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ECOGRAPHY

Research

Understanding complex spatial dynamics from mechanistic models through spatio-temporal point processes

Patrizia Zamberletti, Julien Papaix, Edith Gabriel and Thomas Opitz

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Landscape heterogeneity affects population dynamics, which determine species persistence, diversity and interactions. These relationships can be accurately represented by advanced spatially-explicit models (SEMs) allowing for high levels of detail and precision. However, such approaches are characterised by high computational complexity, high amount of data and memory requirements and spatio-temporal outputs may be difficult to analyse. A possibility to deal with this complexity is to aggregate outputs over time or space, but then interesting information may be masked and lost, such as local spatio-temporal relationships or patterns. An alternative solution is given by meta-models and meta-analysis, where simplified mathematical relationships are used to structure and summarise the complex transformations from inputs to outputs. Here, we propose an original approach to analyse SEM outputs. By developing a meta-modelling approach based on spatio-temporal point processes (STPPs), we characterise spatio-temporal population dynamics and landscape heterogeneity relationships in agricultural contexts. A landscape generator and a spatially-explicit population model simulate hierarchically the pest–predator dynamics of codling moth and ground beetles in apple orchards over heterogeneous agricultural landscapes. Spatio-temporally explicit outputs are simplified to marked point patterns of key events, such as local proliferation or introduction events. Then, we construct and estimate regression equations for multi-type STPPs composed of event occurrence intensity and magnitudes. Results provide local insights into spatio-temporal dynamics of pest–predator systems. We are able to differentiate the contributions of different driver categories (i.e. spatio-temporal, spatial, population dynamics). We highlight changes in the effects on occurrence intensity and magnitude when considering drivers at global or local scale. This approach leads to novel findings in agroecology where, for example, we show that the organisation of cultivated patches and semi-natural elements play different roles for pest regulation depending on the scale considered. It aids to formulate guidelines for biological control strategies at global and local scale.

Keywords: landscape heterogeneity, meta-model, multi-type spatio-temporal point process, spatially explicit model, spatio-temporal pattern, system dynamics



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Introduction

Community structure, population dynamics and species interactions within and between trophic levels are not limited within single plot's borders but depend on the spatial context (Delaune et al. 2019) and on ecological processes at different spatial scales (Pickett and Siriwardena 2011). The key to understanding and predicting community structure and population distribution lies in the explication of the latent mechanisms and causes underlying observed patterns, which may emerge from the collective behaviour at smaller scale units or may be imposed by larger-scale constraints and the related temporal scale (Levin 1992). Moreover, the influence of different spatial and temporal scales is closely related with species life-history traits, such as their ability to disperse, body size, competition, habitat specialisation or trophic position (Rusch et al. 2010, O'Rourke et al. 2011). For example, foraging range and dispersal ability may determine the landscape elements that contribute to population dynamics and trophic interactions (Eber 2001, Fahrig 2001, Tscharntke and Brandl 2004).

Hence, the complex interplay of processes within the landscape and over different scales is one of the key factors in influencing population dynamics across ecosystems. To account for this complexity, the development of spatially explicit computer modelling and simulations are central for addressing theoretical questions. Many spatially explicit model (SEM) types have been proposed, such as continuous-space reaction–diffusion partial differential equations (Roques 2013), patch models (Hanski and Thomas 1994), cellular automata neighbourhood models (Hogeweg 1988) or individual-based models (IBM) (Grimm and Railsback 2005). SEM implementation is commonly realised through numerical approaches that allow for system dynamics simulation. DeAngelis and Yurek (2017) show the importance and the benefits of using SEMs compared to spatially implicit models (SIMs) through different examples, including a savanna ecosystem. They find that the details and small-scale processes captured by SEMs are fundamental drivers of the ecosystem and its dynamics.

The development of advanced numerical models has greatly improved our ability to accurately describe complex dynamics incorporating fine-grain interactions over a large extent. However, as model behaviour depends on the spatial resolution of input, the spatio-temporal extent is often properly adapted by scaling decisions (Fritsch et al. 2020). In-model scaling methods give control over simplifications when building the model or allow us to incorporate and transfer relevant information across different scales. Scaling techniques may also be used before or after building the model, to define model parameters or analyse model outputs.

In this work, we focus on post-model scaling and propose a parsimonious approach to deal with the complexity of SEM outputs while preserving fine-scale information on the ecological dynamics. A solution to deal with this complexity could be the application of non-spatial analysis methods via spatial and temporal output aggregation (Gotelli 2000,

Webb 2000, Fritsch et al. 2020). In this case, however, all fine-scale information is lost, thus impeding any analysis of the drivers acting across different scales. An alternative solution is represented by meta-models, which offer the possibility of reducing model output complexity by establishing a simplified mathematical relationship between the input and output of the system (Simpson et al. 2001, Ratto et al. 2012, Saint-Geours 2012, Jia and Taflanidis 2013). Where possible, an elegant way to build meta-models is the approximation through an analytical model, which is fitted to the large-scale output and allows for simplification (Grimm and Railsback 2005, Johst 2013). Spatial statistic techniques are potential candidates of great interest and should be further explored (Fritsch et al. 2020). For example, (Jia and Taflanidis 2013) present a systematic implementation and optimisation of kriging meta-models for hurricane wave and surge prediction maps based on high-dimensional outputs to reduce complexity while preserving spatial dimension. In functional magnetic resonance imaging analysis, (Kang et al. 2014) synthesise brain mapping information from images and propose a spatial point process approach to model local maxima of brain activation area, explaining the brain task involved.

Here, we show how spatio-temporally explicit outputs of population dynamics models in landscape ecology can be analysed through a meta-modelling approach. Such outputs are simplified to point patterns composed of individual positions, key events or significant hotspots defining local dynamics. The resulting patterns can be modelled as spatio-temporal point processes (STPP). Predictor variables that seek to explain the process are related to the structure of the spatial domain, and its temporal changes (Diggle 2003, Illian et al. 2012, Renshaw 2015, Illian and Burslem 2017). Point processes can be defined over continuous space and time, such that there is no need to work with fixed spatial and temporal units; they can be used for descriptive analyses and stochastic modelling of patterns. For example, Law et al. (2009) apply STPP tools for characterising observed plant patterns; (Gabriel et al. 2017, Opitz et al. 2020, Pimont et al. 2020) develop models for wildfire occurrences through STPPs accounting for the multi-scale structure of data and strong non-stationarities.

The main novelty of our work resides in the characterisation of spatio-temporal population dynamics through STPPs. As a case study application, we focus on the relationships among agricultural landscape structure and the dynamics of a pest and its natural enemy. A hierarchical framework is developed (Fig. 1): 1) a stochastic landscape model, characterised by parameters determining the landscape configuration and composition, is constructed and simulated; 2) a spatially explicit population dynamics model, characterised by parameters determining the pest–predator structure and its spatial heterogeneity, is constructed and simulated. 3) We represent spatio-temporally explicit outputs returned by this modelling chain as point patterns identifying space-time-indexed key events of pest dynamics, that we subsequently model by constructing and estimating statistical regression equations for multi-type STPPs. This approach allows us to investigate the role of

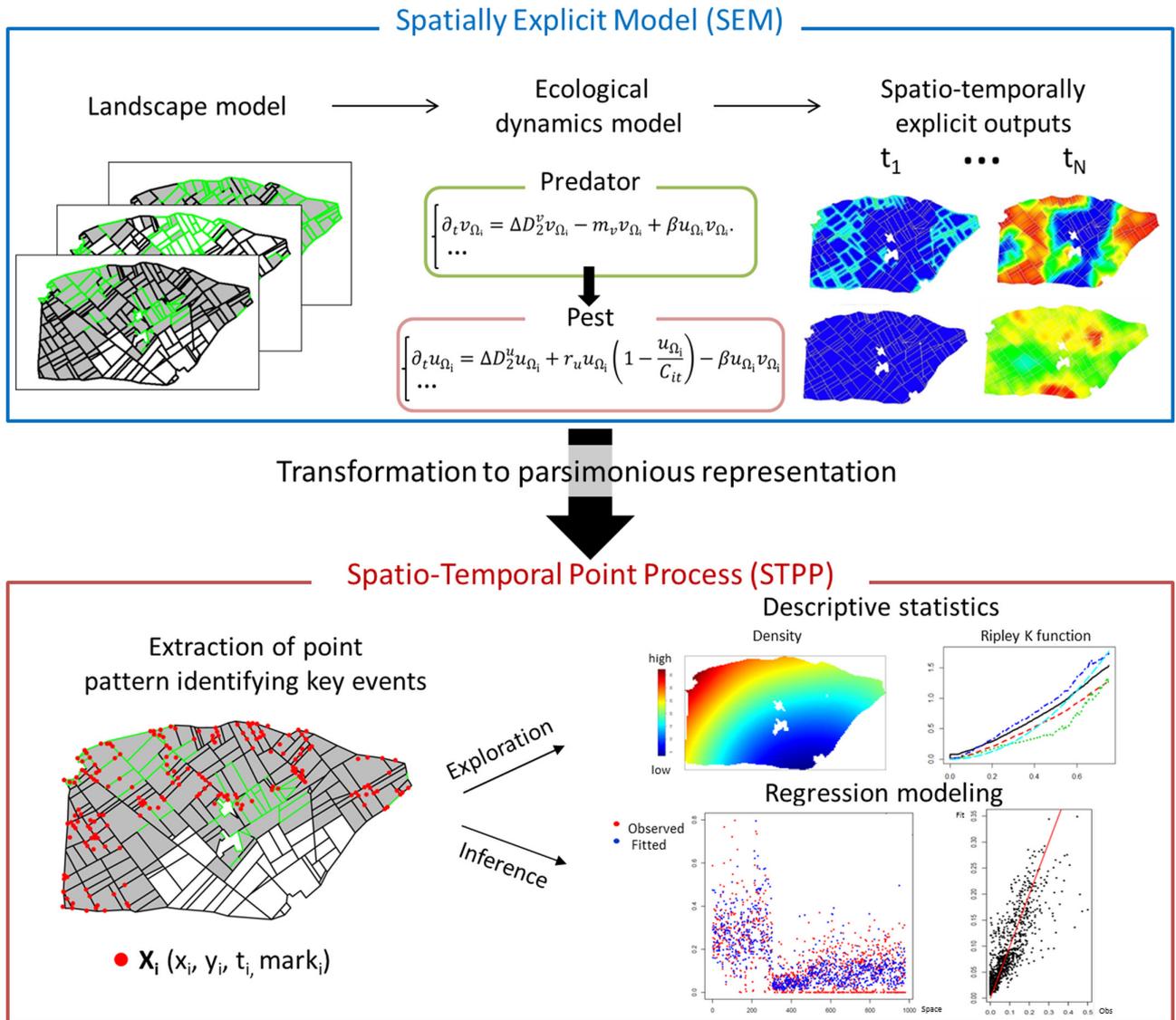


Figure 1. Overview of meta-modeling workflow.

landscape structure in influencing the point process intensity summarising the pest–predator dynamics, and we address two questions: 1) How can spatially-explicit model outputs be parsimoniously represented while conserving key system dynamics information? 2) How can this method be applied to decipher the interplay between landscape effects and population dynamics traits at different spatio-temporal scales?

Simulation models for landscape–pest–predator dynamics

Pest–predator models within agricultural landscapes

We model agricultural landscapes composed of crops, semi-natural areas and hedges through a stochastic landscape generator. Landscape simulations are the spatial domain for a spatially explicit population model of natural enemies and

pests with opportune pesticide treatments on pests. We generate a wide variety of structurally different landscape composition and configuration scenarios for the allocation of crop over patches and of hedges over linear elements by varying representative parameters (i.e. crop and hedge proportion and their aggregation); details are provided in the Supporting information. Within these generated spatial domains, we then simulate the dynamics of the codling moth *Cydia pomonella* pest and of one of its main predators, the family of ground beetles (*Carabidae*), in apple orchards. The pest–predator model is defined by a spatially explicit and density-based model of reaction–diffusion type, allowing for dispersal both on agricultural patches and on hedge network (Roques and Bonnefon 2016).

Codling moths respond strongly to the spatial distribution of apple orchards over landscapes (Tischendorf 2001, Ricci et al. 2009). Franck et al. (2011) have found both low genetic differentiation among their populations over large

distances, indicating that they can disperse over large distances in agricultural landscapes without substantial impact of hedges, and strong effects of insecticide treatments on genetic differentiation resulting from spatial and temporal population size variations (Franck et al. 2011). Thus, in the model, we assume that the pest can be encountered only in patches and that it has positive growth only in patches allocated with crop. In addition, patch boundaries do not affect the pest population dynamics, i.e. the life cycle of *Cydia pomonella* is mostly based in apple orchards, meaning that it perceives the landscape as a heterogeneous environment of crop and semi-natural patches. Finally, we impose the application of local pesticide treatments when the pest density exceeds a fixed threshold on average in a crop patch.

The presence of semi-natural areas, such as hedges, promotes the presence of pest natural enemies (Thies and Tschardt 1999, Maalouly et al. 2013) by offering shelter and by providing complementary resources when pests are not present in patches. Lefebvre et al. (2017) present a field study investigating the routine movement of arthropods among apple orchards and adjacent hedgerows. They found that there are frequent movements for foraging (to apple orchards) and for escaping treatments (to hedges), demonstrating the important influence of hedgerows on the presence of numerous predators in apple orchards. Thus, in our model, we consider that hedges form the main habitat of the predator. The predator can spill over from hedges to patches and there feed on pests in patches as an alternative resource. However, it is generally attracted to hedges, which are its preferred habitat, so that migration from patches to hedges is relatively high compared to migration from hedges to patches (Lefebvre et al. 2017).

Details about the pest–predator dynamics among linear elements and patches are fully presented in Roques and Bonnefon (2016). All the parameters are shown in the Supporting information. To fix parameter ranges, we had performed a sensitivity analysis in a preliminary step since observation data of pests and predators are not available (Zamberletti et al. 2021). Variations in predator population density are mainly explained by predator migration and by hedge proportion. For the pest population density and the average number of pesticide treatments, the most important parameters to explain model output variability are crop proportion and pest growth rate.

Initially, the predator is present in all hedges at carrying capacity. The pest is introduced randomly in space and time. The time unit can be considered as the day. Model parameters are summarised in Table 1.

Pest–predator spatio-temporal patterns

Simulations provide the spatio-temporal pest and predator densities. We characterise the influence of landscape spatio-temporal structure on the pest–predator dynamics by using point patterns. Following our modelling framework, we identify as events 1) the spatio-temporal treatment occurrence (i.e. pest threshold exceedance or pest peak) and 2) the spatio-temporal

pest introductions. For example, when pest threshold exceedance occurs in a patch, we apply a treatment in this patch and, to define the event episode as a point, we extract the time t of threshold exceedance, the pest density maximum in the patch with its Euclidean coordinates (x, y) , and the average pest density over the patch. In Fig. 2, two simulations are shown for different time steps, where the spatio-temporal occurrences of pest introductions and treatments within different landscape allocations are highlighted. This example also illustrates the conjecture that the spatial hedge structure plays a role for pest dynamics. Deeper exploratory quantitative analyses of spatio-temporal relationships between different types of points are proposed in the Supporting information, while we focus on statistical model-based analyses in what follows.

Methods: STPP-based analysis of pest–predator dynamics

Pest densities represented as spatio-temporal point processes (STPPs)

Point patterns representing individual or event distributions in space and time can be modelled as STPPs (Diggle 2003, Illian et al. 2008, Baddeley et al. 2015). Each point can be endowed with additional qualitative or quantitative information defined as a ‘point mark’. In our application, the pattern of events was defined by the coordinates in space and time of pest peaks with both qualitative (pest introduction) and quantitative (pest maximum density) marks. Thanks to the theory of STPPs it is possible to analyse the point distribution properties locally in space and time, and to estimate models for predictive purposes (e.g. number of events, point-to-point correlations and distribution of their numerical or categorical marks). We focused on modelling the point process intensity function (local point density) (Illian et al. 2013). Our modelling goal was to predict the intensity of pest density peaks and the associated values of maximum pest density, and explain their variability in space, through time and across different simulations. We divided the spatial domain in a relatively large number of small cells, and we set a time interval (10 days) to identify an elementary volume (Fig. 3), where we assumed as homogeneous point process intensity. The spatio-temporal discretisation and background on its structure and construction is provided in the Supporting information.

Pest density peak meta-modelling

For predicting the intensity of pest density peaks and associated values of maximum pest density, we developed and estimated regression equations for multi-type STPPs. Both global and local landscape features, species life-history traits and the occurrences of pest introductions, pest peaks and treatments were used as covariate information. We constructed two separate generalized linear model (GLM) formulas as meta-models that incorporated the available covariate information. Response variables and

Table 1. Covariates used in the space-time regression model of pest density peak patterns. The temporal unit d stands for day.

Index	Covariate	Spatial reference	Range	Unit
Spatio-temporal (STC)				
1	No. of treatments in the patch at $t - 1$	Patch	0–40	–
2	No. of treatments in the patch cumulated up to $t - 2$	Patch	0–97	–
3	No. of treatments in neighbour patches at $t - 1$	Patch	0–337	–
4	No. of treatments in neighbour patches cumulated up to $t - 2$	Patch	0–861	–
5	No. of pest density peaks at $t - 1$	Cell	0–15	–
6	No. of pest density peaks cumulated up to $t - 2$	Cell	0–36	–
7	No. of pest density peaks in neighbour cells at $t - 1$	Cell	0–45	–
8	No. of pest density peaks in neighbour cells cumulated up to $t - 2$	Cell	0–97	–
9	No. of pest introduction in cell at $t - 1$	Cell	0–30	–
10	No. of pest introduction in cell cumulated up to $t - 2$	Cell	0–30	–
11	No. of pest introduction in neighbour cells at $t - 1$	Cell	0–30	–
12	No. of pest introduction in neighbour cells cumulated up to $t - 2$	Cell	0–39	–
Spatial (SC)				
13	Cell dimension	Cell	0–0.069	km ²
14	Binary indicator if the cell intersects 2 patches	Cell	0–1	–
15	Binary indicator (1/0) if the cell intersects 3 or more patches	Cell	0–1	–
16	Proportion of hedges within the buffer centred in the cell	Buffer	0–1	%
17	Proportion of crops within the buffer centred in the cell	Buffer	0–1	%
18	Landscape crop and hedge aggregation	Landscape	0–5.54	–
19	Landscape crop proportion	Landscape	0–1	%
20	Landscape hedge proportion	Landscape	0–1	%
Population dynamics (PDC)				
21	Pest diffusion in crop patch	Landscape	0.06–12	km ² d ⁻¹
22	Predator diffusion in crop patch	Landscape	0.07–12	km ² d ⁻¹
23	Predator migration from hedge to crop	Landscape	0.1–1	–

covariates were evaluated over each elementary volume (Fig. 3). The spatio-temporal $STC(s, t) = \sum_{k=1}^{12} \beta_k z_k(s, t)$, spatial $SC(s) = \sum_{k=13}^{20} \beta_k z_k(s)$ and population dynamics $PDC = \sum_{k=21}^{23} \beta_k z_k$ covariates put the spatio-temporal event patterns, landscape structure and population dynamics into relation. The $\beta \in R^{23}$ vector gathered the covariate coefficients to be estimated separately for each model, and the values z_k were covariates summarised in Table 1 and provided for each space-time cell. More information on their selection and computation is given in the Supporting information.

Meta-model for the occurrence intensity of pest density peaks

To model the occurrence intensity of pest density peaks, we considered a GLM with Poisson response:

$$\lambda(s, t) = \exp(\beta_0^\lambda + STC(s, t) + SC(s) + PDC) \quad (1)$$

with global intercept β_0^λ and coefficients of the other variables to be estimated. The value $\lambda(s, t)$ represented the average number of pest peaks occurring in a unit of space and time around the point (s, t) , and was assumed to be constant within each cell of the mesh during each time interval of 10 days. Interactions among covariates were not considered to keep the model simple and relatively parsimonious at this stage, as the number of covariates (and therefore of coefficients to estimate) was already high.

Meta-model for magnitudes of pest density peaks

To model the maximum pest density value associated with each pest peak point, we considered a log-Gaussian GLM:

$$P_{\max}(s, t) = \exp(\beta_0^{P_{\max}} + STC(s, t) + SC(s) + PDC + \varepsilon(s, t)) \quad (2)$$

with global intercept $\beta_0^{P_{\max}}$ and coefficients of the other variables to be estimated, where $P_{\max}(s, t)$ was the maximum pest density value associated to the point where the treatment was applied conditional to the occurrence of such a point. The term $\varepsilon(s, t) \sim N(0, \sigma^2)$ corresponded to the spatially and temporally independent and identically distributed Gaussian error terms.

Model evaluation

Model performances were evaluated according to 1) their predictive capacity, by computing the root mean squared error (RMSE) and the area under the ROC curve (AUC); the latter allowed us to evaluate the prediction of the presence of a pest peak or the exceedance of given threshold in the case of pest density value; 2) the accuracy of parameter estimation by computing standard error ratio (SE-ratio) and estimated coefficient difference (EC-diff). The benchmark scenario consisted of 11 500 parameter combinations with 15 repetitions each, to account for landscape stochasticity. Space and time were discretized over 979 cells for 10 time steps. To investigate the sensitivity of model performances, we defined subsets (Supporting information and Table 2)

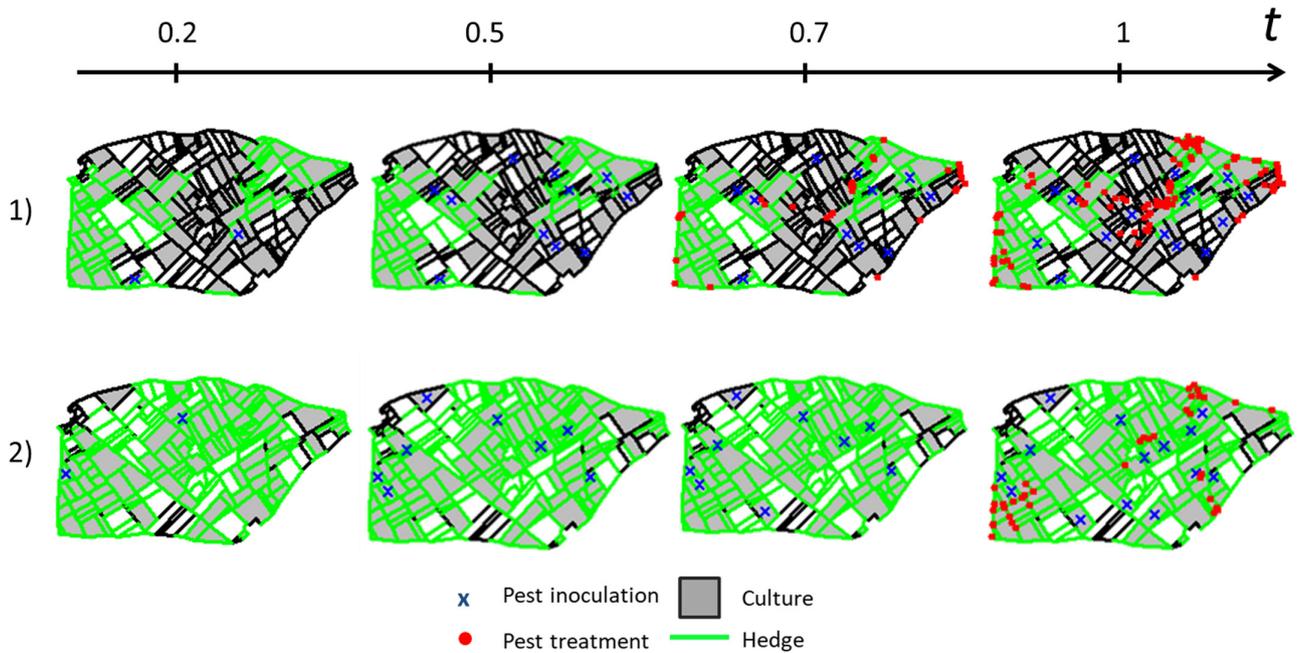


Figure 2. Two simulation examples (by row) illustrating the spatio-temporal pest dynamics depending on landscape structure through pest introductions, and through pest density peaks after threshold exceedances.

reducing repetitions, parameter combinations, spatial cells and time steps. These subsets were used for preforming coefficient re-estimation, while remaining data were used for validation by computing above-mentioned metrics.

Results

Model performances

Table 2 summarizes the results and, generally, shows robust and stable behaviours for both models on peak number and peak value. Reducing the number of parameter configurations led to a decrease in the AUC for the prediction of the presence of a peak in the validation set (but not for the pest density value). As indicated by the RMSE, removing half of consecutive time steps strongly impacted the prediction of the number of peaks and the pest density value. In addition, as indicated by the AUC, the prediction of the magnitude of the pest density value was also impacted but not prediction of the presence of a pest peak.

A reduction of the parameter combinations did not substantially impact model performances with respect to parameter estimation. However, it was necessary to consider more than 5 repetitions to precisely estimate values of model coefficients for peak numbers (EC-diff). Spatial and temporal censoring of the pest dynamics led also to changes in parameter values but to a lesser extent. Similar behaviour was observed for the model of the peak value of pest density, which was particularly sensitive to spatial and temporal censoring.

Spatio-temporal drivers of pest hotspots

We present in Fig. 4 main results obtained by estimating the GLMs in Eq. 1 and 2. Additional results of a covariate correlation analysis and of residual analysis are reported in the

Supporting information, respectively; they showed that the models defined in Eq. 1 and 2 appropriately capture the spatio-temporal variability of the population dynamics model outputs. Prior to estimation, covariates have been scaled to compare more easily the magnitudes of estimated effects.

The proportion of crop at local (%crop buffer) and global (%crop landscape) scales favoured the abundance of suitable habitat for pests, which could easily spread and find resources, leading to a higher number of pest peaks (Fig. 4a). However, the proportion of crop at the landscape scale reduced the magnitude of the pest density at these peaks (Fig. 4a). Hedge proportion in the buffer (Fig. 4a) showed a negative effect of on both variables describing pest activity. Interestingly, however, there was a weaker but positive effect of the hedge proportion over the whole landscape (Fig. 4b). In addition, our model showed that the landscape aggregation had a weak positive effect on peak occurrence numbers while it increased pest density value (Fig. 4b).

Pest diffusion (Fig. 4a) had the strongest negative effect on pest peak values, it may have been due to a dilution effect. Predator diffusion (Fig. 4b) had weaker but similar effects. Predator migration from hedge to crop (Fig. 4b) resulted in a decrease of the number of pest peaks, but it might have increased pest peak values.

High numbers of pest peaks along with high peak values were favoured by the presence of previous peaks in the same cell or in the surrounding ones (Fig. 4a–b, peaks variables). Similarly, an elevated number of introductions in neighbouring (i.e. adjacent) cells led to high pest concentration due to pest spillover (Fig. 4b, introduction variables). The application of pesticide treatments locally in the patch or in neighbouring patches at previous time steps generally led to a decrease of both the number of peaks and the pest density value (Fig. 4b, treatment variables).

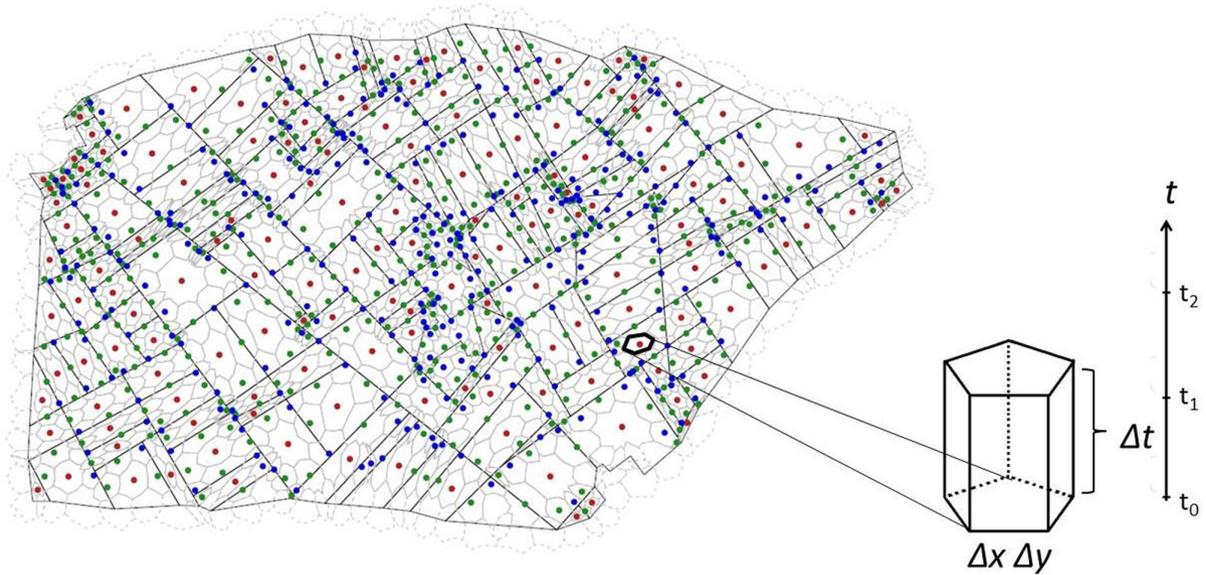


Figure 3. Spatio-temporal discretisation of the regression models for the identification of an elementary volume spatial mesh discretisation (grey dotted line), mesh cells (grey), landscape patches (black). Cell centroids of different colour refer to different cell types: cell in patch center (red), cell connecting exactly two patches (green), cell connecting more than two patches (blue).

Discussion

We propose post-model scaling using regression meta-models based on marked spatio-temporal point processes (STPPs). This approach enabled us to assess and compare the contribution of different spatio-temporal covariates and life-history traits to the direction and strength of variation in crucial

events of population dynamics issued from spatially explicit models. Our approach is flexible and easy to implement, while numerous and diverse covariates describing local and global characteristics can be incorporated. In addition, our methods leverage spatio-temporal and multivariate point pattern techniques, while the state-of-the-art in point pattern analyses deals mostly with purely spatial patterns or does

Table 2. Model performance under different scenarios based on smaller subsets. In predictive performance, the subset was used for re-estimating coefficient (tr) and remaining data were used for validation (val). In estimation capability, the subset is contrasted with the benchmark.

Scenario	Subset	Predictive performance				Estimation capability	
		RMSE (tr)	RMSE (val)	AUC (tr)	AUC (val)	SE-ratio	EC-diff
Occurrence intensity of pest density peaks							
Benchmark	–	0.368	NA	0.909	NA	NA	NA
Repetitions	1/15	0.084	NA	0.94	NA	0.345	323.9
	5/15	0.195	NA	0.905	NA	0.682	35.735
Parameter combinations	50%	0.372	0.401	0.908	0.717	0.71	3.426
	10%	0.379	0.405	0.907	0.693	0.322	11.239
Spatial cells	50%	0.365	0.374	0.907	0.905	0.767	23.467
	10%	0.371	0.367	0.91	0.902	0.715	31.243
	50% crop	0.377	0.377	0.902	0.902	0.716	22.5
Time steps	50%	0.227	3.286	0.949	0.864	0.298	173.71
	10%	0.373	0.376	0.905	0.9	0.667	29.693
Magnitudes of pest density peaks							
Benchmark		0.012	NA	0.762	NA	NA	NA
Repetitions	1	0.013	NA	0.751	NA	0.286	66.933
	5	0.012	NA	0.757	NA	0.621	25.754
Parameter configurations	50%	0.012	0.013	0.76	0.766	0.716	8.14
	10%	0.013	0.012	0.763	0.758	0.308	27.272
Spatial cells	50%	0.013	0.012	0.767	0.756	0.743	1735.933
	10%	0.013	0.012	0.768	0.76	0.019	1735.682
	50% crop	0.012	0.012	0.778	0.762	0.401	1737.931
Time steps	50%	0.013	0.155	0.727	0.637	0.275	2069.302
	10%	0.012	0.012	0.76	0.761	0.651	1728.561

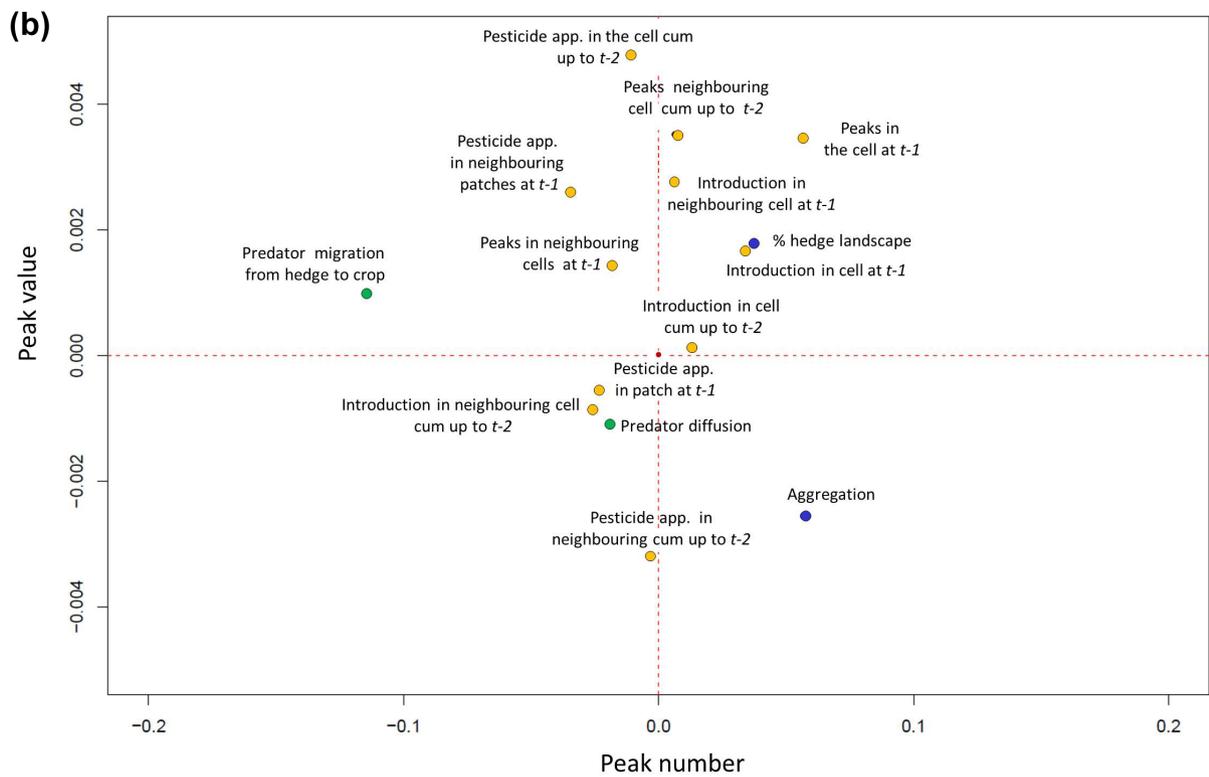
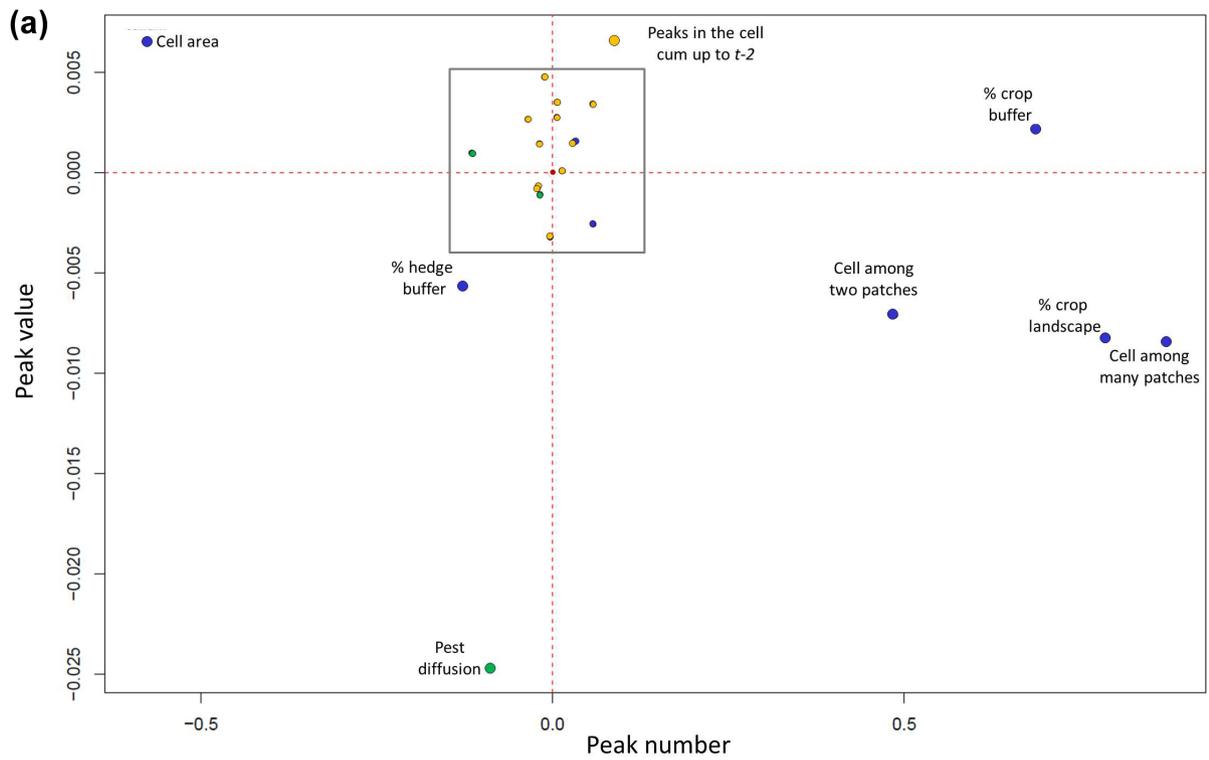


Figure 4. Estimated regression coefficients for the models of peak occurrence intensity (x-axis) and the model of the peak value (y-axis). Dot colours indicate covariate types: STC (orange), SC (blue), PDC (green). (b) is the magnified version of the rectangle in (a).

not well represent the temporal dimension (Wiegand et al. 2017). We applied our methodology to the outputs of a SEM describing the dynamics of a crop pest and its predator.

A large body of literature on meta-models (or surrogate models, or emulators) in various disciplines focuses on Gaussian processes or machine-learning techniques (Forrester et al. 2008, Kleijnen 2015). Discrete events data localized in continuous time and space are also assessed through machine learning (Reinhart 2018, Chen et al. 2020, Zhu et al. 2020, Dong et al. 2021). For example, Du et al. (2016) and Zhang et al. (2020) model discrete events using neural-network-based point process models with the aim of presenting highly performing approaches for reproducing and predicting spatio-temporal patterns observed in the data. Dong et al. (2021) develop a non-stationary spatio-temporal point process for COVID epidemic and introduce a neural network-based kernel to capture the spatially varying triggering effect. However, even if these machine learning-based approaches are very fulfilling, they have been designed for predictive purposes and may lack of interpretability. Their black box nature renders difficult parameter interpretation and driver-process relationship identification. By contrast, our STPP model allowed for a relatively complex spatio-temporal local analysis of system dynamics. It therefore provided insights into the role of different effects and takes process-specific scales into account by using categorical or numerical marks. Through statistical inferences it becomes possible to identify significant relationships of key events with their drivers focusing on biotic interactions and habitat heterogeneity (Baddeley et al. 2015). More generally, our work strikes a pragmatic balance with respect to the inevitable trade-off between model simplicity, to obtain clear insights into important factors, and model complexity, to achieve a more complete and realistic representation of the system (Lacy et al. 2013).

The adaptation of our approach of defining a marked STPP meta-model may be relevant and insightful in various contexts. Examples are occurrence locations and times of earthquake epicentres (Lombardo et al. 2019), wildfires (Opitz et al. 2020), epidemiological outbreaks (White et al. 2018), biodiversity hotspots and species distribution (Soriano-Redondo et al. 2019), pollutant concentrations (Lindström et al. 2014) or local maxima or minima in meteorological events (Heaton et al. 2011). In most ecological process space and time are closely intertwined and not separable as in our case, where pest introductions and subsequent peaks depend on local temporal dynamics driven by local spatial structure. Thus, here, we designed our approach to allow for joint analysis of spatial and temporal scales. White et al. (2018) address how landscape structure impacts simulated disease dynamics in an individual-based susceptible-infected-recovered model. They quantify disease dynamics by outbreak maximum prevalence and duration, coupled with landscape heterogeneity defined by patchiness and proportion of available habitat. Our work had similar thrust by exploring the effect of landscape heterogeneity on pest density peaks. However, by taking advantage of the STPP modelling, we

focused on spatio-temporal positions of peaks, and we investigated which factors locally influence occurrence intensity and magnitude of these events.

In a similar context, Le Gal et al. (2020) highlight the important influence of the interplay between the landscape structure and the timing of CBC measures on the delivery of pest control services. They show that increased semi-natural habitat proportion at the landscape level enhances the visitation rate of pest-colonised crop cells, but it also reduces the delay between pest colonisation and predator arrival in the crop patches. Here, we have opted for simulating the time and position of pest arrival according to a Poisson process with intensity proportional to crop area. We found that locations showing frequent and high density peaks in previous time steps are likely to incur new peaks. On the other hand, local previous treatments in a patch negatively influenced the dynamics since they efficiently reduced the pest density in this patch. Introductions of pest acted as an accelerator of local pest dynamics, and after a short period we often assisted to both high frequency and high magnitudes of peaks in the surrounding patches.

Spatial covariates (SC) in our regression meta-models were time-invariant landscape characteristics that may have influenced pest peaks. Crop proportion was the main driver for pest in our models, and led to a clear positive response of pest insects to increasing cover of a suitable crop (Tscharntke et al. 2007, Avelino et al. 2012, Rand et al. 2014, Zhao et al. 2015, Ricci et al. 2019). Crop proportion at local scale or at global scale led to different peak patterns. When crop aggregation and percentage coverage were high in the whole landscape, pest density threshold exceedances occurred homogeneously over large areas of contiguous crop, but these peaks were of relatively small magnitude because hotspots with high pest clusters and concentration did not build up. Instead, in local aggregates of crop patches, pests found their preferred habitat in a more limited space and tended to concentrate there.

Hedge distribution and proportion can be viewed as a proxy for predator presence and reveal when predators may play a role in reducing pest density (Bianchi et al. 2006, Tscharntke et al. 2007). The effects attributed to semi-natural habitat are ambiguous with both positive, negative or neutral impacts on conservation biological control (Chaplin-Kramer et al. 2011, Karp et al. 2018). In our models, hedge proportion at the landscape scale had a small but positive effect on both the number and the magnitude of peaks. This result might have appeared counter-intuitive at first glance. Since response variables were evaluated at cell scale, having a large hedge proportion in the whole landscape, but a low proportion of hedges in the buffer clearly results in a concentration of pest where hedges were missing. In addition, hedges helped to keep the pest below the treatment threshold and therefore favoured its propagation through the landscape (Zamberletti et al. 2021); therefore, the pest might have reached areas of lower predation pressure more easily and pulled out. Indeed, when focusing on local buffers around a cell, local hedge structure and the resulting predator concentration, played a positive role by reducing both number of pest peaks and their magnitude.

Population dynamics covariates (PDC) in our models were related to species traits. We focused on how the structure of landscape elements influences species spread with respect to the studied events considering parameter related to species mobility. We found that predator diffusion ability over the landscape was fundamental to reduce the presence of pest, as predator were able to rapidly move in the whole landscape. Interestingly, we did not notice the same effect for predator migration speed from hedge to patch. This predator trait acted strongly at locations close to hedges, i.e. around patch borders, with a strong decrease in the number of peaks, while the peak value was not affected but was high mainly in the patch core areas.

To conclude, our approach shows potential to reveal properties in ecological systems that are difficult to identify when considering only the complex model output with large data volumes as a whole. In the context of biological pest control for agricultural landscapes, we have devised an approach for disentangling the effects of local and global drivers acting on the spatio-temporal pattern of pest outbreaks. Our work can help to schedule specific local control strategies by targeting the locations that frequently suffer from pest peaks and the moments when local control strategies can be expected to be most efficient to control pest dynamics.

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Data availability statement

Code and data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.r7sqv9sdr>> (Zamberletti et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

References

- Avelino, J. et al. 2012. Landscape context and scale differentially impact coffee leaf rust, coffee berry borer and coffee root-knot nematodes. – *Ecol. Appl.* 22: 584–596.
- Baddeley, A. et al. 2015. Spatial point patterns: methodology and applications with R. – CRC Press.
- Bianchi, F. J. et al. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. – *Proc. R. Soc. B* 273: 1715–1727.
- Chaplin-Kramer, R. et al. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. – *Ecol. Lett.* 14: 922–932.
- Chen, R. T. et al. 2020. Neural spatio-temporal point processes. – arXiv preprint arXiv:2011.04583.
- DeAngelis, D. L. and Yurek, S. 2017. Spatially explicit modeling in ecology: a review. – *Ecosystems* 20: 284–300.
- Delaune, T. et al. 2019. Spatio-temporal drivers of crop pests and pathogens abundance at the landscape scale. – *Ecography* 44: 1429–1442.
- Diggle, P. 2003. Statistical analysis of spatial point patterns, 2nd edn. – Hodder Arnold Education.
- Dong, Z. et al. 2021. Non-stationary spatio-temporal point process modeling for high-resolution COVID-19 data. – arXiv preprint arXiv:2109.09029.
- Du, N. et al. 2016. Recurrent marked temporal point processes: embedding event history to vector. – *Proceedings of the 22nd ACM SIGKDD international conference on knowledge discovery and data mining*, pp. 1555–1564.
- Eber, S. 2001. Multitrophic interactions: the population dynamics of spatially structured plant–herbivore–parasitoid systems. – *Basic Appl. Ecol.* 2: 27–33.
- Fahrig, L. 2001. How much habitat is enough? – *Biol. Conserv.* 100: 65–74.
- Forrester, A. et al. 2008. Engineering design via surrogate modeling: a practical guide. – Wiley.
- Franck, P. et al. 2011. Genetic inferences about the population dynamics of codling moth females at a local scale. – *Genetica* 139: 949.
- Fritsch, M. et al. 2020. Scaling methods in ecological modelling. – *Methods Ecol. Evol.* 11: 1368–1378.
- Gabriel, E. et al. 2017. Detecting and modelling multi-scale space-time structures: the case of wildfire occurrences. – *J. Soc. Franc. Stat.* 158: 86–105.

- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. – *Ecology* 81: 2606–2621.
- Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology, vol. 8. – Princeton Univ. Press.
- Hanski, I. and Thomas, C. D. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. – *Biol. Conserv.* 68: 167–180.
- Heaton, M. J. et al. 2011. Spatio-temporal models for large-scale indicators of extreme weather. – *Environmetrics* 22: 294–303.
- Hogeweg, P. 1988. Cellular automata as a paradigm for ecological modeling. – *Appl. Math. Comput.* 27: 81–100.
- Illian, J. B. and Burslem, D. F. 2017. Improving the usability of spatial point process methodology: an interdisciplinary dialogue between statistics and ecology. – *AStA Adv. Stat. Anal.* 101: 495–520.
- Illian, J. B. et al. 2012. Using INLA to fit a complex point process model with temporally varying effects—a case study. – *J. Environ. Stat.* 3: 1–25.
- Illian, J. B. et al. 2013. Fitting complex ecological point process models with integrated nested Laplace approximation. – *Methods Ecol. Evol.* 4: 305–315.
- Illian, J. et al. 2008. Analysis and modelling of spatial point patterns, from spatial data to knowledge. – Wiley.
- Jia, G. and Taflanidis, A. A. 2013. Kriging metamodeling for approximation of high-dimensional wave and surge responses in real-time storm/hurricane risk assessment. – *Comput. Methods Appl. Mech. Eng.* 261: 24–38.
- Johst, K. et al. 2013. Scaling up: How do exogenous fluctuations in individual-based resource competition models re-emerge in aggregated stochastic population models? – *Popul. Ecol.* 55: 173–182.
- Kang, J. et al. 2014. A Bayesian hierarchical spatial point process model for multi-type neuroimaging meta-analysis. – *Ann. Appl. Stat.* 8: 1800.
- Karp, D. S. et al. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. – *Proc. Natl Acad. Sci. USA* 115: E7863–E7870.
- Kleijnen, J. P. 2015. Design and analysis of simulation experiments. – In: Pilz, J. et al. (eds), *International workshop on simulation*. Springer, pp. 3–22.
- Lacy, R. C. et al. 2013. Metamodels for transdisciplinary analysis of wildlife population dynamics. – *PLoS One* 8: e84211.
- Law, R. et al. 2009. Ecological information from spatial patterns of plants: insights from point process theory. – *J. Ecol.* 97: 616–628.
- Le Gal, A. et al. 2020. Modelling the interactions between landscape structure and spatio-temporal dynamics of pest natural enemies: implications for conservation biological control. – *Ecol. Model.* 420: 108912.
- Lefebvre, M. et al. 2017. Bayesian inferences of arthropod movements between hedgerows and orchards. – *Basic Appl. Ecol.* 21:76–84.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. – *Ecology* 73: 1943–1967.
- Lindström, J. et al. 2014. A flexible spatio-temporal model for air pollution with spatial and spatio-temporal covariates. – *Environ. Ecol. Stat.* 21: 411–433.
- Lombardo, L. et al. 2019. Numerical recipes for landslide spatial prediction using R-INLA: a step-by-step tutorial. – In: Pourghasemi, H. R. and Gokceoglu, C. (eds), *Spatial modeling in GIS and R for earth and environmental sciences*. Elsevier, pp. 55–83.
- Maalouly, M. et al. 2013. Codling moth parasitism is affected by semi-natural habitats and agricultural practices at orchard and landscape levels. – *Agricult. Ecosyst. Environ.* 169: 33–42.
- O'Rourke, M. E. et al. 2011. A multi-scale, landscape approach to predicting insect populations in agroecosystems. – *Ecol. Appl.* 21: 1782–1791.
- Opitz, T. et al. 2020. Point-process based Bayesian modeling of space–time structures of forest fire occurrences in Mediterranean France. – *Spat. Stat.* 40: 100429.
- Pickett, S. R. and Siriwardena, G. M. 2011. The relationship between multi-scale habitat heterogeneity and farmland bird abundance. – *Ecography* 34: 955–969.
- Pimont, F. et al. 2020. Prediction of regional wildfire activity with a probabilistic Bayesian framework. – *Ecol. Appl.* 2021: e02316.
- Rand, T. A. et al. 2014. Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes. – *Agricult. Ecosyst. Environ.* 186: 135–143.
- Ratto, M. et al. 2012. Emulation techniques for the reduction and sensitivity analysis of complex environmental models. – *Environ. Model. Softw.* 34: 1–4.
- Reinhart, A. 2018. A review of self-exciting spatio-temporal point processes and their applications. – *Stat. Sci.* 33: 299–318.
- Renshaw, E. 2015. *Stochastic population processes: analysis, approximations, simulations*. – Oxford Univ. Press.
- Ricci, B. et al. 2009. The influence of landscape on insect pest dynamics: a case study in southeastern France. – *Landsc. Ecol.* 24: 337–349.
- Ricci, B. et al. 2019. Local pesticide use intensity conditions landscape effects on biological pest control. – *Proc. R. Soc. B* 286: 20182898.
- Roques, L. 2013. *Modèles de réaction-diffusion pour l'écologie spatiale*. – Editions Quae.
- Roques, L. and Bonnefon, O. 2016. Modelling population dynamics in realistic landscapes with linear elements: a mechanistic-statistical reaction–diffusion approach. – *PLoS One* 11: e0151217.
- Rusch, A. et al. 2010. Biological control of insect pests in agroecosystems: effects of crop management, farming systems and seminatural habitats at the landscape scale: a review. – In: Bertsch, P. M. et al. (eds), *Advances in agronomy*, Vol. 109. Elsevier, pp. 219–259.
- Saint-Geours, N. 2012. Sensitivity analysis of spatial models: application to cost-benefit analysis of flood risk management plans. – PhD thesis.
- Simpson, T. W. et al. 2001. Metamodels for computer-based engineering design: survey and recommendations. – *Eng. Comput.* 17: 129–150.
- Soriano-Redondo, A. et al. 2019. Understanding species distribution in dynamic populations: a new approach using spatio-temporal point process models. – *Ecography* 42: 1092–1102.
- Thies, C. and Tschardtke, T. 1999. Landscape structure and biological control in agroecosystems. – *Science* 285: 893–895.
- Tischendorf, L. 2001. Can landscape indices predict ecological processes consistently? – *Landsc. Ecol.* 16: 235–254.
- Tschardtke, T. and Brandl, R. 2004. Plant–insect interactions in fragmented landscapes. – *Annu. Rev. Entomol.* 49: 405–430.
- Tschardtke, T. et al. 2007. Conservation biological control and enemy diversity on a landscape scale (erratum: 2008 may, v. 45, issue 2, p. 238–253). – *Biol. Control* 43: 294–309.

- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – *Am. Nat.* 156: 145–155.
- White, L. A. et al. 2018. Disease outbreak thresholds emerge from interactions between movement behavior, landscape structure and epidemiology. – *Proc. Natl Acad. Sci. USA* 115: 7374–7379.
- Wiegand, T. et al. 2017. Spatially explicit metrics of species diversity, functional diversity and phylogenetic diversity: insights into plant community assembly processes. – *Annu. Rev. Ecol. Evol. Syst.* 48:329–351.
- Zamberletti, P. et al. 2021. More pests but less pesticide applications: ambivalent effect of landscape complexity on conservation biological control. – *PLoS Comput. Biol.* 17: e1009559.
- Zamberletti, P. et al. 2022. Code and data from: Understanding complex spatial dynamics from mechanistic models through spatio-temporal point processes. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.r7sqv9sdr>>.
- Zhang, Q. et al. 2020. Self-attentive Hawkes process. International conference on machine learning. – *Proc. Mach. Learn. Res.* 119: 11183–11193.
- Zhao, Z.-H. et al. 2015. Effects of agricultural intensification on ability of natural enemies to control aphids. – *Sci. Rep.* 5: 8024.
- Zhu, S. et al. 2020. Interpretable deep generative spatio-temporal point processes. – arXiv preprint arXiv:1906.05467v2.