, they usually are studied from a steady-state angle. This kind of approach inspired us working with mechanistic descriptions of lower-scale processes. However, steady-state resolutions are fairly unsuitable for insect pest management in which population distributions are dealt with as seasonal invasion processes (as they frequently consist of seasonal colonisations) which are inherently dynamic (Fagan et al., 2002). Apart from those mechanistic approaches, individual-scale processes are usually assumed to be of lesser concern in the spatial population dynamics, or often ignored because of their complex links with landscape features and their non-intuitive integration into population models. Yet numerous studies pledge for the convergence of such population and individual processes in multi-scale approaches (Turchin, 1991; Mueller and Fagan, 2008).

We propose to account for foraging processes and their determinants in order to ensure the population model a strong dependence on the resource distribution and hence, on the landscape. In heterogeneous environments, foraging relies on informed movements requiring both perceptive and navigational abilities (Nathan et al., 2008). It determines, among other things, how individuals aggregate in space (*i.e.* habitat selection) depending on resource distribution and foraging strategies (see *e.g.* Olsson and Bolin, 2014). Quality and distribution of resources used by a given species can be highly heterogeneous over space and time. Therefore we developed a spatialised approach accounting for landscape features considered as resource locations or not. The landscape and the population are thus mediated *via* foraging. The type of resources searched is often closely related to the energy supply of the forager, dealt with as a latent metabolic variable. In the present study we focused on feeding and laying resources, of which the utilisation greatly influences the energy supply of an individual. In our approach, foraging is therefore composed of two processes: resource perception and energy supply management. Foraging has already been modelled interacting with perception to explain population distributions (Vuilleumier and Perrin, 2006) and with metabolic currency (of which energy supply is a theoretical example) to explain individual foraging strategies (Houston and McNamara, 2014). Combining these processes in a landscape-based approach brings us closer to an emerging theoretical field: metabolic landscape ecology. In such a multi-scale context, we ought to dispose of a population model highly responsive to landscape structure and composition, thus providing an insightful tool for further landscape oriented studies.

We applied our multi-scale approach to an insect pest as a case study: the cabbage root fly *Delia radicum* L. (Diptera: Anthomyiidae), an important pest of Brassicaceous crops (cauliflower, cabbage, radish, turnip, etc.) (Finch, 1989; Josso, 2012). *D. radicum* is a very common species in temperate regions of the holarctic zone (Sondgerath and Muller-Pietralla, 1996). Its biology has been described in earlier papers (*e.g.* Finch and Ackley, 1977; Lepage et al., 2014) but some simple and important aspects can be briefly outlined. In our study area, this insect (Holometabola, *i.e.* which develops through distinctive larval, pupal, and adult stages) is active from April to October. In April, adult flies emerge from diapausing pupae, the resistant stage for the cold season. Adults oviposit (*i.e.* lay eggs) on the ground close to plant stems or directly on stems, and after hatching, larvae develop inside the root causing damage. Before ovipositing in Brassica crops, adults need to mate and to feed on flowers from hedgerows and field-banks (Coaker and Finch, 1970; Josso et al., 2013). Both resources affect the energy supply either positively (*i.e.* feeding) or negatively (*i.e.* ovipositing) and hence, impact population dynamics. We used spatialised population data obtained from a two-year survey (2010–2011) in an agricultural area of Brittany, an important cole crop production region in northwestern France where the cabbage root fly is a very problematic pest. The locations of the resources of interest were georeferenced allowing us to use a landscape-based approach relying on geomatic information. Fig. 1synthesises the scales involved in the framework.

We built a stage-structured demographical model composed of 5 Ordinary Differential Equations (ODE) whose parameters were estimated from literature data (see details in Appendix A). We spatialised it to account for agricultural landscape heterogeneity and adult fly ability to disperse through a diffusion term (thus we have one Partial Differential Equation, PDE, and four ODE). Then we accentuated its landscape dependence *via* two individual-scale processes of resource utilisation. First we introduced perception kernels of landscape features (here, resource locations) to define a spatially heterogeneous diffusion. Secondly, we added an energetic dimension in which adult flies evolve depending on the landscape element (*i.e.* feeding or oviposition sites) they are located on, thus simulating the evolution of individual energy supply according to resource exploitation. Therefore two kinds of individual-landscape interactions, namely resource perception and energy supply management, were included as additional driving forces of the spatial population dynamics. We address the following question: can we consider this perception-based foraging as a determinant of pest spatial population dynamics regarding our biological model? If so, the mechanistic descriptions of both the individual landscape-based processes would factually ensure our model an additional responsiveness to the landscape substrate.

Fourteen non-experimentally identified parameters were tuning the perception process, the energy supply management and the demographical death rates of the 5 development stages. Their effects on specific responses of the model (regarding both pest reproductive success and model predictions adequacy to data) were studied by the means of a Global Sensitivity Analysis (GSA) (Morris, 1991; Saltelli et al., 2004) providing rankings of importance of the parameters and hence, ranking of the processes they tune. The significance of the individual-scale processes were tested and discussed. To go further, some of the model properties were assessed and discussed after comparing the spatial configurations of the elementary effects (*i.e.* the outcome of the GSA) depending on the nature of the response variables using a procrustes analysis (Klingenberg and McIntyre, 1998).