



Foraging as the landscape grip for population dynamics—A mechanistic model applied to crop protection



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ABSTRACT

Individual ability to survive and reproduce is driven by the foraging for various kinds of resources. In agricultural landscapes, accounting for the distributions of the resources foraged by a pest can help in assessing whether or not its population may damage crops. Such outcome results from landscape-dependent processes occurring at several biological scales. We present a reaction–advection–diffusion population dynamics model accounting for the foraging process as a driver of an insect pest redistribution in space. It is based on three individual-scale components: resource perception, energy supply management, as well as their optimal interaction determining the optimal foraging strategies. These elements depend on the distribution of two competing resources (namely, feeding and laying sites) affecting (resp. positively or negatively) the energy supply of an insect pest. Here, resource distribution affects the population dynamics through (1) directed motions towards needed resources in response to their perception, and (2) a metabolic currency materialised by a limited laying ability and an additional death by starvation. Building on its multiscale and mechanistically enhanced sensitivity to landscape modifications, we applied this calibrated tool to a theoretical landscape planning problem. Eventually, the model appears as an efficient tool to achieve pest control, used to propose landscape arrangements more resilient to pest outbreaks.

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1. Introduction

The recent incentives for modern crop protection slowly direct pest management towards less chemically driven practices (European Commission, 2013). Diverting our focus from symptomatic relief towards more integrated protection strategies requires a deep understanding of the field colonisation processes governing pest dynamics.

Pest abundance in fields is an intricate output of the agro-ecosystem. It results from different spatial structures (Jonsen and Fahrig, 1997; Ostman et al., 2001; Josso et al., 2013), whose effects apply on multiple scales (Thies et al., 2003; Gonthier et al., 2014), and which generally cause our insights to be too contextual (Veres et al., 2013). Depending on the pest species, some landscape features can be fairly identified as refuges, overwintering sites, laying sites, feeding sites, etc. Their relative abundances have obvious

effects on pest distribution as they determine the available habitat quantity (Maisonhaute et al., 2010; Jonsson et al., 2015). More interestingly, the actual benefit induced by habitat units is modulated by their spatial arrangements, as they offer differential reachabilities for dispersing species (Haenke et al., 2014; Olsson et al., 2015). In this perspective, the spatial rearrangement of land-covers is often seen as a lever for action to control species abundances with regard to landscape compositional constraints (see e.g. With and King, 2001; Roques and Hamel, 2007; Polasky et al., 2008). The landscape features composing the pest habitat are not likely to be encountered at small spatial scales (such as the field) in sufficient and meaningful spatial distributions. The landscape, precisely the agricultural mosaic, is therefore the relevant working scale to design pest resilient agro-ecosystems that can minimise the use of pesticides (Tschardt and Brandl, 2004). Unfortunately, experimenting crop protection strategies across the landscape can only be done at great expense, with scarce replicates (see e.g. Marrec et al., 2015). In such context, *in silico* approaches can help in getting insightful responses from the agro-ecosystem (e.g. Retho et al., 2008; O'Rourke and Jones, 2011; Papaix et al., 2014).

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Our understanding of the pest impacts on crops, a first step towards their biocontrol, can benefit from population-scale models (Fagan et al., 2002). Regarding insect pests, our focus in this study, the damage caused by one individual are negligible. The population distribution in space is therefore a key determinant of the subsequent yield losses, and hence, the most intuitive proxy for them. Moreover, the damage on crops (often caused by the development of larval stages of the pest) and the pest population density follow entangled dynamics, sustaining each other along the pest activity season. In a nutshell, predicting the pest impact on crops is clearly a matter of population dynamics.

Spatially explicit population dynamics models have been useful for decades now, accounting for the effects of spatial substrates on dispersing species (Okubo, 1980; Shigesada and Kawasaki, 1997; Turchin, 1998; Cho and Kim, 2013). They generally consist of partial differential equations (for continuous time simulations) and some studies have focused on the landscape scale (e.g. Richter, 2008; Tyutyunov et al., 2008; Potgieter et al., 2015; Bourhis et al., 2015; Parisey et al., 2016). Such mathematical tools instantiate population densities across space and time, which is very convenient dealing with insect pests and their inherently dynamic and spatially structured field colonisation processes (Bianchi and Werf, 2003; Vinatier et al., 2011; Sivakoff et al., 2012; Ferreira et al., 2014; Evans et al., 2015).

The spatial structure of the simulated populations mostly results from the landscape dependence (or more broadly speaking, the spatial substrate dependence) of the hosted process, *i.e.* the population dynamics. This is generally ensured by land-cover dependent demographic rates (e.g. Skellam, 1951; Soubeyrand and Roques, 2014; Potgieter et al., 2015; Parisey et al., 2016), or dispersing rates (e.g. Cho and Kim, 2013; Bourhis et al., 2015; Bengfort et al., 2016). These spatial dependencies result from meaningful land-cover classifications (often very simple like *habitat vs. non-habitat*) that influence the local behaviours of the population model. However, sometimes they might be too tangential (*i.e.* not so closely connected to the population biology, or not significantly driving it) and unable to properly account for the spatial determinants of the redistribution processes (*sensu* Turchin, 1998). This is especially so when the local behaviours of the population model should be driven by distant elements of the landscape. Theoretically, it is relevant to consider some of the redistribution processes from an individual angle. For instance, foragers redistribute themselves depending on the resources they need and the resources they perceive (Nathan et al., 2008). Their movements are consequently driven by the resource distributions in space and time (see e.g. van Moorter et al., 2013). Perception and internal state are substantially individual information that can hardly be scaled up and accounted for in population dynamics, even though they determine survival and reproductive efficiencies. Although they are rare, a few studies attempted to provide more individual-scale insights for population models, by including e.g. age-dependent diffusion (Okubo, 1980), starvation driven diffusion (Cho and Kim, 2013) or perception driven diffusion (Bourhis et al., 2015).

We propose here a reaction–advection–diffusion model of a theoretical pest population; a multiscale approach in which we developed an acute landscape dependence based on few parsimonious and mechanistic assumptions on individual redistribution determinants. We considered the foraging for two competing resources: feeding and laying sites, which have opposite effects on the survival and reproductive success of the pest. Building on the idea of age-dependent dispersal of the McKendrick-von Foerster equation (Okubo, 1980; Hastings, 1991; Murray, 2002), we included an additional dimension to our 2D-space model to account for the energy supply of the pest, one aspect of its internal state. Using a kernel convolution, we modelled the perception of resources, which here results in advective flows (*i.e.* directed

motions) towards both kinds of resource depending on the energy supply of the pest (non-local spatial dependence). Two coupled equations define a two-stage population dynamics with mobile and foraging adults, and sessile young causing damage on crops. We simulated seasonal dynamics starting from a stock of overwintering young individuals (standing for eggs, larvae and pupae, grouped indiscriminately), developing into foraging adults which go extinct by the end of the season. We believe this theoretical pest with coarse traits to fit a lot of the most common flying insect pests of the Northern hemisphere from the Diptera (e.g. *Delia radicum*, *Psila rosae*) or the Lepidoptera orders (e.g. *Pieridae* or *Noctuidae* families), all of which feed on nectariferous field banks and lay on crops (Finch, 1989; Harvey and Wagenaar, 2006). Eventually, resource perception and energy budget allow the model to encompass the pest foraging strategies, a critical individual-scale aspect of the redistribution process. The strategies emerge from an optimisation procedure, which brings our population model in the scope of optimal foraging theory.

We applied the model to a theoretical landscape planning problem where it is used to assess and limit the landscape exposure to pest outbreak. The focus is set on the spatial co-occurrence of the competing resources, which determines the actual benefit the dispersing species can get from its habitat. We developed a simple landscape model to instantiate resources aggregation gradients for given compositions (standing here for the agronomic productive constraints). Taking advantage of the mechanistically enhanced landscape dependence of the model, we tested our ability to propound parsimonious landscape modifications improving crops protection across the landscapes.

2. Multiscale and mechanistic model

2.1. Theoretical assumptions

A mechanistic model describes the behaviours of a system focusing on the mechanisms its underlying basic elements interact through. Mechanistic descriptions of the population spatial redistribution processes include numerous environmental determinants like e.g. terrain steepness and prey density (Moorcroft and Lewis, 2006; McKenzie et al., 2012), conspecific avoidance (Moorcroft and Lewis, 2006; Giuggioli et al., 2013), conspecific perception (Shcherbacheva and Kauranne, 2013) or pursuit of vegetation cover (Potts et al., 2014). Such approaches allow sound understanding of the ecological processes involved in animal movement. As those determinants apply mostly on the individual scale, their implementations in population dynamics model are not straightforward. Still, studies advocate for such multiscale endeavours (Turchin, 1991; Mueller and Fagan, 2008; Petrovskii et al., 2014).

We defined a population dynamics model which fits the coarse traits characterising a theoretical pest. We have in mind flying insect pests with a quite high dispersion power and directed flight, mostly from the Diptera and Lepidoptera orders (see e.g. Josso et al., 2013, for the characteristics of *Delia radicum* L.). It encompasses two stages (see Eq. (1)):

- the *young* stage includes indiscriminately the sessile stages of the pest, and is responsible for the damage on crops,
- the *adult* stage, foraging for resources, is here characterised by the mechanistic redistribution processes.

To simulate a seasonal dynamics, we specified a mortality increasing during the activity season, thus mimicking phenomenologically the increasing affluence of natural pest regulators and the

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