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Conservation biological control at the landscape level: measuring and modelling

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Abstract: The incorporation of landscape management into Conservation Biological Control (CBC) strategies is a priority area of research but is hindered by a lack of harmonisation of the means to describe and measure the effectiveness of CBC, the organisms under focus and the landscape. This paper provides a set of recommendations that represents the consensus amongst experts of the ENDURE network. The most important data values that were identified were: pest population level; natural enemy population or % parasitism/predation; crop damage; estimate of mobility of study organisms (dispersal function) and non-explicit spatial measurements such as the proportion of the landscape offering resources and the connectivity between resource patches. For all these measurements, careful consideration should be given to the appropriate spatial and temporal scale of assessment. For analysis, we advocate an iterative use of modeling tools, particularly individual-based models, and statistical approaches: the former to understand mechanisms underlying the population dynamics of pests and their natural enemies in landscapes and the latter to characterize the observed patterns of these populations in a given landscape.

Key words: CBC effectiveness; pest ecology, resource patch, dispersal behaviour, spatial and temporal scales, individual-based models

Introduction

The incorporation of landscape management into Conservation Biological Control (CBC) strategies is a priority area of research (Ferguson and Alomar, 2010) but poses two important challenges. The first relates to the current diversity of descriptors, measurements and methodologies used in CBC studies, which limits the ability to compare and conduct meta-analyses of studies done so far. A second difficulty is that landscape dynamics classically described in landscape ecology are often not appropriate to pests and natural enemies living in agricultural environments. These factors limit the development of policy for encouraging landscape management for CBC to reduce the need for chemical pesticides.

In the present paper, we make proposals to facilitate CBC studies at the landscape level. We identify key measures that are needed to relate pest organisms to agricultural landscapes and discuss analytical approaches for understanding the regulating effect of landscape on pests.

Measuring CBC effectiveness

The need for meaningful assessment of CBC effectiveness must be the first consideration when planning studies of the effect of landscape on CBC. This governs the choice of measurements made, with important implications as to i) the selection of organisms to assess and ii) the appropriate spatial and temporal scales over which to set up the assessment. Determining CBC effectiveness is also critical to the end-point of the study as it will ultimately be used to validate outputs from predictive models. There are a number of criteria that could be used to assess the effectiveness of CBC.

Reductions in crop damage at harvest and in pesticide use are the agronomic measurements that would be the most direct indicators of the economic and environmental benefits associated with CBC. However, as CBC impacts are likely to be partial and to interact with those of other changes in agricultural practices, in practice, it is difficult to quantify the influence of CBC in an integrated system. As a result, direct measures of CBC effectiveness are difficult to obtain and surrogate measurements are reported in papers.

The most frequent measurement of CBC success reported in the literature is that of natural enemy abundance and/or diversity during the growing season. It would seem most appropriate that this measure is taken at times when the enemies are most likely to control pest populations (often at the beginning of pest infestation). Measurements made before and after pesticide applications can also provide evidence of the impact of pesticides on natural enemy abundance. However, data on natural enemy abundance and diversity must be treated with caution as they are not necessarily directly linked to the effectiveness of predation and parasitism or to levels of pest damage. This is particularly true for non-specialist enemies that may prey on a range of species and may be involved in intra-guild predation with other predators (Straub *et al.*, 2008). Measurements of rates of pest predation or parasitism are somewhat more informative but are often difficult to collect. Exposing sentinel pest organisms for short periods can be a valuable source of information on natural enemy activity, particularly in relation to parasitic wasps or pathogens (Thies *et al.*, 2003).

We suggest that assessments of both pest and natural enemy populations, backed up by sound ecological knowledge of their trophic relationships, are the minimum data required to infer effects of landscape variables on CBC. Methods for monitoring populations should be tailored to each specific pest or beneficial organism. The optimal timing for assessments will depend on the phenology of pest damage and the timing of the pest life-stage vulnerable to natural enemies. Limitations on time and manpower are likely to impose constraints on sampling and the most efficient best temporal and spatial distribution of sampling points should be carefully considered.

Ecology of pests and natural enemies

We often lack knowledge of basic elements of pest and/or natural enemy biology that are essential to understanding the behavioural and ecological responses of organisms to the landscape. For example, a low pest population and an absence of landscape effects on that population could be due (i) to an absence of a critical resource for the pest throughout the landscape (bottom up control) or (ii) to the ubiquity of predators due to their mobility (Rand

& Louda 2006) and/or the optimal distribution of resources to support them (top down control). These two scenarios could lead to very different conclusions as to the design of landscapes for CBC were the ecological requirements and behaviour of the organisms are not understood.

Identification of the resources and bottlenecks in the lifecycle of an organism is the first prerequisite to understand its interaction with the landscape in which those resources are distributed. This equates with defining the ‘suitable’ habitat for the organism under consideration, both in space and time. There are cases when such an assessment is fairly straightforward, e.g. when a pest is associated with a specific crop at a specific stage of development. However, many organisms are more generalist and often, little information is available as to what constitutes a suitable habitat patch. Some pests (e.g. weed species) have wide ecological requirements and their habitat encompasses several crop types. In such instances, the association between a given organism and the resources it requires can be assessed by mining existing databases on its distribution and phenology. Alternatively, *de novo* measurements can be made, i.e. counts of pests in mosaics of crops. For generalist natural enemies such as carabid beetles, trophic relationships with their prey can be particularly hard to establish with confidence and the lack of quantitative data is acute. Although some information may be gleaned from consumption preference tests in the laboratory (e.g. carabids feeding on weed seeds; Honek *et al.*, 2007), such tests are artificial. Statistical analysis of data on the co-occurrence of predators and prey in the landscape can make a valuable contribution to the study of feeding choices and to predicting the value of habitats, both for predators of invertebrates and of weed seeds (Bell *et al.*, 2010; Brooks *et al.*, in preparation).

Knowledge of the dispersal behaviour of organisms is essential to understanding the geographical scale of the functioning of pest and natural enemy communities and how this functioning might be optimized for CBC. Here, measurements depend on the type of organism under focus and will encounter limitations met in classical landscape-scale studies such as the difficulty with estimating the tail of dispersal functions. However, the latter problem is likely to have fewer implications than in conservation biology as the promotion of CBC probably only requires measures that are tailored to the core dispersal range of organisms to achieve significant effects on populations of species that are (by definition) not rare. The body size of organisms can be used as a surrogate of dispersal capacity within some groups (such as Hymenoptera). A number of internal and external marking techniques (e.g. fluorescent dyes, trace elements such as rubidium, stable isotope ratios) are available for mark-recapture studies and there are tracking techniques using e.g. electronic tags and harmonic radar (Lavandero *et al.*, 2004). Each method has advantages and limitations but all may allow some estimation of home range and some can provide information about longer distance movement. Genetic markers can shed some light on the degree of relatedness between individuals at different spatial scales, but translating these results into direct dispersal events is extremely challenging.

Measuring the landscape

A general limitation in landscape studies of CBC is that authors usually attempt to relate pest abundance to general landscape variables for which data are most readily available or observed (e.g. composition as land-use types, proportion of semi-natural habitats) and that these descriptors often do not match the perception of the landscape of the organism under study (Veres et al., 2010).

Here we argue that the 'pest' landscape should primarily be a spatial and temporal representation of resources used by the organism (e.g. for a pest, dates of crop sowing/ flowering/ fruiting/ harvest and for a natural enemy, the phenology of the pest) in a mosaic of crops and uncultivated areas. Secondly, if landscape management is to be a CBC measure, the resources manipulated must be landscape elements that can be managed through actions of policymakers, as the scale is beyond that of the economic unit (individual farmer), and this must be possible without adverse effects on crop productivity.

A detailed quantitative record of the spatial and temporal relationships between the resources used by the organism(s) in the landscape is also fundamental and careful thought should be given to the appropriate spatial scale at which landscape measurements should be made, which should be relevant to the study organism. *The minimum spatial resolution* (grain size and sampling unit) of the studied landscape should in general be the size of the 'habitat patch' defined by the biology of the studied organism. Usually a field is the appropriate sampling unit for a pest (resource patch), but in perennial crops, where plants may be larger and harbour less mobile pests, it may be necessary to sample at the plant level (e.g. tree). *The maximum size limit* of the landscape that should be sampled should match the scale at which the most mobile of the species under consideration operates during the timescale at which landscape effects are expected (or can be studied, see below). If a smaller limit to the landscape is used there is a risk that an important factor is not measured and that the influence of a process operating at a larger scale is not accounted for or understood. Extending the sampled landscape beyond this scale would reduce the efficiency of the sampling effort. It is also important to select *the correct temporal scale* which should be great enough in relation to the biology of the organism to enable meaningful change to be detected. The duration of the study is likely to be limited by the period that users of the landscape consider reasonable for benefits to accrue, or by cost. Increasing sampling locations is generally of more value than increasing sampling frequency and sampling should, in any case, be stratified as much as possible (e.g. sampling from resources in different landscape types).

The degree of complexity necessary in the measurement of the landscape context in CBC studies will then depend on the organism under focus and on the way it uses the landscape. It may range from simple landscape representations for organisms that interact only with few landscape elements (all landscape elements not used could be classified as 'matrix'), to complex and explicit representations for organisms whose functioning is influenced by many of the habitats in the landscape (e.g. landscape elements that cannot be considered as resources may yet affect dispersal probability or mortality during dispersal).

Although the quality of a resource is often much less important than its quantity or its mere presence, it is necessary to measure changes that have a major affect on its value, for example the start and end of the flowering period for pollen beetle pests of oilseed rape (Cook *et al.*, 2002). Perhaps the most important of such changes is the application of a pesticide.

Policymakers work with generic landscape types and use 'implicit' measurements (e.g. proportions of different landscape elements, length of field boundary per km^2) to characterise them rather than explicitly describing (mapping) landscapes. If studies of landscape management for biocontrol are to indicate to policymakers how the landscape could in general be manipulated then they must also deal with descriptors that provide 'implicit' descriptions of landscapes. Mapping can be labour intensive and there are risks that conclusions are specific to the mapped landscape; it is therefore probably only appropriate for special cases.

Analytical approaches for CBC at the landscape level

Statistical approaches

Many published papers investigating the effects of landscape characteristics on pests or pest enemies are based on correlations or regressions relating pest or natural enemy variable to some landscape characteristics (e.g. non cultivated area, arable field area). These approaches are efficient as a preliminary/exploratory step to investigate what factors and variates may have a role in the landscape, particularly when used to test a hypothesis. However, as noted by most authors, such approaches face the difficulty that explanatory variables frequently co-vary at landscape scale and effects of variables can easily be confounded. Overcoming these short-cuts is only feasible by, in as much as possible, carefully stratifying the choice of sampling points (generally fields) according to landscape variables that are expected to affect pests or pest enemies based on prior knowledge, as described above, and by identifying a range of meaningful alternative hypotheses (McIntire & Fajardo, 2009).

In situations where a type of regression model can be fitted to the data, its predictive value can be tested over different sampling points within the same sampling region (e.g. other fields in the same production basin) for internal validation or in another region for external validation. External validation ensures that the predicted effects of landscape variables are not specific to the landscapes used for the original model.

Spatially explicit modeling of interactions

Modeling tools allow landscape arrangements to be tested at scales not experimentally feasible, allowing greater spatial and temporal scales to be addressed, more replication, uncertainty testing and scenario testing. They are also helpful for predicting population properties, such as spatial patterns at the landscape scale, on the basis of individual traits. Among the modeling approaches that may be used to analyze landscapes, spatially explicit models in general and individual-based models (IBM) in particular are the most suitable for simulating population dynamics based on individual behaviour in interaction with spatial structure. This type of model requires classical demographic parameters (fecundity, longevity), specific parameters that describe individual dispersal, e.g. distance of dispersal, and behavioural parameters linked to habitat choices.

Model-driven design of landscapes to optimize CBC has now become a real possibility. Currently, IBMs are frequently used to determine the optimal spatial and temporal arrangement of resources for pests (different habitats) in order to minimize both migration of the pest into crops and the overall population of the pest. With the increasing availability of computing power, there is now the opportunity to extend this to address CBC in the landscape by including in these models biological control agents of the pest such as parasitoids and predators. IBMs represent a suitable framework for studying interactions between these organisms, including the spatial dimension. They can be used in two ways, either to model a specific scenario to predict the effectiveness of different options, or as a research tool looking more generally at the interplay of biological, habitat and agronomic attributes in determining CBC success. For example, simulating the spatial epidemiology of pests in virtual landscapes would allow alternative biological processes to be explored. Sensitivity testing could be used to identify the most important parameters affecting CBC efficiency, including parameters intrinsic to the organism (e.g. dispersal distance) and spatial configurations of different habitats. Spatially explicit modeling could also help tackle more theoretical questions applied to CBC, for example the interaction between distribution of resources, the specificity of trophic interactions, and the life traits of pest and CBC organisms.

We propose that an iterative use of i) modeling tools, particularly IBMs, to understand underlying mechanisms of epidemiology of pests in landscapes, and ii) statistical approaches, to characterize the observed patterns of pest populations in a given landscape, should represent the corner stone of comprehensive pest management at the landscape level.

Summary of recommendations

Knowledge-based hypotheses
Studies should be based on the exploration and testing of hypotheses based on sound biological and ecological knowledge. As much information as possible should be obtained about the biology/ecology of the organisms studied, particularly the resources in the landscape that are used. The main factors relevant to its significance in the agronomic situation should be identified. Mechanistic models may be of value for testing whether all important factors influencing pest populations have been recognised.

Essential parameters
The most important data values are: pest population; natural enemy population or % parasitism or % predation; crop damage; estimate of mobility of study organisms (dispersal function); non-explicit spatial measurements of landscape: e.g. % of the landscape offering resources; distance between resource patches; ecologically and practically relevant time limit of study. Careful consideration should be given to the appropriate spatial and temporal distribution of measurements. Major changes in resource quality, e.g. at pesticide application, should also be recorded. We suggest that landscapes for CBC should be described using implicit and relative spatial information (e.g. distribution of patch size and connectivity) and including spatio-temporal information on land cover (e.g. crop rotations). Virtual landscapes described in this way are more readily compared with real-world landscapes than those that are explicitly described and mapped. They could be compared with the characteristics of landscapes at a regional scale that could be addressed by policymakers.

Data-analysis
Statistical approaches should be used either as a preliminary and exploratory step to investigate what factors in the landscape may have a role or to test predictions from computer or conceptual models. Models should be used to explore landscape configurations to optimize the effect of those factors on CBC. Given that we are dealing with interacting species, that interactions may be context (landscape) dependent and that spatially explicit modeling is needed, we believe that IBMs are appropriate, even though they have some limitations. The model should incorporate as much relevant biological knowledge as possible in order to test the sensitivity of CBC to factors such as the intrinsic biological parameters of organisms, spatial configurations of resources and the specificity of trophic interactions.

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