

## CHAPTER 8

# SCALE EFFECTS IN BIODIVERSITY AND BIOCONTROL: METHODS AND STATISTICAL ANALYSIS

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## I Definitions of scale, and an outline for this chapter

The structure of agricultural landscapes is likely to influence organisms living in these landscapes, and in particular, insect pests and their natural enemies (Gámez-Virués et al., this volume). Interactions at a local scale (for example an individual field) are likely to be influenced by processes acting at larger scales (for example the surroundings of that field; Plate 9.1). This is often called scale dependence or context dependence (Pearson 2002).

This chapter serves as an introduction to the design and analysis of studies on biocontrol at different spatial scales. Spatial scale can be described by two factors, grain and extent (Wiens 1989; Fortin and Dale 2005). Grain is the size of an individual sampling unit (for example a plot measuring 4 m<sup>2</sup>); extent is the total size of the study area (for example a landscape measuring 100 ha). The grain size used for individual study units should be carefully chosen to match the spatial structure of the phenomenon being studied. For example, a grain size of 0.5 cm could be necessary in a study of insects inhabiting wheat stems (where the spatial arrangement of damaged vs. intact wheat stems is of interest). In addition, the grain size can also be important when it comes to data analysis - that is, when data are aggregated for statistical analysis. Hence, "spatial scale" can refer to an individual study organism, an individual sampling unit, or an individual unit of

statistical analysis (see also Dungan et al. 2002).

Knowing now what we mean by "scale", we may now ask: How can scaling effects be included in studies on pest control? Before addressing scale effects out in the landscape, it is often useful to start with smaller-scale laboratory systems where it is easier to control for confounding variables. We therefore start this chapter with an introduction to the problem of "upscaling", that is, the extrapolation from smaller to larger scales. We then move on to the landscape scale, and provide an overview of field methods used to study the movement of organisms through the landscape. This section is followed by two sections on data analysis and modelling. Finally, we conclude the chapter with some guidelines likely to be useful for practitioners who want to incorporate scale effects in their own biocontrol studies.

## 2 From the laboratory to the field: upscaling problems

In traditional biocontrol studies, it is often necessary to start with a series of smaller-scale laboratory experiments before moving to the field scale. For example, we need to understand the host specificity of biocontrol agents, or the food plant spectrum of individual insect herbivores, before we can begin to understand what is happening in the field. Often, the underlying interactions between the biological



**Plate 9.1:** Scale transitions and landscape complexity in agroecosystems. (a) Wheat spikes are attacked by pest insects (e.g. aphids) interacting with biocontrol agents on a local scale; (b) a complex agricultural landscape near Holzminden (Central Germany); (c) a simple agricultural landscape in the cereal plain of Chizé (France). All photographs by C. Scherber.

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control agent and the pest organisms occur at the individual level at a scale of centimeters and smaller. To develop efficient biological control measures, we need to understand individual-level ecological processes such as herbivory, parasitism, colonization, and competition and then upscale this knowledge to the level of whole plants or whole stands. However, upscaling is not a straightforward task for ecological and methodological reasons. The ecological processes that drive small-scale and large-scale patterns are usually not the same and do not necessarily overlap (Hartley et al., 2004; Teodoro et al., 2009; see also Gámez-Virués et al., this volume). For instance, the foraging pattern of gall-forming insects differs across scales from the leaf over the branch to the tree level (Lill, 1998). Similarly, parasitism by different parasitoids of the forest pest *Malacosoma disstria* was affected both by spatial scale and by parasitoid body size (Roland & Taylor, 1997). Hence, ecological mechanisms between scales cannot always be easily compared. The main methodological challenge is to maintain the high resolution (grain, see introduction) of small-scale laboratory studies when increasing the extent of a study to the field scale (e.g. Xia et al., 2003). This is often not possible due to logistic constraints such as limited manpower, facilities, or computing power. The methodological alternative is to decrease the resolution of a study when moving from the laboratory to the field scale. Aggregation procedures can be used to achieve this decrease in resolution. However, nonlinearities and thresholds often complicate aggregation procedures, so that aggregation provides no simple upscaling solution, either.

These difficulties of scaling up from small to large scales are reflected in the scarcity of upscaling approaches and of studies that adopt or test these approaches by using scales as explanatory variables. The simplest approach is to take samples at different scales, ideally in a nested manner (hierarchical sampling approach). Due to the logistic constraints mentioned above, the resolution of the samples will in most cases change across scales (for an exception see Roland & Taylor, 1997). If the relationship between the ecological variable of interest and the scales on the x-axis is linear, upscaling of the ecological process can be performed based on this relationship. Unfortunately, most studies adopting this approach have found scale-dependence of the ecological process, preventing straightforward upscaling (e.g. parasitism: Lill, 1998; Matsumoto et al., 2004; mite predation: Zhang Anderson 1993; 1997; foraging in multitrophic systems: Heisswolf et

al., 2006; pathogenic nematode attack: Efron et al., 2001). We are aware of one exception, where upscaling of parasitoid foraging from the local to the landscape scale yielded consistent results (Fraser et al., 2008).

Three general approaches can be taken to scale up from small to large scales: Sampling at different scales, interpolating between local estimates to cover larger scales, and extrapolating from local estimates to larger scales (Table 9.1). The first approach of taking (hierarchical) samples at different scales is often analyzed with scale-area plots to determine the scale-dependence of ecological processes (Table 9.1). When sampling is not possible at multiple scales, local estimates have to be used to reach larger spatial or temporal scales, either by interpolating or extrapolating. In the second approach, the space or time between estimates is interpolated to cover larger areas or time frames. Methods of spatial interpolation include Voronoi polygons and thin plate spline interpolation (Table 9.1) and have been applied to species distribution modelling (Jarvis & Collier, 2002). Species distribution modelling is also the major field of application of the third approach in which bioclimatic models extrapolate local estimates to larger scales using regression techniques (Table 9.1). However, non-climatic factors such as biotic interactions, rapid evolutionary change and dispersal may also affect species distributions, but are often not included in bioclimatic models (Pearson & Dawson, 2003).

For a successful extrapolation across scales, critical scale transitions (He and Hubbell 2003) and the extent and direction of change in the interactions between organisms at these transitions have to be identified. Critical scale transitions are characterized by abrupt changes in a landscape parameter (e.g. field perimeter) with changing spatial scale (for details, see He and Hubbell 2003).

A useful starting point to study such scale transitions is the biological control of microbial leaf pathogens. Population sizes of microorganisms on the leaf surface vary unpredictably across scales and are highly aggregated at all scales from leaf segments to tree stands (Kinkel et al., 1995, Kinkel 1997; Hirano & Upper, 2000). Hence, there is no optimal sampling scale from which population sizes at other scales can simply be extrapolated (Kinkel et al., 1995). This is also reflected in the variable efficiencies of biological control measures observed at the seed and at the field scale (Kildea et al., 2008).

**Table 9.1:** Commonly used methods of upscaling from smaller to larger scales

Purpose	Method	Selected references	Applications
Analysing the impact of scales on an ecological process	Scale-area plots	Kunin, 1998	Hierarchical sampling Assessment of scale-dependence of range sizes of plant species (Hartley et al., 2004) Prediction of species distributions
	Voronoi polygon method (=Dirichlet tessellation)	Dale, 1999	Interpolation of local temperature estimates to the landscape level to predict phenological events in the life cycle of three pest species (Jarvis & Collier, 2002)
Interpolating between local estimates to cover larger scales	Thin plate spline interpolation	Hutchinson, 1991	Thin plate spline interpolation performed better than the Voronoi polygon method (Jarvis & Collier, 2002) Inference of actual or potential species distributions via climate envelopes
	Bioclimatic modelling	Pearson & Dawson, 2003	Inference of the distribution of the biological control agent <i>Podisus maculiventris</i> (Legaspi & Legaspi, 2007), cautioning against basing field-level decisions on bioclimatic models due to the lack of sufficient data for their parameterisation and validation

Microbial systems can be a worthwhile starting point to test the performance of current and new upscaling approaches before transferring the results to insect biological control agents.

The lack of overarching upscaling approaches indicates that, probably, each scale requires its own approach, so that we should advance the coupling of existing approaches rather than aiming at developing the universal up-scaling approach (Meyer et al., 2010). One example of a coupled approach is the pattern-oriented modelling strategy (Grimm et al., 2005) where small-scale mechanisms are derived from large-scale patterns. Pattern-oriented modelling can be used to distinguish between alternative hypotheses on the transition from one scale to the other and thus identify the most appropriate upscaling approach for a particular biological control study.

Overall, upscaling studies show that it can be difficult to compare results obtained in laboratory systems to the field or landscape scale. It is therefore inevitable to move one step further and try to follow organisms out in the agricultural landscape. In the next section, we will see how we can track the movement of insects through real landscapes - a prerequisite for many approaches that follow.

### 3 Field methods for understanding landscape-scale patterns

Moving from smaller laboratory systems to the field and landscape scale, researchers often have to become detectives – simply because there is so much space available for study-organisms to hide and escape. This is not so much of a problem under small-scale laboratory conditions, but is central to the success or failure of large-scale field studies. Up-scaling from the laboratory to the field thus requires a whole new set of approaches to track arthropods at the large scale. During the last few decades, a series of different marking and tracking techniques have been developed to study arthropod movement and dispersal. These techniques can be used to identify the land uses that (1) act as sources of movement into crops, for both pests and natural enemies, and (2) act as alternative resources and resource subsidies for natural enemies. In the following brief overview of marking and tracking techniques we outline how different techniques have been used to investigate the movement and spatial ecology of arthropods and suggest areas for future focus. Due to the limits on space, however, the following section is by no means an in-depth review of this subject (more detailed reviews are highlighted in Table 9.1)

Following animals from one point to another is the basic requirement of any marking and tracking technique. The fact that “old fashioned” techniques

such as fluorescent dyes have continued to be used (e.g. Schellhorn et al., 2004; Bianchi et al., 2009) despite the high-tech revolution of recent decades illustrates the power of the basic guidelines (for example outlined by Hagler and Jackson, 2001) that a marking technique should be simple to apply, readily detectable, inexpensive, safe and not affect the biology or ecology of the target species. Fluorescent dyes score well in all of these categories (see Table 9.1). For example, despite the relatively low recapture rates compared with rare-earth labels (Hagler & Jackson, 2001; Prasifka et al., 2001), fluorescent dyes are cheaper to apply and there is no need for specialised laboratory equipment with trained technicians to process the samples. And while rare-earth labelling techniques may offer much greater capture rates, in mark-capture trial (e.g., see Prasifka et al. 2001), rare-earth labelling requires intensive background sampling before the mark-capture is conducted (in order to firstly establish the naturally occurring variation, within the local population, of the elements to be used as a marker (e.g., rubidium). Similarly, the enormous potential, for mass mark-capture, offered by marking with cheap proteins for ELISA analysis (described by Hagler and Jones 2010) may be overshadowed, for many researchers, by the need for specialised equipment for identification. Although fluorescent dyes may offer a good, cheap, all-purpose type of marking solution, they are perhaps best suited to mark-release-recapture type investigations (where a large number of collected or laboratory-reared individuals are marked and release, en masse, from a central point and subsequently recaptured). The emerging potential of marking with cheap proteins (for example, milk and egg protein as described in Hagler and Jones 2010) offers the opportunity to apply the marker to unprecedentedly large areas of vegetation in order to mark wild populations of arthropods in mark-

recapture type investigations.

Traditional mark-capture techniques suffer from several disadvantages. In particular, mark-recapture techniques require equal catchability of marked individuals, and often high numbers of individuals need to be marked. Often, a technique described as "self-marking" may be preferable, where arthropods obtain the mark, for example through foraging, rather than being directly and intentionally marked by the observer. The extra ecological information from such studies can be useful in habitat management and conservation biological control. For example, HPLC nectar analysis (Wäckers, 2007), pollen marking (Silberbauer et al., 2004) and the use of stable carbon isotopes (to identify C<sub>3</sub>/C<sub>4</sub> feeding, e.g. Prasifka & Heinz, 2004) can identify the resources, resource subsidies and alternative habitats utilised by pests and natural enemies. However, these approaches may not have the critical information about the origin of the 'mark' (unless there is a unique source of pollen, nectar or C<sub>3</sub> plants in the area). It is here that rare-earth labels are perhaps most useful (e.g. Lavandero et al., 2005; Scarratt et al., 2008), because plants can be intentionally marked via the vascular system, leaving no doubt about how and where the mark had been obtained (stable isotopes can also be employed in this fashion, e.g. Wanner et al., 2006; see Table 9.1). Rare-earth elements, such as rubidium and strontium, have the advantage of moving through trophic levels (as do stable isotopes), they may, therefore, provide information on the foraging habits of captured insects (Prasifka et al. 2004). The identification of sugars in the gut contents of natural enemies can also help to inform on the use of resource subsidies or the foraging of pest-originated sugars such as melezitose included in lepidopteran frass and homopteran honeydew (Heimpel et al., 2004).

Perhaps the greatest potential for marking and

**Table 9.2:** An overview of marking and tracking techniques commonly employed in landscape-scale biological control studies.

Technique	Characteristics		Recent Examples		Reviews
	Simplicity	Cost	Requires specialist equipment	Resource use (self-marking) studies	
Dyes	simple	low	no	Bianchi et al., 2009	Schellhorn et al., 2004
Rare Earths	moderate	relatively low	yes	Prasifka et al., 2004	Lavandero et al., 2005; Southwest Entomologist Special Issue 14 1991
Sugar analysis	moderate	relatively low	yes	Desouhant et al., 2010	Winkler et al., 2009
Stable Isotopes	moderate	relatively low	yes	Prasifka & Heinz, 2004	Wanner et al., 2006
Protein marking	increasingly simple	relatively low	yes	Jones et al., 2006	See Jones et al., 2006
					Hood-Nowotny & Knols, 2007; Prasifka and Heinz, Hagler & Jones, 2010; Horton et al., 2009

tracking techniques in biological control, especially with a focus on biodiversity, is the use of multiple markers to adapt techniques to more complex field situations; for example, to simultaneously identify multiple resources (i.e. different source habitats or different resource subsidies). The recent advances in identifying common proteins with ELISA (Hagler & Jones 2010) offers great potential in this endeavour; e.g., to use milk proteins to mark one field, or one prey species, and egg proteins to mark another field or prey species.

Great potential is also offered by combining different disciplines, for example in 'landscape genetics'. In recent years, the use of landscape genetics, which is the combination of high resolution genetic markers with spatial data analysis, has been particularly relevant when assessing the influence of landscape characteristics on the genetic variability and the identification of barriers to gene flow (Storfer et al., 2007). Examples of the assessment of suppressive landscapes using landscape genetics are still scarce, although molecular markers are available for many species (Behura, 2006), and area-wide pest management programs provide valuable information about landscape attributes (Calkins & Faust, 2003; Carrière et al., 2004; Beckler et al., 2005; Park et al., 2006). Correctly identifying sinks and sources of pests and natural enemies can inform on refuge placement and determine whether a landscape is pest suppressive or not. As different parasitoid races can be specific to different host species (for parasitoids with a great host range), genetic and allozyme studies have shown that there is gene flow between refuge-alternative hosts and the target pest on the target crop (Blair et al., 2005; Forbes et al., 2009; Stireman et al., 2006). Thus, the ability of a parasitoid to control different hosts on different host plants may not

be constant, even among different genotypes of a single species (Henry et al., 2010). In a recent study in Central Chile's main apple production area, the relationships between aphid (*Eriosoma lanigerum*) and parasitoid (*Aphelinus mali*) population genetics were studied. Samples were taken from commercial apple orchards and from a different *E. lanigerum* host (*Pyracantha coccinea*) in a farm hedge dominated by the plant genus *Pyracantha*. Prior studies had shown geographic barriers interrupting gene flow of the aphid host between neighbouring populations independently from geographical distances (Lavandero et al., 2009). Evidence of extensive gene flow between sites, and no evidence of reproductive barriers for the parasitoid were found, suggesting no host-plant related specialisation and therefore indicating that *Pyracantha* hedges are a source of parasitoids for the crop. Based on this knowledge, future integrated pest management programs could rely on the use of refuges of alternative hosts to increase migration of parasitoids to areas where they are more rare, aiding the augmentation of the parasitoid population after disturbances.

Overall, the approaches highlighted in this section show a wide range of methods available to the researcher - from marking and tracking to landscape genetics. We will now move on to another important area, which is experimental design and statistics.

#### 4 Design and statistical analysis of large-scale biological control

Knowing how to mark and track insects in agricultural landscapes, we can now move on to think of how to apply this knowledge to conduct a biocontrol study on a landscape scale. First, we need to consider the spatial arrangement of study sites and treatments (experimental design). Second, we need to come up with sampling schemes that work for our study organisms (sampling design).

##### 4.1 Experimental design

Of the wide variety of available experimental designs (e.g. Fig. 1 in Hurlbert 1984), the completely randomized design will probably be the least useful. It is almost certain that our study sites will need to be arranged in blocks in space and time. Blocks share similar abiotic conditions (e.g. soil parameters) and help reduce the unexplained variation in

#### Box 9.1 The spatial population dynamics of insects exploiting a patchy food resource (Dempster et al. 1995)

Movements between plant patches were studied with the use of chemical markers (Rb, Sr, Dy and Cs) which were applied as chloride salts to individual patches, and which were translocated to the flowerheads and so to insects feeding on the seed, and to their parasitoids.

These analyses showed that individual of all species moved considerable distances, with movements of up to 2 km being commonly recorded. Estimates of rates of immigration to patches showed that movement plays an important role in the population dynamics of these insects. There was some evidence that immigration was density-dependent: it was highest when the resident populations (numbers per flowerhead) were low.

data. To reduce workload and costs, it is often advisable to apply split-plot designs in which smaller subplots are nested within larger plots. Experimental treatments (for example bagging, caging, pesticide application etc.) are then applied at random at increasingly smaller spatial scales.

#### 4.2 Sampling design

After deciding on the experimental design to be used in our biocontrol study, we need to define an appropriate sampling scheme to estimate organism abundance, species richness, predation rates and so forth. To decide on an appropriate sampling method, we need to know our study organisms: How large are they, how mobile will they be, and how will they respond to landscape features (Wiens, 1989)? Secondly, we need to employ sampling, marking and tracking procedures that are as unbiased as possible (Hagler & Jackson, 2001). This requires setting-up traps and other devices according to systematic or random schemes (Fortin & Dale, 2005; see Table 9.3). At this stage, we will also need to know which types of analyses we want to conduct with the data after they have been collected. For example, grid-based sampling will lead to different types of geostatistical procedures than random sampling (Fortin and Dale 2005).

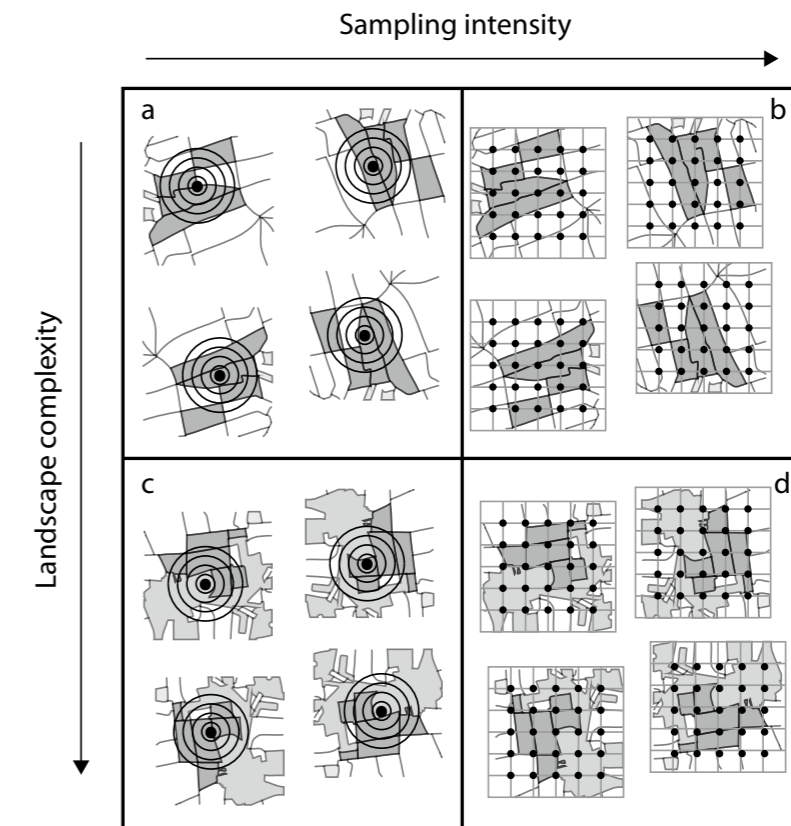
#### 4.3 Combining observational and experimental

##### approaches

In landscape-wide biocontrol studies, observational data (“mensurative experiments” sensu Hurlbert, 1984) should be combined with experiments to achieve what is called “strong inference” (Platt 1964). For example, if we study multitrophic interactions in oilseed rape, it is a good idea to experimentally establish own oilseed rape plots in addition to fields already existing in the landscape (Thies & Tschardtke, 1999). Additionally, experimental plant individuals (“phytometers”) may be used to study local-scale phenomena (Gibson, 2002). Such approaches may help to standardize plant cultivars, soil conditions and other confounding variables. Experimental plots can then be used for specific treatments on a subplot scale (e.g. fertilization, insecticide treatment, or caging experiments). In general, an “ideal” landscape-scale study always involves experimentation (“manipulative experiments” sensu Hurlbert 1984): Experimental establishment of hedges (e.g. Girma et al., 2000), experimental fragmentation of habitats (e.g. Lindenmayer et al., 1999; Debinski& Holt, 2000), experimental application of herbicides, insecticides and biocontrol agents (e.g. Cochran & Cox, 1992). However, in many cases, experimentation will be impossible for logistical reasons. Landscape-scale studies cover large areas, and individual fields often belong to landowners who individually manage their fields. Under these circumstances, we can study gradients in landscape complexity, composition or configuration. Paired designs using “pseudo-treatments” can also yield insights - for example if organic and con-

**Table 9.3:** Experimental or sampling designs employed in landscape-scale biocontrol studies

	Experimental studies	Observational studies
	Completely randomized design	Landscape gradients (e.g. gradients in landscape complexity)
Most frequent experimental or sampling schemes applied	Randomized blocks designs	Concentric circles design (to study landscape context)
	Paired designs	Grid sampling schemes Paired designs (e.g. paired comparisons between organic-conventional farms)
Main advantages	Clear separation of response and explanatory variables	Realism
	Classical hypothesis testing, strong inference	Direct application to real-world scenarios possible
Main disadvantages	Sometimes unrealistic	Causes and effects may be difficult to separate
	Small power if sample sizes is low	Unanticipated block-by-treatment interactions
	Upscaling problems	



**Figure 9.1:** Sampling designs in biocontrol studies on a landscape scale. Sampling sites are indicated by filled black dots within landscapes; (a) and (c), low sampling intensity (N=4 datapoints in 4 landscapes), landscape structure around each sampling site is measured in concentric circles with increasing radii. (b) and (d) high sampling intensity (N=25 datapoints in 4 landscapes); landscape structure and spatial information about sampling locations are measured simultaneously. Landscape complexity increases from (a) to (c) and from (b) to (d). Figure created by C. Scherber.

ventional farming systems are studied (e.g. Kleijn et al., 2006). Below, we list some of the most important features to consider for successful experimental design of biocontrol studies.

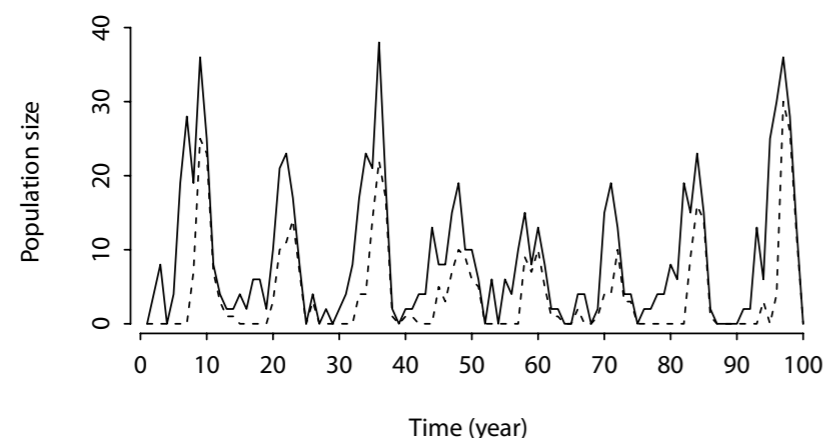
#### 4.4 Importance of blocking

Blocks are still among the most useful “devices” to control for variations in abiotic conditions in both experimental and observational studies on a landscape scale. For example, individual countries can form blocks in continent-wide studies (Billetter et al.; 2008; Dormann et al., 2007). Likewise, pairs of farms can be considered as blocks (Kleijn et al., 2006). Further, individual observers moving through the landscape can be “applied” to different groups of study plots and “observer effects” can then easily be incorporated into the block effect in

statistical models.

#### 4.5 Proper use of random effects

Every study site has its own characteristics, and we will never be sure which of these characteristics will exactly be important for a given study. In the statistical design and analysis of landscape-wide studies, it is therefore important to be very clear about which factors should be treated as ‘random’ (McCulloch & Searle, 2001; Bolker et al., 2009). Imagine you begin your study with a selection of 30 study sites, scattered through a larger landscape. If someone else would have selected these 30 sites, he or she would probably have chosen different ones. Hence, the population of possible sites may probably have been almost infinitely large. The sites you chose just happened to be that particular 30. Hence, your sites are actually random effects, and this should be clear from the beginning of the study (Zuur et al., 2009). As a final note, random effects should always have at least two levels, and ideally as many as possible



**Figure 9.2:** Population density of adult hosts (black line) and parasitoid larvae (dotted line) oscillating with time in one exemplary cell; simulation run with landscape parameters as visualised in Figure 9.3. Adapted from Visser et al., 2009.

(Giovagnoli&Sebastiani, 1989; McCulloch & Searle, 2001).

#### 4.6 How to incorporate the landscape context

Observations at a single site may be influenced by the surrounding landscape; these indirect influences are commonly termed “landscape context” (Pearson, 2002). The traditional approach has been to use individual sampling points, scattered through landscapes differing in landscape complexity. These points were then surrounded by concentric circles in which landscape parameters were assessed (Figure 9.1a, c). However, this means that landscape effects can only be guessed from correlations between what we observed at an individual plot, and some features of the landscape surrounding that point. It is more desirable to also collect replicated samples in space, for example using replicated grids of sampling points at every study site (e.g. Billeter et al., 2008; Dormann et al., 2007; see Figure 9.1b, d). Note, however, that the grid cell size needs to match the cell size of the expected spatial pattern (Fortin & Dale, 2005). Alternatively, stratified random sampling may be employed; that is, each habitat forms an own ‘stratum’ and is sampled separately. The sample size will then be a function of habitat area and costs of sampling (for details, see Krebs, 1999).

#### 4.7 Know your response and explanatory variables

It is always a good idea to set up an artificial dataset before the beginning of a study. You can then already try out different statistical models and do power analyses to estimate the sample sizes needed

(e.g. Crawley, 2002). In biocontrol studies, we will often encounter count data (numbers of insects) or proportion data (proportion parasitised hosts). These data types usually require special types of statistical models such as generalised linear (mixed) models (McCulloch & Searle, 2001).

#### 4.8 How to do the statistical analysis of landscape-scale biocontrol studies

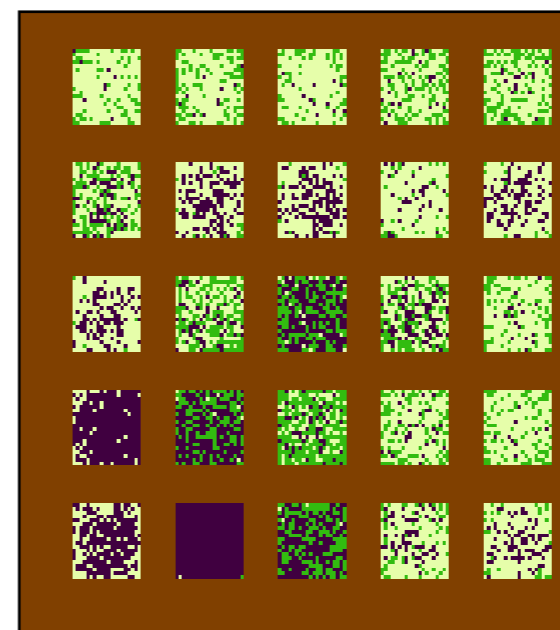
After successful data collection, we usually want to draw inferences from these data using statistical techniques. In the past, many datasets have been analysed using standard regression techniques, although datasets actually had a clearly spatial na-

##### Box 9.2 Persistence of parasitoid populations and parasitism rate

We focus on two measures that are widely used to assess the performance of biocontrol: persistence (a measure of the parasitoid’s reliability), and parasitism rate. The first measure is commonly used in theoretical studies and the latter in field studies.

Persistence of parasitoid populations and parasitism rate are measures often applied in theoretical and field studies, respectively. Each of them reveals important properties of biocontrol, namely reliability and effectiveness, respectively.

Visser et al. (2009) found that the amount of habitat in a landscape modulates the effect of fragmentation on parasitoid persistence. Parasitism rate, on the other hand, decreased with fragmentation regardless of the habitat amount in a landscape. Consequently, the effect of fragmentation and isolation on the performance of biocontrol as an ecosystem service hinges on whether the focus is on persistence or parasitism.



**Figure 9.3:** Snapshot of a virtual landscape of the scenario with low amount of habitat (habitat amount 2500 cells, number of patches 25, patch distance 10 cells) during a simulation run; white: cells with only host population, dark pink: cells with host and parasitoid population, brown: matrix cells, green: empty habitat cells. Adapted from Visser et al., 2009.

ture (Dormann, 2007). The most important steps in the analysis of datasets on landscape-scale biocontrol are the following:

(1) Decide on how to deal with count and proportion data. Usually, you may wish to analyse them using generalized linear (mixed) models, but current software packages often lack methods to incorporate spatial and/or temporal autocorrelation into these models (for an overview, see Bolker et al., 2009). The best solution often is to transform the response variable, or to use variance functions to account for non-constant variance.

(2) Decide on what to do with space and time. If you are interested in spatial trends, decide if you want to interpolate between sampling locations (kriging), or if you simply want to account for spatial autocorrelation (correlation structures in the residuals); a good introductory reference is Fortin and Dale (2005). If you are interested in temporal trends, make sure that your observations are regularly spaced in time and that there is sufficient temporal replication (Zuur et al., 2009). Treat temporal pseudoreplication using time series analysis or by incorporating time as a random slope. Avoid incorporating time as a pseudo-“subplot” because this may violate the sphericity assumption (sphericity is a measure of variance homogeneity in repeated

measures analyses; for details, see von Ende, 2001).

(3) Plot the data, together with the model predictions, instead of plotting linear regressions provided by graphics software. Remember that model predictions from generalised linear models look nonlinear on the untransformed scale.

## 5 Modelling scale effects in biological control

Even the most sophisticated statistical analysis often opens up new questions. For example, we may find that landscape context influences the distribution of a specialist parasitoid, but we may be unclear about the mechanisms. Modelling can be a useful tool to understand the spatiotemporal dynamics of pests and their biocontrol agents in the field. Modelling is also needed as a final step in designing pest-suppressive landscapes. In order to be able to give management recommendations towards promotion of biodiversity and biocontrol via design of pest-suppressive landscapes, a good understanding of the ecological processes acting at different scales (e.g. Levin, 2000, Turner 2005) is important. Key questions are: Which species are promoted/threatened in a given landscape structure and what are the species and landscape characteristics making these species abundant/prone to extinction in such a landscape? How can a landscape be altered to promote beneficial species and suppress pest species?

The basic idea of ecological modelling is to reconstruct the basic features of ecological systems in simulation models. In other words, these models are a representation of all essential factors of the real system that are relevant with respect to the scientific question being addressed (Wissel, 1989). In case of rule-based simulation models, these essential factors and their interactions are being described using ‘if-then-rules’ (Starfield et al., 1994). For example, one rule in the model might be: *if* a parasitoid finds a host individual at a specific location, then the parasitoid lays an egg into the larva and at this location no host but a new parasitoid will develop. Experts that know from field experience which factors shape the system are a great help to model development.

Typically, several model variants are developed that can be used to test specific hypotheses on the functioning of the system. Factors can be added or

removed, parameter values are being increased or decreased and thereby our understanding of the system can be greatly improved. Models can also be used to help the planning of new field experiments. Using virtual experiments, different landscapes can be created and the (insect) species are being placed into these landscapes and their populations develop according to the model rules. In such experiments, long time series can be investigated, which would not be possible in the field.

There are two main classes of models that are most frequently used to model large-scale spatiotemporal dynamics of organisms: Individual-based models (IBM) and grid-based models. In IBM, each individual is tracked explicitly, along with its properties (e.g. size, sex, developmental stage). Population processes emerge from the combined behaviour of many individuals (e.g. Bianchi et al. 2009).

In grid-based models (e.g. Bianchi & van der Werf 2003), space is represented as a grid of cells. This means each of these cells represents a small subunit of space in a certain position and contains specific information for example about its suitability for the regarded species (e.g. "habitat") or the presence of the organisms to be studied (e.g. "occupied by host population") (see also the grid-based sampling approach shown in Figure 9.1b,d). Within a cell, non-spatial processes such as reproduction can take place. Cells are interlinked via dispersal and this way the reproduction and spread of a local insect population can be depicted. Inspecting the landscape-level patterns emerging from such a model can help to scale up local insect dynamics to the landscape.

Visser et al. (2009) developed a grid-based host-parasitoid model based on the ecology of the rape pollen beetle *Meligethes aeneus* (Fabricius) and its specific parasitoids in semi-natural habitats. In fragmented landscapes, parasitoids have been found to go extinct before their hosts do, which suggests that species at different trophic levels experience a landscape differently (Kruess & Tschamntke, 1994; Tschamntke et al., 2002). Parasitoids are often antagonists of important pest insects and therefore a good understanding of host-parasitoid systems in agricultural landscapes is of great interest to biocontrol.

One grid cell in the model represents a 100 m × 100 m area of an agricultural landscape which can be either suitable "habitat" for the host (e.g. set asides)

or unsuitable 'matrix' (e.g. other crops, but not rape). Each cell can contain a subpopulation of host and parasitoid and is the place for the local processes reproduction, parasitism, and mortality. Local subpopulations are linked by dispersing host and parasitoid individuals. For model details see Visser et al. (2009).

Habitat fragmentation was studied by varying the number, size of, and mutual distance between habitat patches in the virtual landscapes of the host-parasitoid model (Visser et al., 2009). A habitat patch is defined as a continuous area of adjacent habitat cells. Across all scenarios, host parasitoid dynamics in a given cell is oscillating in time (Fig. 9.2). Generally, these local oscillations of host and parasitoid densities lead to a wave-like or chaotic spatial pattern (Fig. 9.3) with increasing local host populations at the wave front, followed by increasing parasitoid populations (see also Hirzel et al., 2007). These waves of hosts and parasitoids move across the landscape with time. As the parasitoid populations cause the local extinction of the host, they leave a zone of empty cells behind. Analyses across fragmentation scenarios show the following trends: (1) Parasitism rates decrease with the number of patches and decrease with patch distance, and (2) host outbreak duration increases with the number of patches, and (3) parasitoid persistence is additionally modulated by habitat amount: if habitat is abundant persistence decreases with the number of patches and with patch distance, if habitat is scarce persistence is highest at intermediate levels of fragmentation (Visser et al., 2009)..

In summary, the amount of habitat in a landscape modulates the effect of fragmentation on parasitoid persistence. Parasitism rates, on the other hand, decreased with fragmentation regardless of the habitat amount in a landscape. Consequently, the effect of fragmentation and isolation on the performance of biocontrol as an ecosystem service hinges on whether the focus is on persistence or parasitism rates.

Although the dispersal of both hosts and parasitoids is hindered by increasing fragmentation and isolation, this effect is much stronger for the parasitoid. This is due to the fact that the parasitoid depends on a more ephemeral resource (host) than the host (habitat). With increasing fragmentation, the disadvantage of the parasitoid increasingly leads to the decoupling of the host population from the control of the parasitoid, which results in pro-

longed host outbreak duration and decreased average parasitism rates. Thus, the modelling study by Visser et al. (2009) confirms the findings of several field studies that increasing fragmentation and isolation can decrease parasitism rates (Kruess & Tschamntke, 1994), increase prey outbreak duration (Kareiva, 1987) and reduce prey tracking at a certain scale (With, et al. 2002). It also reveals that the basic mechanism underlying their observations may be neither the difference in dispersal abilities of host and parasitoid (which were kept identical in the model) nor the predator searching behaviour interacting with landscape features (which was not incorporated in the model), but the decoupling of the population dynamics of pest and antagonist due to habitat structure.

The example of the host-parasitoid model illustrates that modelling can improve our understanding of complex systems beyond the possibilities of field studies. The model shows that landscape effects on biological control agents can be found without any significant differences in local dispersal abilities and even without any specific active response of the organisms to the landscape features. This was greatly facilitated by the fact that, within a model, properties such as dispersal ability and degree of interaction with landscape features can be changed while keeping all other properties constant.

## 6 Summary and conclusions

Data collection, sampling design, tracking and marking techniques, statistics as well as modelling of data on a landscape scale can be challenging for the individual researcher. In this chapter, we have tried to cover the areas that we believe are most relevant for landscape-scale studies. As everywhere in science, innovation is often based on methodological or technological advancements. For example, landscape genetics would be unthinkable without the rapid developments in molecular biology. Likewise, analyses of landscape structure are greatly aided by advances in multiband satellite imagery and image processing and classification software. Finally, new types of sampling design, such as grid-based landscape-wide sampling, may provide new insights and opportunities for modelling. All in all, we think that there are several key steps that can be followed to make the most of an individual study:

(1) Start off with a small-scale study (for example with your favourite biocontrol agent and insect

pest), and try to predict what might happen on larger spatial scales.

(2) Choose from selected marking and tracking techniques, and do preliminary studies in your type of landscape. Find out which spatial and temporal scales you can reasonably cover.

(3) Know your study organisms, their biology, life cycle and dispersal behaviour.

(3) Invest time into finding an appropriate sampling or experimental design. If your design is solid, your study will also be (provided you know your organisms). If you have too low replication, or block-by-treatment interactions, you can often not cure this at the statistics stage.

(4) Use established, robust and well-documented statistical procedures for data analysis. This doesn't mean you should use "canned" solutions, but don't become too excited about approaches that are still under development (such as generalized linear mixed models). Always graph your data before you start any analyses.

(5) Use the advantages of modelling and simulation techniques to derive predictions that extend across the scales of your study.

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