

Factors and mechanisms explaining spatial heterogeneity: a review of methods for insect populations

Fabrice Vinatier^{1*}, Philippe Tixier¹, Pierre-François Duyck¹ and Françoise Lescourret²

¹CIRAD, UPR 26, B.P. 214, F-97285, Le Lamentin, Martinique, France; and ²INRA, Unité Plantes et Systèmes de Culture Horticoles, UR 1115, Domaine St. Paul, Site Agroparc, Avignon Cedex 9, 84914, France

Summary

1. The spatial distribution of populations is affected by the dispersal abilities of the species, interactions among individuals, or habitat selection. Linking these ecological processes to spatial patterns is of primary importance for understanding and prediction purposes.
2. We review both statistical and mechanistic methods for studying the spatial distribution of populations. Statistical methods, such as spatial indexes and nearest-neighbour analyses help characterizing the spatial pattern. They allow testing the effect of environmental variables on spatial patterns using regression analyses.
3. Mechanistic modelling can be used to analyse the effect of mechanisms underlying the spatial pattern. We review mechanistic models (e.g. metapopulation, individual-based and cellular automaton models) devoted to represent dispersal abilities, interactions among individuals and habitat selection.
4. We illustrate each method by works on insects, which cover a broad range of spatial patterns. Strengths and limitations of methods are discussed according to the process and type of data set.
5. Scientists can use statistical or mechanistic methods in an iterative manner to infer process from spatial pattern. New approaches such as ‘pattern-oriented modelling’ or ‘space as a surrogate framework’ determine whether alternative models reproduce an observed pattern. It allows selection of the process that best explain the observed pattern.

Key-words: ecological process, mechanistic model, spatial analysis, spatial pattern

Introduction

Spatial heterogeneity is of great importance in the study of populations, communities, ecosystems, and landscapes (Shaver 2005). Spatial heterogeneity is defined either as the variation in space in distribution of a point pattern, or variation of a qualitative or quantitative value of a surface pattern (Dutilleul & Legendre 1993). It can be caused by habitat factors (Tscharntke *et al.* 2002) and their temporal variations (Leyequien *et al.* 2007), individual traits (Tilman & Kareiva 1997), and neutral processes (Rosindell, Wong, & Etienne 2008). Habitat factors include resource density and heterogeneity that may result in a series of suitable patches of different size and of different isolation level in an unsuitable matrix (Tscharntke *et al.* 2002). When habitat is fragmented, the dispersal behaviour of individuals explains much of the variation of population densities in corresponding patches (Coombs

& Rodriguez 2007). Individual traits such as dispersal abilities (Tscharntke & Brandl 2004), sexual attraction by pheromone, or aggregative behaviour have consequences for population dynamics and species distributions.

Linking ecological processes, such as dispersal, interactions among individuals, or habitat selection, to spatial patterns is of primary importance in both basic and applied ecology. It may help the conservation of endangered species (Matern *et al.* 2007) based on the comprehension of the effects of habitat fragmentation on population dynamics (McIntire, Schultz, & Crone 2007), and to control pest species by relating their spatial distribution to their damages (Rodeghiero & Battisti 2000; Eber 2004).

Methods used to analyse the spatial heterogeneity of populations are statistical or mechanistic. Statistical methods based on spatial correlations or multiple regressions on landscape variables help reveal the link between landscape elements and populations. They allow the researcher to characterize spatial patterns and to test the explanatory power of candidate variables using a correlative approach. Mechanistic methods deal

*Correspondence author. E-mail: fabrice.vinatier@cirad.fr
Correspondence site: <http://www.respond2articles.com/MEE/>

with underlying mechanisms of spatial distribution of populations that are studied at the population or individual scale. The combination of statistical and mechanistic models in ecological research can provide new insights into the comprehension of spatial heterogeneity.

In this review, we argue that the comprehension of spatial heterogeneity requires an iterative process including three steps. The first part of the review presents the use of statistical methods to detect the characteristics of spatial patterns (Fig. 1: arrow 1). The second part of the review presents the statistical models used to identify exogenous or endogenous factors explaining a spatial pattern (Fig. 1: arrow 2). The third part of the review exemplifies the use of mechanistic models to study the mechanisms that produce spatial patterns. In the last part of the review, we discuss the methodological ways to link spatial patterns and ecological processes, and especially how statistical and mechanistic methods complement each other to achieve a full understanding of spatial heterogeneity of population (Fig. 1: arrow 3). Rather than presenting in detail methods, which has been done elsewhere for statistical methods (e.g. Cressie 1993; Dale *et al.* 2002; Fortin & Dale 2005), mechanistic methods (e.g. Tilman & Kareiva 1997; Huffaker & Gutierrez 1999), and pattern-process approach (Illian *et al.* 2008), our review aims at providing a framework for choosing the right method or the best combination of methods to explain the spatial pattern of a population. We illustrate the strengths and limitations of methods with insect case studies, because of the wide range of spatial patterns and life-history

traits in insect populations (Schowalter 2006). Tables 1 and 2 illustrate the topics of the research conducted on spatial heterogeneity of insect population during the last 15 years by statistical or mechanistic methods, respectively. Each table allows researchers to know existing methods already used to address a given topic.

Characterization of the spatial pattern of insect populations

Spatial and temporal resolutions of the sampling area are of primary importance to capture the process under study and should be adapted in consequence (Fortin & Dale 2005). For example, the distribution of a population of aphids may seem to be aggregated, random, or regular depending on whether the forest, tree, or leaf is chosen as sampling unit (Begon, Harper, & Townsend 1996). Geostatistical methods have to be chosen among indexes of spatial autocorrelation [e.g., Moran and Geary, Spatial Analysis by Distance Indices (SADIE[®]), Mantel] and analysis of neighbouring distances (e.g., Nearest-neighbour distance or K-function) (Table 1, Fig. 1: arrow 1).

OVERVIEW OF SAMPLING METHODS

Sampling methods include direct observation, capture–mark–recapture (Kreyer *et al.* 2004), radiotelemetry (Vinatier *et al.* 2010), or interception trapping using pitfall traps (Botes *et al.* 2006), trunk traps (Rodeghiero & Battisti 2000),

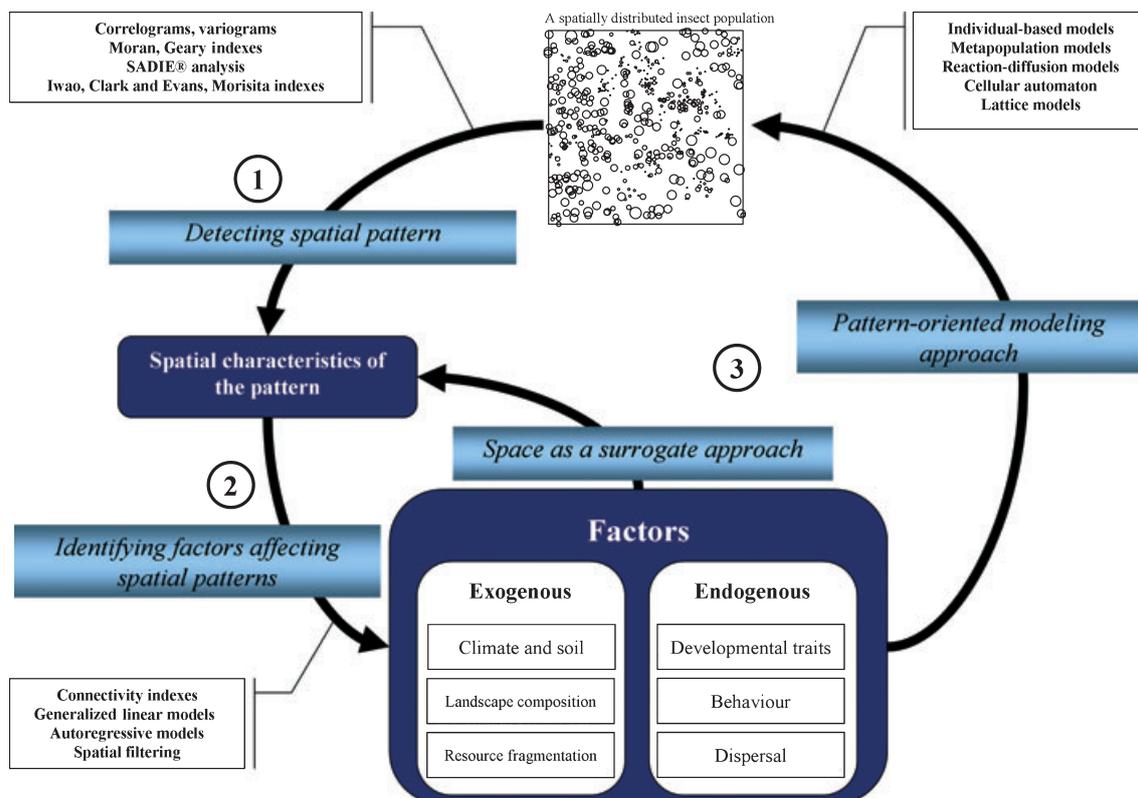


Fig. 1. Schematic diagram of the different steps necessary to understand spatial heterogeneity of organisms and the type of methods involved.

Table 1. Overview of statistical models used to characterize spatial patterns of insect populations and corresponding references

Topic	Method	References
Characterization of the spatial population pattern		
Evaluation of distribution of species	Kriging	(Franceschini, Cannavacciuolo, & Burel 1997; Moral García 2006; Trematerra <i>et al.</i> 2007)
	Trend surface analysis	(Felizola Diniz-Filho & Fowler 1998)
	Moran eigenvectors	(Jombart, Dray, & Dufour 2009)
Identification of species patterning (aggregation)	SADIE®	(Thomas <i>et al.</i> 2001; Ferguson <i>et al.</i> 2003; Nansen, Subramanyam, & Roesli 2004)
	Mantel test, Moran and Geary indexes	(Rodeghiero & Battisti 2000; Judas, Dornieden, & Strothmann 2002; Ellis 2008a)
	Lloyd's index	(Kianpour <i>et al.</i> 2010)
	Ripley's K-function, Taylor's power law	(Powers <i>et al.</i> 1999; Lancaster, Downes, & Reich 2003; Schroff, Lindgren, & Gillingham 2006)
	Iwao's patchiness regression	(Arnaldo & Torres 2005; Peña <i>et al.</i> 2007)
	Morisita's index	(Gilbert, Vouland, & Grégoire 2001)
	Clark & Evan's index	(Chamorro-R, Montealegre-Z, & Gonzalez-O 2007)
	Nearest-neighbour distance	(He & Alfaro 1997; Dodds, Garman, & Ross 2006)
	Bayesian approach	(Augustin <i>et al.</i> 2007)
	Nearest-neighbour distance	(Potts & Willmer 1998; Moravie, Borer, & Bacher 2006)
Egg-laying pattern	Frequency distribution fitting	(Desouhant, Debouzie, & Menu 1998; Zu Dohna 2006)
Identification of factors affecting spatial patterns at the landscape scale		
Landscape factors	Multiple regression analysis	(Holland & Fahrig 2000; Den Belder <i>et al.</i> 2002)
*Habitat unsuitability (border effects...)	Stepwise regression	(Elliott <i>et al.</i> 1999; Buse, Schroder, & Assmann 2007; Matern <i>et al.</i> 2007)
*Habitat suitability	Generalized linear mixed models	(Taboada <i>et al.</i> 2006)
	Correlation with proximity indexes	(Hanski & Heino 2003; Beckler, French, & Chandler 2004; Fred, O'Hara, & Brommer 2006)
	ANOVA analysis	(O'Rourke, Liebman, & Rice 2008)
	Autoregressive models	(Kadoya <i>et al.</i> 2009)
	Spatial-filtering	(Hamasaki <i>et al.</i> 2009)
	Generalized linear models	(Botes <i>et al.</i> 2006)
Climate factors	Autoregressive models	(Aukema <i>et al.</i> 2008)
	Spatial-filtering	(Fergnani, Sackmann, & Cuezco 2008)
	Nearest-neighbour distance	(Scharf <i>et al.</i> 2008)
Habitat fragmentation	Generalized linear mixed models	(Powers <i>et al.</i> 1999; Tschardtke <i>et al.</i> 2002; Rabasa, Gutierrez, & Escudero 2005; Fred, O'Hara, & Brommer 2006; Li <i>et al.</i> 2007)
*Patch indexes	Multiple regression analysis	(Krauss, Steffan-Dewenter, & Tschardtke 2003)
	Field study and ANOVA analysis	(Kreyer <i>et al.</i> 2004; Haynes, Diekötter, & Crist 2007a; Haynes <i>et al.</i> 2007b)
*Source/sink effects	Ring correlation	(Carrière <i>et al.</i> 2004; Ricci <i>et al.</i> 2009)
*Connectivity indexes	Multiple regression analysis	(Diekötter, Billeter, & Crist 2008; Ricci <i>et al.</i> 2009)
Human population	Generalized linear models	(Pautasso & Powell 2009)

suction traps (Bommarco, Wetterlind, & Sigvald 2007), and pheromone traps (Moral García 2006). Other methods are based on pest damage in agroecosystems (Augustin *et al.* 2007). Trapping data and pest damage data are considered to be 'marked point processes', where traps or plants are mapped objects for which the number of trapped individuals or the intensity of attacks are recorded. Direct observations are considered as 'point pattern processes', where the position of each individual is recorded on a two-dimensional Euclidian space. Trapping methods capture only a part of the real population, are generally affected by environmental factors, and they are often sex-biased, for example with pheromone traps. It is important to recognize that these limitations in sampling could affect our understanding of spatial heterogeneity.

TYPES OF SPATIAL POPULATION PATTERNS

Spatial patterns are usually divided into three types: random, aggregated, or regular (Begon, Harper, & Townsend 1996). Random distributions can be modelled by negative binomial or Poisson distributions (Desouhant, Debouzie, & Menu 1998). Distribution patterns may also be of a gradient type (Judas, Dornieden, & Strothmann 2002). Spatial patterns could be the result of the superposition of different types of patterns. Wiegand, Martinez, & Huth (2009) found that spatial pattern of tropical tree species is composed of a random component and a component with two critical scales of clustering. This pattern can be modelled by Thomas processes (Thomas 1949) consisting of a set of clusters and points for each given cluster. Position of points relative to each cluster follows a

Table 2. Overview of mechanistic models used to investigate spatial patterns of insect populations and corresponding references

Topic	Method	References
Population spatial pattern results from...		
Insect behaviour		
*Dispersal	Lattice model	(Lee <i>et al.</i> 2007)
*Mate-finding behaviour	Individual-based model	(Byers 1991; Tyson <i>et al.</i> 2008)
*Aggregation	Metapopulation model	(De Gee, Lof, & Hemerik 2008; Lof <i>et al.</i> 2008)
	Network model	(Yakob, Kiss, & Bonsall 2008)
	Individual-based model	(Depickere, Fresneau, & Deneubourg 2004)
	Cellular automaton	(Perfecto & Vandermeer 2008)
*Egg-laying tactic	Probabilistic model	(Horng 1997; Gilbert, Vouland, & Grégoire 2001; West & Paul Cunningham 2002; Zu Dohna 2006)
	Individual-based model	(Byers 1996)
Habitat heterogeneity results from...		
Insect damages	Cellular automaton	(Kondoh 2003; Bone, Dragicevic, & Roberts 2006; Lee <i>et al.</i> 2007)
	Differential equations	(Lopes <i>et al.</i> 2007; Lopes, Spataro, & Arditi 2010)
	Individual-based model	(De Knegt <i>et al.</i> 2008)
Insect behaviour	Individual-based model	(Theraulaz & Bonabeau 1995)
Habitat heterogeneity affects population dynamics or population resistance to insecticide		
Landscape factors	Network model	(Yakob, Kiss, & Bonsall 2008)
	Reaction-diffusion model	(Tyson, Thistlewood, & Judd 2007; Roques, Auger-Rozenberg, & Roques 2008)
	Individual-based model	(Parry, Evans, & Morgan 2006; Arrignon <i>et al.</i> 2007)
	Leslie matrix model	(Benjamin, Cédric, & Pablo 2008)
Climate factors	Lattice model	(Kizaki & Katori 1999)
	Individual-based model	(Parry, Evans, & Morgan 2006; Arrignon <i>et al.</i> 2007)
Habitat fragmentation	Leslie matrix model	(Pichancourt, Burel, & Auger 2006)
	Cellular automaton	(Cerdeira & Wright 2004)
	Metapopulation model	(Ovaskainen <i>et al.</i> 2002; Hanski & Heino 2003; Kondoh 2003; Fred, O'Hara, & Brommer 2006)
Planting management	Individual-based model	(King & With 2002; McIntire, Schultz, & Crone 2007)
	Metapopulation model	(Banks & Ekblom 1999)
	Individual-based model	(Levine & Wetzler 1996; Potting, Perry, & Powell 2005; Vinatier <i>et al.</i> 2009)
Resource quality	Differential equations	(Helms & Hunter 2005)

bivariate Gaussian distribution, and position of cluster can be randomly and independently distributed (single cluster). Clusters can be themselves clustered, leading to a double cluster.

The spatial distribution of populations can change across years, as illustrated by He & Alfaro (1997). The authors explained that white pine weevils were restricted to some trees early in the infestation (giving an aggregated distribution); the weevils then dispersed randomly to the other trees (giving a random distribution); and finally the weevils attacked all trees at the peak (giving a regular distribution).

METHODS TO DEFINE THE KIND OF SPATIAL PATTERN

For point pattern processes (see Subsection OVERVIEW OF SAMPLING METHODS), indices are mainly based on counts of individuals per unit of a grid, called quadrat. The simplest indices are based on the variance (S^2) and the mean (μ) of population density per quadrat. Lloyd's (1967) *mean crowding* is defined as $\mu^* = \mu + (S^2/\mu) - 1$ and represents the mean number per individual of other individuals coexisting in the same quadrat. *Patchiness* corresponds to the relative magnitude of spatial, quadrat-to-quadrat variations of population density (Kuno 1991). Taylor's *empirical power equation*

$S^2 = a \cdot \mu^b$ makes it possible to assess the level of aggregation by means of slope b that indicates a uniform ($b < 1$), random ($b = 1$), or aggregated ($b > 1$) distribution of population (Arnaldo & Torres 2005). Morisita's *index of dispersion* (Morisita 1971) is based on the probability that two randomly selected individuals will be in the same quadrat. In addition, Iwao's *patchiness regression* (Iwao 1968) between mean crowding μ^* and mean density μ indicates the contagiousness inherent to the species (intercept of the regression) and the manner in which individuals distribute themselves in their habitat with change in the mean density (slope of the regression).

In contrast to the indices presented above, a statistical method termed SADIE[®] (Perry 1995) takes into account spatial coordinates of quadrats. Given a number of individuals in each of several quadrats, two indexes can be computed from this method: one referring to distance to crowding and one to distance to regular. The first SADIE[®] index is based on the total distance that individuals would have to move in order to get them all in one quadrat. The second SADIE[®] index is based on the total movement necessary to get the same number of individuals in each quadrat (Fortin & Dale 2005). SADIE[®] has been successfully applied to insect counts determined by regular trapping (Ferguson *et al.* 2003). Contrary to Taylor,

Morisita, and Iwao indices, SADIE[®] is able to analyse counts of a given species at different times and counts of multiple species (Thomas *et al.* 2001).

Concurrently to methods applied at the quadrat scale, nearest-neighbour methods are used to analyse patterns of small populations at the individual level (Dodds, Garman, & Ross 2006). For example, the Clark & Evans (1954) index gives a measure of dispersion. It is calculated as the ratio between the mean observed nearest-neighbour distance and the mean expected nearest-neighbour distance in case of randomness. The Clark & Evans index cannot be computed when a large part of the area of observation is not classified because of missing values (Dodds, Garman, & Ross 2006). To test the occurrence of different patterns at different spatial scales within the same population, it is necessary to associate a goodness-of-fit test and the Pielou test to the Clark & Evans index, as shown by Potts & Willmer (1998) in their study of the spatial distribution of bee nests. The nearest-neighbour techniques gather the K -function (Ripley 1976) and its modified forms: the L -function usually defined as $L(r) = \sqrt{\frac{K(r)}{\pi}}$ for $r \geq 0$ (Besag 1977), and the pair correlation function $g(r) = \frac{dK(r)}{2\pi r dr}$ for $r \geq 0$ (Dietrich & Helga 1996). They help determining the radius r at which a collection of mapped points exhibits clustering (negative values) or overdispersion (positive values). As $K(r)$ is expected to be proportional to r^2 in planar case with deviations of interest for small values of r , the L -function has the main statistical and graphical advantage to be directly proportional to r in planar case (Illian *et al.* 2008). The pair correlation function g has the advantage to isolate specific distance classes in a ring dr (Wiegand & Moloney 2004).

In contrast to point pattern processes, marked points processes include the abundance of population at each sampling point. It is relevant to employ spatial autocorrelation indexes that compare the similarity between pairs of sampling points within a given radius to randomly distributed pairs of points (Legendre & Fortin 1989). The spatial autocorrelation is described with Geary or Moran indexes (Legendre & Legendre 1998) and is represented in correlograms that show the relationship between autocorrelation and distance classes between sampling points (Legendre & Fortin 1989). Such indexes allow identifying patchy or gradient distributions and estimating the size of population patches. A particular case of marked point patterns includes the discrete number of individuals per host plant. The fit of frequency distributions on the total number of individuals per host plant (including the non infested ones) can be used to characterize spatial patterns (Warren, McGeoch, & Chown 2003).

Identification of factors affecting spatial pattern

As emphasized by McIntire & Fajardo (2009), various processes can create the same spatial pattern, and therefore characterizing the spatial pattern is insufficient to elucidate the mechanisms that generated it. The possible role of exogenous or endogenous factors must be identified by statistical analyses (Fig. 1: arrow 2 and Table 1). Biological factors such as species

dispersal abilities, aggregation behaviour, or sexual attraction, and temporal variation of species population due to mortality and fecundity, could affect population pattern and will be illustrated in Section Mechanistic modelling approaches. Insects are affected by various environmental factors such as landscape composition, fragmentation of resource, or climate (Huffaker & Gutierrez 1999). Environmental factors are either continuous (e.g. temperature) or discrete (e.g. soil type).

INTERPOLATION AS A METHOD TO EVALUATE CONTINUOUS ENVIRONMENTAL FACTORS AT UNSAMPLED LOCATIONS

Kriging can be used to predict a continuous variable distributed in space or in time at unsampled locations based on data from sampled locations (Stein 1999). Temperature, an important driver of insect populations, is a good example of a variable that could require kriging because the density of climate stations is sometimes less than the resolution of the study (Aukema *et al.* 2008). The use of interpolated temperatures instead of temperature from the nearest climatic station helped Jarvis & Collier (2002) to model the phenology of pests in horticultural crops.

Stationarity is the major condition for applying kriging, i.e. mean and variance of the data must be the same throughout the area under study (Legendre & Fortin 1989). Ordinary kriging considers that values fluctuate locally and that stationarity is limited to local areas (Deutsch & Journel 1998). Interpolation can be performed for specific coordinates (punctual kriging) or for an area (blocked kriging) (Fortin & Dale 2005). More details on the kriging technique can be found in Cressie (1993).

Spatial variation of environmental variables can be interpolated using 'trend surface analysis' (Legendre & Legendre 1998) in which each variable is treated as a polynomial function of the longitude and latitude of the observation area. This method allows extracting simple spatial structures, such as gradient, a single wave, or a saddle. The sample area must be approximately homogeneous, and the sampling design must be close to regular (Norcliffe 1969). Moran's I eigenvectors are suited for extracting features at finer spatial scales than trend surface analysis (Dray, Legendre, & Peres-Neto 2006; Griffith & Peres-Neto 2006).

ASSESSMENT OF LANDSCAPE ELEMENTS

Landscape is considered as a mosaic of discrete spatial elements such as forest patches, field crops, or hedgerows. Landscape elements are usually represented as points, lines, or polygons using a Geographic Information System (GIS) framework (Beckler, French, & Chandler 2004). GIS helps to define their geometrical properties, like shape, edge length, and orientation, often established from aerial photographs. Such properties are important for assessing the effects of barriers or corridors on insect dispersal (Bhar & Fahrig 1998; Den Belder *et al.* 2002). Landscape composition can be evaluated by conducting in-person field surveys (Den Belder *et al.* 2002; Suzuki,

Kawaguchi, & Toquenaga 2007), by using satellite reflectance values to characterize vegetation types (Despland, Rosenberg, & Simpson 2004), or colour-infrared air photographs (Powers *et al.* 1999).

Investigating the connectivity between landscape elements and populations is simple when those elements are represented by lines (Holland & Fahrig 2000). Studying this linkage can be more complicated in the case of ‘polygons’ or ‘patches’ that refer to an area that encompasses elements of the same habitat type. A common practice is to calculate the connectivity between two patches as the product of the migration rate of the studied insect, the distance between the two patches and the area of the patches. The distance between two patches has been formalized by the spatial graph theory (Fall *et al.* 2007) that describes patch connectivity with nodes, links (connection between two nodes), and weights of link (accumulated ‘cost’ along the link’s line that reflects the cost of a movement along the line in terms of energy or of mortality risk). For example, patches are assimilated to their centres when patch area is small compared to the observation area of the study (Rabasa, Gutierrez, & Escudero 2005); when patch area is large compared to the observation area, the distance between two patches is the nearest edge-to-edge distance (Diekötter, Billeter, & Crist 2008). It is also possible to determine the area of each landscape element inside rings defined around each sampling location (Carrière *et al.* 2004; Ricci *et al.* 2009), providing a good description of source-sink effects of landscape elements. For example, Carrière *et al.* (2004) characterized Bt crops (i.e. crops that produce insecticidal proteins from the bacterium *Bacillus thuringiensis*) as sinks of pink bollworms because of the drastic decrease of populations inside these elements, and characterized non-Bt crops as sources of pink bollworms.

METHODS TO LINK CANDIDATE FACTORS TO POPULATION PATTERNS

Landscape features are assessed, and then they get the status of explanatory variables and are selected using various regression analyses. Spatial pattern, such as habitat fragmentation level (Haynes, Diekötter, & Crist 2007a), can be assessed in a factorial design with replications. Effect of spatial pattern on population level is, therefore, evaluated through an ANOVA that helps studying interactions between variable. Explanatory variables could be selected by a stepwise procedure, as exemplified by Elliott *et al.* (1999) on factors affecting aphid predator populations, or with a Bayesian approach (Augustin *et al.* 2007). Generalized linear models (GLM) (McCullagh & Nelder 1989) are suited to non-normally distributed response variables. They put up with counts, proportions or occurrence data based on an appropriate choice of both statistical distribution representing the data (Poisson, Binomial, or Gamma distributions) and the link function relating the mean value of the response to a linear predictor (linear combination of explanatory variables). Beyond the GLM, the Generalized Linear Mixed Model is suitable for multiple scale analysis, as exemplified by Rabasa, Gutierrez, & Escudero (2005) on egg-laying of a butterfly assessed at the scales of patch, plant, and fruit.

The spatial-filtering method transforms a variable containing spatial dependence into one free of spatial dependence (Griffith & Peres-Neto 2006). The original data is partitioned into a spatial-filter variable capturing latent spatial dependency and a non spatial variable (Borcard, Legendre, & Drapeau 1992). This flexible approach generates a very large number of spatial variables for which the most relevant ones need to be selected (Blanchet, Legendre, & Borcard 2008). Among spatial-filtering methods described by Griffith & Peres-Neto (2006), the Principal Coordinates of Neighbour Matrices (PCNM) (Borcard & Legendre 2002) is based on an eigenfunction decomposition of a truncated matrix of geographic distances among the sampling site. The resulting eigenvectors are considered as new variables that can be used in any statistical approaches (e.g. GLM, ordinary least square regression, canonical analyses such as redundancy or correspondence analyses). For example, Hamasaki *et al.* (2009) found spatial autocorrelation as the most important factor explaining odonate assemblages using PCNM, within-habitat environment and land use having comparable effects.

More specialized methods have been proposed to partition the spatial variation in species composition, defined as the ‘beta diversity’ (Whittaker 1972), among environmental and spatial factors. Recently, Legendre, Borcard, & Peres-Neto (2005) have compared two major methods in the domain, the Mantel approach (Legendre & Legendre 1998) based on distance matrices and canonical analysis operating on raw data, either canonical redundancy analysis or canonical correspondence analysis. They showed that the canonical approach is more appropriate to partition the spatial variation of species composition than the Mantel approach that underestimates the amount of explained variation. The Mantel approach, however, is appropriate to analyse variation in species composition among groups of sites.

Mechanistic modelling approaches

Mechanistic models deal explicitly with the processes underlying spatial patterns (Table 2). According to Grimm *et al.* (2005), modellers have to find the optimal level of resolution, called the ‘Medawar zone’, between a too-complex and a too-simple model. Discretizing the population, e.g. by considering age classes, the time, and the space increase the resolution of the model and, accordingly, its complexity. Subsequently, we focus on the capacity of models to account for the spatial arrangement of resources and the interaction among individuals, two key points of the spatial distribution of populations.

CHOICE OF MODELLING APPROACHES IN RELATION TO THE RESOLUTION OF THE MODEL

Spatial patterns may be age-structured, and this calls for explicit consideration of age in corresponding models (Pichancourt, Burel, & Auger 2006; Yoo 2006). In the contrary, models without consideration of age-structure are based on differential equations considering the population of insects as a whole (Lopes *et al.* 2007). The Leslie matrix (Williamson 1959)

divides the population into different age classes and is based on transition probabilities from one class to another, based on mortality and fecundity ratios. Space can be included in these models, leading to a Multisite Leslie Matrix (Lebreton 1996) in which transitions from one habitat element to another are modelled (Pichancourt, Burel, & Auger 2006).

Space, another key point of model resolution, can be considered implicitly, i.e. the exact position of each habitat element or patch density can be considered to be unknown. Among them, metapopulation models such as the Levin's model (Levins 1969) calculate the number of sites occupied by a species. Dispersal is considered as unconstrained in implicit models, and local dispersal is therefore not considered (Tilman & Kareiva 1997). Implicit approaches are thus suitable for insect species with large dispersal capacities, such as winged species, or when local dispersal can be neglected. Lopes, Spataro, & Arditi (2010) developed an aphid model on this basis and reproduced observed population structure comprising both patches of highly infested plants for aphids that do not disperse and a spatially uniform distribution for long dispersers.

In spatially explicit models, the position of each habitat element, patch density, or individual is known. Among them, cellular automata are composed of a grid of cells with different states and are discrete in time, space, and state (von Neumann 1949). Cell states change according to transition rules and to their neighbourhood (Balzter, Braun, & Kohler 1998). The lattice model (Hassell, Comins, & May 1991) offers a more complex framework in which states of cells are directly linked to population densities simulated by differential equations (Lee *et al.* 2007). As the lattice model, the network model (Yakob & Bonsall 2009) considers spatially located subpopulations with their own dynamics, but with variability in the connection structure of subpopulations. A very different category of spatially explicit models is that of reaction-diffusion models, which consider time, population, and space as continuous variables. They are suited for studying spatial patterns of invasion in systems with little or no spatial heterogeneity of resources (Roques, Auger-Rozenberg, & Roques 2008).

When local movements and individual behaviour are considered as important processes affecting the spatial pattern, an individual-based modelling (IBM) approach will better describe the system, based on emergence of population properties from individual behaviour (Grimm & Railsback 2005). In IBMs, each individual is explicitly modelled and acts according to a set of rules depending on the landscape structure which is represented by a grid. Space and time are generally discrete. Because they have a high level of resolution, IBMs are parameter consuming, and the best combination of parameters that describes the spatial pattern must be selected to avoid exceeding the computation capacity.

MODELS AS EXPLORATORY TOOLS FOR STUDYING THE SPATIAL ARRANGEMENT OF RESOURCES

The effects of habitat fragmentation on population dynamics can be studied by means of metapopulation models, considering group of sites that are suitable or unsuitable. They are

well suited for populations with large dispersal ranges relative to the landscape area (Ovaskainen *et al.* 2002). Metapopulation models, however, cannot be used to investigate the effects of element boundaries on movement or the effects of temporal variation in element quality (Pichancourt, Burel, & Auger 2006). More sophisticated models allow studying the effect of various spatial arrangements of plants on population dynamics, and therefore can be seen as 'virtual laboratories' (Charnell 2008). They can guide the arrangement of attractive, repulsive, or resistant plants that are grown with a cultivated crop (Potting, Perry, & Powell 2005; Tyutyunov *et al.* 2008).

MODELLING INTERACTIONS AT THE LOCAL OR INDIVIDUAL SCALE

Cellular automata and IBM are commonly used to represent interactions between individuals or between local populations of insects. Cellular automata are particularly suitable for modelling interactions between neighbours when dispersal is weak relative to the landscape area under study. The combination of a cellular automaton and a GIS environment is common (see Bone, Dragicevic, & Roberts 2006 for an example on forest insect infestation). Using a cellular automaton, Kondoh (2003) showed that the spatial heterogeneity of a plant can lead to overgrazing by herbivores.

Individual-based models have been used to study aggregation by ants (Depickere, Fresneau, & Deneubourg 2004) and fruit flies (Lof *et al.* 2008) as well as mate-finding behaviour of other insects (Byers 1991; Tyson *et al.* 2008). The elucidation of how individual behaviour affects the mating rate is relevant for the use of sterile insect techniques in the control of pest populations (Marsula & Wissel 1994). Yamanaka, Tatsuki, & Shimada (2003) used an IBM to investigate the effect of wind on pheromone trap efficiency and found that the modelled population clustered around the pheromone plume.

Linking spatial patterns and ecological processes

Spatial patterns of insect populations can be studied by inductive or deductive procedures (McIntire & Fajardo 2009). The inductive procedure characterizes the pattern and then suggests hypotheses about the underlying processes. The deductive procedure tests multiple hypotheses of underlying processes by comparing them with the pattern, either by experimentation or with mechanistic or statistical models. The aim of fitting a model to empirical data is to gain an understanding of the pattern (Illian *et al.* 2008). Inferring processes from spatial patterns is a new approach motivated by advances in statistical and mechanistic modelling (Grimm *et al.* 2005; McIntire & Fajardo 2009) (Fig. 1: arrows 3). These two procedures are discussed in the following paragraphs. Few studies attempt to link statistical and mechanistic methods, regarding the references figuring both in Tables 1 and 2 (Gilbert, Vouland, & Grégoire 2001; Hanski & Heino 2003; Fred, O'Hara, & Brommer 2006; Zu Dohna 2006).

INDUCTIVE PROCEDURE

Explaining a spatial pattern is sometimes reduced to the suggestion of processes from the characterization of the spatial pattern. For example, woodlots could physically restrict the dispersal of onion thrips and increase thrips mortality because of enhanced enemy abundance (Den Belder *et al.* 2002). The egg-laying decisions of *Apion onopordi* may reflect their limited dispersal abilities (Moravie, Borer, & Bacher 2006). Broad *et al.* (2008) assumed that the spatial pattern of lepidopteran herbivores could result from interference with host location and egg-laying processes. In some cases, these suggestions merely require time to be further tested. However, testing complex mechanisms by means of models or experiments such as learning behaviour of insects (West & Paul Cunningham 2002) or the Allee effect (Takasu 2009) appears a hard task.

DEDUCTIVE PROCEDURE USING EMPIRICAL STUDIES

In some cases, the type of spatial pattern detected suggests underlying simple mechanisms that motivate empirical studies. For example, Chamorro-R, Montealegre-Z, & Gonzalez-O (2007) used nearest-neighbour analyses to determine that the spatial distribution of males of *Panacanthus pallicornis* tended toward randomness or uniformity; based on this pattern, the authors hypothesized that the spacing of males was due to the calling song. They validated this hypothesis by studying dispersal of two groups of released males, one group with torn tympanic membranes and the second with intact tympanic membranes. Ellis (2008b) estimated that the spatial distribution of offspring of the tree mosquito was aggregated. Using both a capture–mark–recapture study and the same spatial indices, he then compared different scenarios for explaining the roles of habitat selection, passive aggregation, and egg-laying preference in the spatial population patterns.

DEDUCTIVE PROCEDURE USING STATISTICAL MODELS

McIntire & Fajardo (2009) proposed a new approach, called ‘Space as a surrogate’, that combines mechanism and statistical models for inferring processes from spatial patterns. The approach is based on (i) the determination of all the relevant processes affecting the system under study, (ii) the development of the resulting spatial patterns these processes would create, and (iii) the comparison of these hypothesized, process-based patterns with the real patterns. For example, McIntire (2004) tested multiple hypotheses concerning the spatial pattern of the mountain pine beetle and found that factors such as weather and surface vegetation affected the boundary formation of beetle outbreaks. This framework helps the researcher to infer mechanisms without additional empirical study. Finally, the framework should be applied to the construction of multiple hypotheses around processes, e.g. random or correlated walks, long or weak dispersers, aggregative or repulsive behaviours.

Autoregressive models combine *per se* mechanism and statistical methods. They are well suited for modelling the

abundance of species whose distributions are controlled by a combination of exogenous factors and biological properties (Lichstein *et al.* 2002). The spatial autoregressive process can occur (i) only in the response variable (‘lagged-response model’), (ii) both in response and predictor variables (‘lagged-mixed model’), (iii) only in the error term of the model (‘spatial error model’) (Dormann *et al.* 2007). Such models can account for ecological processes, such as density dependence (Bommarco, Wetterlind, & Sigvald 2007; Bjørnstad, Liebhold, & Johnson 2008), spatial dependence of the population at neighbouring locations (Kadoya *et al.* 2009), or both spatial and temporal dependencies (Aukema *et al.* 2008). The regression also includes exogenous factors concerning climate (Aukema *et al.* 2008) or landscape composition (Kadoya *et al.* 2009). These autoregressive models usually provide a better prediction of the population distribution than simple regression (Latimer *et al.* 2006). Autoregressive models may be unsuitable for very large georeferenced data sets because of computation time required for analysing distance matrices (Griffith & Peres-Neto 2006).

DEDUCTIVE PROCEDURE USING MECHANISTIC MODELS

Because a spatial pattern is the result of ecological processes, it is interesting to compare patterns emerging from simulations of those processes with real data. Following ‘pattern-oriented modelling’ approach (Grimm *et al.* 2005), ‘single working hypothesis’ models are constructed and their confrontation to data can lead to the acceptance or rejection of the hypothesis (Hanski & Heino 2003; Fred, O’Hara, & Brommer 2006; Parry, Evans, & Morgan 2006; Arrignon *et al.* 2007; Vinatier *et al.* 2009). When there is a good fit of modelled to real results, it may be difficult to know whether the processes and parameters of the model are relevant because a different set of processes and parameters could simulate the same pattern. When there is a poor fit of modelled to real results, the rejection of the hypothesis does not confirm any particular alternative hypothesis, as emphasized by McIntire & Fajardo (2009).

A further understanding of spatial patterns can be obtained by determining whether alternative models reproduce the observed pattern (Grimm *et al.* 2005), models failing to reproduce the observed spatial pattern being rejected. The objective of this approach is similar to that of the ‘space as a surrogate’ framework described above for statistical models. Gilbert, Voulant, & Grégoire (2001) illustrated this approach in the study of distribution of attacks of *Dendroctonus micans* by both Morisita’s index of dispersion and a probabilistic model. Among a choice of scenarios, the best fit was obtained for the hypothesis of induced host susceptibility following random attack.

Pattern-oriented modelling can also reduce the uncertainty of parameter estimates by estimating parameters that reproduce different patterns simultaneously. This technique, which is known as ‘inverse modelling’, was used by Vandermeer, Perfecto, & Philpott (2008) to study the spatial distribution of ant clusters. The authors constructed a cellular automaton

based on two parameters, ant clusters expansion and mortality, and they used both population density over time and cluster size distribution as criteria for the estimation procedure.

Conclusions

Spatial patterns of insect populations depend on various factors reflecting the behaviour of individuals and the spatial organization of habitat patches. Among methods used to understand spatial patterns, statistical models are widely used to link population levels with habitat traits in a descriptive way, leading to a better knowledge of habitat preferences of insect species. Mechanistic models offer the possibility to understand the mechanisms resulting in population patterns, and to evaluate the role of habitat and other factors. Inferring those processes from patterns relies on a judicious combination of methods, especially of statistical and mechanistic models that can be combined in an iterative process. Statistical models are used to identify factors influencing the spatial distribution. When factors are identified, statistical or mechanistic models are used to understand which mechanism is related to those factors and how it influences the spatial pattern. Simulated patterns are compared to observed patterns using similar statistical indexes.

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