



Reply to comment

Multiscale ecology of agroecosystems is an emerging research field that can provide a stronger theoretical background for the integrated pest management

Reply to comments on “Multiscale approach to pest insect monitoring: Random walks, pattern formation, synchronization, and networks”

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We would like to thank all commentators for their insightful and thought-provoking commentaries [1–4] that also helped to further broaden the scope of our review [5] as well as to extend the list of references. We very much appreciate the positive comments on the relevance, timeliness and comprehensiveness of our work.

Meanwhile, we want to emphasize that multiscale pest monitoring is an emerging research theme rather than a well-established one. Indeed, although the existence and importance of multiple scales has long been known in spatial ecology [6,7], their quantitative investigation has not started in full until relatively recently, e.g. see [8,9] and references therein. For this reason, in our review [5], several relevant aspects might have been either just touched briefly or not mentioned at all. In particular, Rebecca Tyson [1] rightfully brought attention to the importance of transient environmental factors, e.g. temperature, that may control the build-up of pest populations. The effects of temperature on the rates of insect development through their life-stages and on insect population growth are well-known [10,11] and have been utilized in some empirical approaches used in Integrated Pest Management (IPM), e.g. in what is known as degree–day models [12,13]. Models of this type, however, are essentially based on average insect population

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numbers and hence leave largely unaddressed the natural spatial and temporal variability of the insect population between subsequent years and between spatial locations (e.g. agricultural fields) with similar properties. Meanwhile, such variability is typical both on the field and landscape scales, and can often be as large as two orders of magnitude, e.g. see Figs. 23 and 32 in [5] and Fig. 2 in [14]. Multiscale pest monitoring can provide a stronger theoretical background for IPM and to transform empirical models to theory-based models, and, at the same time, take a full account of population variability. The currently available theoretical approaches to the analysis, interpretation and modelling of trap counts (in particular those reviewed in [5]) are relatively straightforward to extend to the fully realistic case of a transient environment, provided sufficient information is available about insect response to all relevant factors. The latter may require additional field studies though, especially in the cases where these responses are not well understood.

Another relevant factor that was only briefly mentioned in [5] is taxis or advection, i.e. directed insect individual movement instead of (or additionally to) diffusive random motion. Directed movement may arise from an insect's behavioural responses to smell or light, or (for airborne species) can be a result of transport by the wind. Whilst the latter was shown to be important on the large (landscape) scale, resulting in the synchronization of population oscillations [5,14], the effect of taxis is likely to be important on the small (single trap) and intermediate (single field) spatial scales. As was pointed out by Luiz Rodrigues in his commentary [2], on the single field scale, many insect species are known to respond to gradients of smell or odour [15] or, more generally, to the gradient in density of a resource [16,17]. Their directed movement along or against this gradient may then lead to pattern formation because of the so-called convective instability [17,18]. The population aggregation emerging due to pattern formation may significantly decrease the accuracy of population size estimation [5,19,20]. On the single trap scale, good understanding of taxis becomes especially important in the case of baited traps (e.g. pheromone-baited or light-baited), that are widely used in practice, and this should indeed become a direction of future research. We mention here that modelling of trap counts by baited traps is more complicated compared to the pitfall traps considered in our review as the effect of the attractant may change insect movement behaviour in a complex way [21,22]. Also, the currently available biological data about the possible effect of an attractant on the insect's movement behaviour are often ambiguous and insufficient.

The need for efficient and reliable pest insect monitoring as a crucial component of IPM was further emphasized by Bernd Blasius [3] and Edward Codling [4] who also pointed out the importance of identification of the physical and biological processes involved. Consequently, this raises the subtle and sometimes controversial issue of an adequate mathematical framework to describe these processes. However, what are adequate mathematical models and/or techniques is not always clear and the whole notion of adequacy may depend on the benchmark information available [23]. Once the process has been identified, usually it is not difficult to build a mathematical model for it, though the model might not necessarily be unique, as different mathematical tools may sometimes be used. For instance, the same movement pattern can be described by a partial differential equation (i.e. the diffusion equation) and by an integro-difference equation (i.e. the master equation); e.g. see [5], Section 2.2. The task of choosing 'the right model' becomes a much bigger challenge when we know the pattern but only part of the information about the actual process behind it is available; the choice of an adequate model then may become context-specific.

Identification of the movement pattern and the choice of the model, in particular as it applies to individual insect movement, was the main point of the commentary by Edward Codling [4]. A situation similar to that outlined in the previous paragraph can arise in the analysis of trap counts collected by a single trap. It appears that the same time course of counts is generated by a population of insects performing Lévy flight (LF), and by insects performing Brownian motion (BM) with a time-dependent diffusivity; see [5], Section 2.5. LF is generally regarded as a movement pattern basically different from BM, yet when considered in the particular context of insect trapping, they appear to be equivalent. Surprising as it may seem, it evokes other recent results showing that, in many cases and for many different reasons, the pattern produced by an animal population performing BM may become indistinguishable from the pattern produced by animals performing LF [24–26]. Altogether, this seems to lead to a paradigm shift: it is not the movement pattern itself that matters but the ecological context where the movement is considered. One relevant context is given by an animal's behaviour, which is likely to become a core component of future movement studies. We also mention here that, although diffusive insect movement with time-dependent diffusivity has been observed in some field studies [17], it can also be used formally as a convenient mathematical framework to approximate Lévy flights [5].

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