

Metapopulation modelling and area-wide pest management strategies evaluation. An application to the Pine processionary moth



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ABSTRACT

Forecasting pest population abundance is a time and resource consuming task, and in particular for area-wide pest management is complicated by demographic and environmental stochasticity. These factors make difficult the development of quantitative tools to design and evaluate different management strategies performances by taking into account various form of variability and uncertainty. Pest management could benefit from methods supporting decision making based on models ease of development under scarce data and high uncertainty. Host plants for many agricultural and forest pests are often patchily distributed, therefore population dynamics can be suitably described in terms of metapopulations. Despite the fact that metapopulation models were originally proposed for pests, they remain a widely used tool in conservation biology but receive little attention in large scale pest management.

The aim of this paper is to propose a framework allowing the ranking of the efficacy of area-wide pest control strategies, taking into account population spatial distribution in discrete patches. The Kullback–Leibler divergence, well known in Information Theory, Probability and Statistics, is used to measure how far the state of the metapopulation as predicted by a spatially explicit metapopulation model is from a suitable reference state.

The method is applied to compare the efficacy of different types of predefined control strategies of the Pine processionary moth (*Traumatocampa pityocampa* (Den. and Schiff)). The analysis of a dataset on metapopulation dynamics of this moth from a fragmented Mediterranean pine forest allows to derive some rules of thumb for the rational allocation of control effort, in terms of spatial and temporal distribution of the interventions.

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1. Introduction

At the local and global levels, the spatial patterns of agricultural and forest pest population dynamics may vary according to the characteristics of a fragmented landscape (Vinatier et al., 2011). Analyses of spatial heterogeneity are either based on correlations that take into account details of landscapes and their effect on population processes (Wiens, 1997; Hunter, 2002), or on simulation models based on complex assumptions on ecological processes (Sheehan, 1989; Sharov and Colbert, 1996).

Metapopulation models deal with the occurrence of individual populations across an ensemble of habitat fragments (or patches) suitable for the occurrence and reproduction of the species (Tscharrntke and Brandl, 2004), connected by dispersal.

Metapopulation models were originally proposed for pests and were based on a simple description of the frequency of occupied patches (Levins, 1969; Ives and Settle, 1997). The need to explicitly represent patches in space has demanded the development of different metapopulation models. Spatially explicit metapopulation models are a widely used tool in conservation biology, but have received little attention in pest control despite their potentiality (Hunter, 2002). The most widely known spatially explicit metapopulation model for instance, the Incidence Function Model (IFM) (Hanski, 1994), uses area and connectivity to predict metapopulation dynamics and has not been applied yet to agricultural and forest insect, to the best of our knowledge. The apparent lack of interest in applying the IFM and its generalizations to pest is surprising, because it would enable managers to take into account the size of habitat (Fleishman et al., 2002), habitat quality (Moilanen and Hanski, 1998; Fleishman et al., 2002), spatial arrangement (patch structure), patch isolation (connectivity, including matrix) (Fleishman et al., 2002), and patch occupancy (description and possibility of modelling variation in local dynamics).

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Traditionally, pest management has disregarded the effects of habitat fragmentation on population dynamics and only recently, attempts have been made to overcome this and other restrictions (Kogan et al., 1999; Elliot et al., 2008). Spatial expansion of pest management has been motivated by increasing interest in the effects of landscape features on pest population dynamics (Hunter, 2002) and further stimulated by research on species assemblages exhibiting different life strategies in a fragmented landscape. The careful consideration of the spatial dimension is also important for obtaining further insight into species interactions, including herbivory, biological control and pollination (Tscharntke and Brandl, 2004; Tscharntke et al., 2005). These interactions depend on species traits but also on the size and the connectivity of habitats (Tscharntke and Brandl, 2004).

Although area-wide pest management strategies are becoming common (Kogan, 1995; Faust, 2008), the advantages of these strategies are difficult to establish with scientific rigour, and their design and evaluation may be done by modelling tools. Pest management could benefit from quantitative methods based on model ease of development under scarce data and high uncertainty. In this respect, metapopulation models have unexplored potentiality (Hunter, 2002; Grimm et al., 2003; Gilioli et al., 2008; van Nouhuys, 2009). However, metapopulation models should be embedded in a decision-making framework to give managers the capability of ranking alternative decisions (Westphal et al., 2003). This means that the objectives of the management should be explicitly and clearly stated in terms of metapopulation model variables (Possingham et al., 2001). In applied ecology, metapopulation models are frequently used in a decision-making framework for conservation purposes mainly, to evaluate metapopulation persistence. To the best of our knowledge, only a few applications concern pest management. For instance, stochastic dynamic programming (SDP) has been recently applied in pest management related issues, coupled with a spatially implicit metapopulation model, e.g. for invasive species control optimization (Bogich and Shea, 2008), or for biological control release strategies optimization (Shea and Possingham, 2000). However, SDP is computationally complex and its applicability limited to small metapopulations (Nicol and Chadès, 2011). Borrowing from epidemiology, a susceptible-infected-susceptible (SIS) model and a finite Markov decision process have been proposed to manage diseases, pest or endangered species in small (<25 nodes) network motifs (Chadès et al., 2011).

In this paper, we propose a methodology based on a spatially explicit metapopulation model and the Kullback–Leibler divergence (Kullback and Leibler, 1951) to rank area-wide single species pest management strategies. Strategies are ranked according to their capability in achieving at a given point in time an explicitly stated objective, defined by means of the Kullback–Leibler divergence. The required computations are relatively simple and fast. The method deals with a mosaic of different spatial units (patches) infested by a monophagous pest and investigates the interplay between pest population dynamics, dispersal and area-wide control strategies. For the target pest we assume that the problem can be solved by focussing on the pest population rather than on the population system composed of the pest and its natural enemies (Hunter, 2002), and that threshold-based management is an appropriate control strategy. Within this pest metapopulation context, we show that if a spatially explicit metapopulation model adequately describes pest population dynamics, management strategies expressed in terms of variations in the components of such a model can be compared and ranked. To do this, we apply the method proposed by Gilioli et al. (2008). We show how this method accounts for metapopulation dynamics and supports the evaluation of short-term strategies (e.g., spatial and temporal distribution of control interventions) aiming at the management of

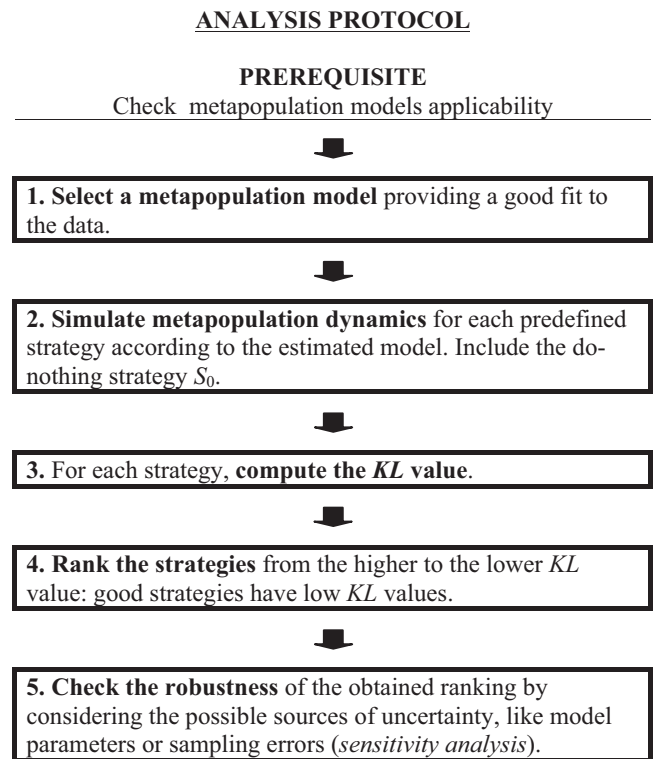


Fig. 1. Scheme of the adopted analysis protocol.

species inhabiting agricultural and forest habitats, where they play the role of pest. Short term strategies are particularly suitable for pests that directly attack essential or yield producing structures of the host plant or pests of significant public health importance, and are an essential component of Integrated Pest Management (Kogan et al., 1999). Fig. 1 summarizes the complete analysis protocol, described in Section 2.

In this paper we consider data from a three years survey of the Pine processionary moth (*Traumatocampa pityocampa* (Den. and Schiff), PPM) populations dynamics in fragmented forest stands of the National Park of Aspromonte, Calabria, Italy. Infestations by PPM cause damage to pine trees that may result in yield loss, negatively affect the value of forests for recreational purposes and diminish the aesthetic value of individual trees in urban environments (Masutti and Battisti, 1990). Pest status is further increased by the production of setae by larvae, often causing serious allergic reactions in humans and various animals (Lamy, 1990). The host plants of the PPM are often patchily distributed in forest areas around the Mediterranean Basin, therefore metapopulation models can be tested to describe PPM population dynamics in a fragmented landscape (Tscharntke and Brandl, 2004; Elliot et al., 2008).

2. Materials and methods

2.1. Study area and data collection

The National Park of Aspromonte consists of Mediterranean-mountain forests characterized by the dominance of the endemic *Pinus nigra* ssp. *calabrica* (= *Pinus laricio* var. *calabrica*), and various conifers in reforestation areas (Brullo et al., 2001). The forest areas considered in our study are predominantly composed of pure *P. nigra* coetaneous forest stands, separated by open grassland or deciduous forests stands which are not inhabited by PPM. The study area faces the Tyrrhenian Sea and covers 817 ha along a 25 km transect extending from Southwest towards Northeast. In

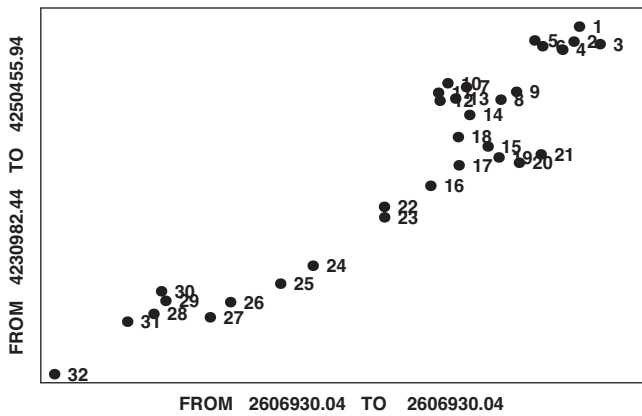


Fig. 2. The set of *Pinus* spp. patches sampled in the National Park of Aspromonte Calabria (Italy). The patches are infested by local populations of Pine processionary moth that make up the metapopulation. Points represent the position of the centroid in the plane of numerical X and Y coordinates (UTM 33 GB40) for each forest patch.

the preparatory phase of the study, maps were obtained from different institutions including the national and regional forest services (Corpo Forestale dello Stato, AFoR) and park authorities (Ente Parco Nazionale d'Aspromonte). Spatial information was completed with soil data made available by the *Corine Land Cover* project (<http://www.eea.europa.eu/publications/COR0-landcover>), digitized aerial colour photographs, georeferenced forest survey data on the dimensions and locations of spatially separated forest fragments, and finally with insect population data from surveys and field observations (Manti and Gilioli, 2006). We consider the isolated forest fragments as patches. A schematic representation of the centroids of the patches in the study area is illustrated in Fig. 2.

In three consecutive years, from 2003 to 2005, PPM nests were sampled in all the 32 forest patches in the study area. During larval development the PPM aggregates into pre-nests that evolve into permanent nests where the larvae overwinter. Monthly counts of pre-nests and nests were taken from October to April, until the number of nests remained constant. The final nests counts were used as an estimation of population abundance. The sample variable consists of the number of nests per tree. Counts were made along a minimum number of 2 and maximum number of 3 transects per patch on 25 neighbouring trees. A random procedure was used to choose the transect position.

2.2. Testing criteria for metapopulation definition

A preliminary step for the application of the proposed approach is to demonstrate that a plant-pest system can be considered as a metapopulation (see Fig. 1). To do this, Hanski (1997) recommends that (a) host plants are distributed as discrete patches, (b) pest populations within patches have a substantial risk of extinction, (c) empty patches are available for colonization, and (d) pest local populations do not fluctuate synchronously. Criterion (a) is satisfied because the occurrence of the PPM is related to the discrete distribution of the host plant. For threshold-based pest control purposes, local pest population dynamics can be described as fluctuating below and above a given target-level of abundance, and empty patches are continuously available for colonization. The last two observations also prove criteria (b) and (c). As far as criterion (d) is concerned, an evaluation of the spatial synchrony among local populations is conducted by means of the Moran's index I , a measure of spatial autocorrelation (Moran, 1950), and of the Mantel test (Mantel, 1967), a measure of the correlation between two sets of

variables based on distance matrices. The index I is computed for different distance classes d as

$$I(d) = \frac{n}{\sum_k \sum_l w_{kl}} \frac{\sum_k \sum_l w_{kl} (x_k - \bar{x})(x_l - \bar{x})}{\sum_k (x_k - \bar{x})^2} \quad (1)$$

where x_k is the value of the observed pest abundance at site k , d is the distance class based on the Euclidean distance between sites, $w_{kl} = 1$ if the pair of observations k and l belongs to the distance class d and $w_{kl} = 0$ otherwise, n is the number of spatial units and \bar{x} is the mean value of the x_k s. A zero value indicates a random spatial pattern. The significance of $I(d)$ is tested using a randomization test (Legendre and Legendre, 1998, p. 20) and the method of Holm used to correct probability levels for multiple testing (Lehmann and Romano, 2005, p. 350). The spatial relationships between pest abundance observed at different dates is assessed using a modified Moran's I statistic, the bivariate Moran's I (Fortin and Dale, 2005, p. 147) and the Mantel correlogram (Oden and Sokal, 1986). The Sturge's rule is used to fix the number of classes, and Euclidean distances are distributed among them by considering both equal distance intervals and equal sized classes (Fortin and Dale, 2005, p. 116).

2.3. The Incidence Function Model

To conform with the usual notations of metapopulation models, we refer to 'presence' or 'absence' (occupied or empty patch, respectively) meaning that the pest local population abundance is above (1) or below (0) the management threshold, respectively.

In this work we adopt the IFM, describing presence/absence of a species in the patches of a highly fragmented landscape at discrete time intervals (years) as the result of colonization and extinction processes, to model the transitions across the management threshold (Step 1 in Fig. 1). In terms of pest metapopulation dynamics, the transition of population abundance from below to above the management threshold is represented as a colonization process. Pest species are often r -strategists that build up high population levels soon after patch colonization, and limited time is taken to reach the threshold. Therefore, in terms of metapopulation dynamics the transition from empty to occupied patches can be considered as the immediate consequence of patch colonization rather than within-patch processes. The documented contribution of the movement to the local dynamics in many forest Lepidoptera species like PPM (Masutti and Battisti, 1990) further justifies the role of connectivity and of the colonization process in metapopulation dynamics.

The transition of population abundance from above to below the management threshold, due to either the decline of the local population or to control intervention, is represented as an extinction process. In the case of the PPM in Aspromonte, for each patch i , the mean number m_i of nests per tree is compared to the threshold level of 0.75 nests per tree, according to the recommendation provided by the Corpo Forestale dello Stato in compliance with the requirements of the Italian Law (D.M. 30 ottobre 2007 – *Disposizioni per la lotta obbligatoria contro la processionaria del pino*). Only if $m_i \geq 0.75$ should treatment be considered.

In the IFM, the process of occupancy of patch i is described by a first-order Markov chain with two states, $\{0, 1\}$ (empty and occupied, respectively). The extinction probability of a population in patch i , E_i , is constant in time and is assumed to decrease with increasing patch area

$$E_i = \min \left[\left(\frac{A_0}{A_i} \right)^x, 1 \right] \quad (2)$$

where A_i is the area of the patch i (km²), A_0 is the critical patch area for which the local population has a unit probability of extinction in

1 year, and x is a parameter reflecting the severity of environmental stochasticity (Hanski, 1994). Here the patch area represents the resources supporting the local population. The colonization probability of patch i at time t , $C_i(t)$, is assumed to be a sigmoidal function increasing with connectivity

$$C_i(t) = \frac{S_i^2(t)}{S_i^2(t) + y^2} \quad (3)$$

where

$$S_i(t) = \sum [\delta_j(t) \exp(-\alpha d_{ij}) A_j : j \neq i] \quad (4)$$

is the connectivity of patch i at time t , $\delta_j(t) = 1$ if patch j is occupied at time t and $\delta_j(t) = 0$ otherwise, d_{ij} is the Euclidean centroid-to-centroid distance (km) between sites i and j , α is a positive constant setting the survival rate of migrants over the distance and y is a parameter describing the colonization ability of the species (good colonizers have small y). In this paper, due to lack of specific information the minimum area A_0 that may support a PPM population is set equal to 400 m². The survival rate over distance $\alpha = 2.3$ (10% survival at 1 km) is obtained from the literature on the maximum distance reached by a flying adult during its short life (Manti, 2006). The uncertainty about A_0 and α is considered in Section 2.6. Parameters x and y are estimated by maximization of the pseudo-likelihood (Moilanen, 1999) corresponding to the initial distribution given by the first observed metapopulation state (year 2003, see Table 1).

Table 1

The study of a Pine processionary moth metapopulation in forest stands of the National Park of Aspromonte, Calabria, Italy. For each forest patch, the size (in m²) and the average annual nest abundance are reported. The average nest abundance per patch is defined in terms of number of final permanent nests per tree. The last row shows the mean values of patch area and nest abundance.

Patch	Patch area (m ²)	Nest abundance		
		2003	2004	2005
1	76,952.12	1.52	1.08	2.16
2	118,040.78	1.13	0.97	1.47
3	75,634.44	0.68	2.20	1.80
4	46,699.49	0.72	1.04	1.72
5	9626.39	1.12	0.72	1.52
6	32,839.29	0.40	0.40	0.40
7	156,918.33	1.10	1.10	1.10
8	80,640.96	0.30	0.30	0.30
9	489,647.84	0.89	1.83	1.91
10	22,778.76	1.80	1.80	1.80
11	124,423.97	1.60	1.60	1.60
12	41,644.60	0.64	2.04	1.34
13	37,503.63	0.92	2.00	1.28
14	368,181.27	0.56	1.10	1.66
15	426,183.47	0.86	1.50	1.77
16	652,758.32	0.48	2.13	1.97
17	407,366.32	0.44	0.84	2.00
18	1,175,910.81	0.90	1.23	1.86
19	100,794.14	1.72	2.28	2.60
20	51,305.24	1.44	1.20	3.40
21	273,488.23	0.80	0.80	0.80
22	69,012.79	0.52	0.84	2.00
23	63,327.84	0.32	0.96	1.32
24	475,172.94	0.84	1.52	1.88
25	369,247.02	0.84	1.88	1.86
26	82,197.46	0.00	0.92	1.68
27	249,482.81	0.01	0.95	1.68
28	41,686.47	0.36	2.04	1.20
29	134,546.93	1.80	1.80	1.80
30	190,317.93	0.44	2.09	1.53
31	1,626,188.30	0.59	1.62	1.66
32	98,395.17	2.60	2.60	2.60
Mean	255,278.56	0.89	1.42	1.68

Table 2

Pine processionary moth metapopulation model: comparison of the model parameter values to the values estimated under the different hypotheses considered for sensitivity analysis in Section 2.6. Bold type denotes the parameter with respect to which sensitivity is assessed. A_0 is the critical patch area for which the local population has a unit probability of extinction in 1 year, α is the survival rate over distance, x reflects the severity of environmental stochasticity and y describes the colonization ability of the species. The last row refers to the hypothesis that the true nest density is overestimated by a factor of 1.25.

Fixed biological parameters	x	y
$\alpha = 2.3$ $A_0 = 400 \text{ m}^2$	0.77724	0.00314
$\alpha = 0.7$ $A_0 = 400 \text{ m}^2$	0.77724	0.09608
$\alpha = 3.9$ $A_0 = 400 \text{ m}^2$	0.77724	0.00014
$\alpha = 2.3$ $A_0 = 40 \text{ m}^2$	0.52239	0.00314
$\alpha = 2.3$ $A_0 = 4000 \text{ m}^2$	1.65224	0.00314
$\alpha = 2.3$ $A_0 = 400 \text{ m}^2$	0.74035	0.00331
Overestimation		

2.4. Strategy definition

The proposed evaluation method compares different strategies of pest control defined in terms of spatial and temporal allocation of treatments irrespective of the adopted control technique. The only requirements are that the patch area is the minimum spatial unit of intervention and control operations target the entire pest populations in a patch. We consider a threshold-based pest management, and therefore local population abundance is kept under a threshold whatever defined (e.g., action threshold) as a consequence of an effective intervention. Then, from the modelling point of view, each strategy considers a set of occupied patches that are forced to be unoccupied (below the threshold, $1 \rightarrow 0$) at selected times. In other words, here 'strategy' means a group of patches to be treated (if occupied, i.e. above the threshold) and the strategies differ in which patches are treated and in the time of the treatments. First, we evaluate the effect of different allocation of the treatments in space and time separately, then we show by an example how to combine space and time.

For the spatial allocation, three kinds of strategies are compared: (a) scattered sites, (b) close sites and, due to the geometry of the PPM metapopulation (see Fig. 2), (c) in line sites. Three levels of intervention are considered, 15%, 30% and 50% of the total area (low, medium and high intervention level). By fixing the intervention area we are implicitly considering a budget constrained problem. Table 3 lists the selected patches for the identified strategies. In each intervention level, strategies are denoted by a capital letter indicating the level (L, M and H) and increasingly numbered. We suppose that a single treatment is applied in 2006 (the first year following the sampling period) and strategies outcomes are evaluated in 2008, for the sake of illustration.

For the temporal allocation, we compare the treatment application in 2006 and 2007 to the treatment application in 2006 and 2008. Strategies outcomes are evaluated in 2010. We apply the treatment to the two largest groups considered in the previously described case of high intervention level (H7 and H8, see Table 3). Finally, to evaluate the role of synchronous and asynchronous spatial treatments (Elliot et al., 2008) we combine specific pattern of spatial high intervention level and temporal allocation of treatment from 2006 to 2009. In particular, treatments are assigned to two subgroups of the patches in the strategy alternately in the four years. We considered the subgroups of H7 and H8 indicated in Table 5.

Table 3

Values of the index KL for different purely spatial control strategies of the Pine processionary moth metapopulation in the national park of Aspromonte (Calabria, Italy) under three levels of intervention: treated area of 15% (low, L), 30% (medium, M) and 50% (high, H). In model simulations the strategies are applied in 2006 and evaluated at year $T=2008$. Bold type denotes the lowest value (the best strategy) for each level of intervention. Parameters: $A_0 = 400 \text{ m}^2$, $\alpha = 2.3$, $x = 0.77724$ and $y = 0.00314$.

$KL(S_0) = 144.3$				
Strategy	Treated sites	Short description	Treated area (km ²)	KL
Low level (~15% of the total area)				
L1	1,7,16,21,28	Scattered sites	1.20	142.5
L2	1,9,15,30	Scattered sites	1.18	143.5
L3	4,18	Scattered sites	1.22	143.4
L4	3,7,21,22,23,27,28,29,30	Scattered sites	1.25	131.4
L5	15,17,19,21	Close sites	1.21	143.5
L6	16,17,19,20	Close sites	1.21	142.4
L7	7,10,11,12,13,14,15,20	Close sites	1.23	142.9
L8	1,2,3,4,5,6,7,8,9,10,11,12,13	In line close sites	1.31	119.5
L9	23,25,26,27,28,29,30,32	In line close sites	1.23	110.3
Medium level (~30% of the total area)				
M1	1,2,3,7,9,11,16,23,24,27	Scattered sites	2.48	130.8
M2	9,12,19,24,26,31,32	Scattered sites	2.91	132.7
M3	3,9,14,15,17,25,26,27	Scattered sites	2.47	133.6
M4	3,4,5,14,25,27,28,31	Scattered sites	2.79	128.1
M5	11,14,16,18,19	Close sites	2.42	140.6
M6	14,15,17,18,20,21	Close sites	2.70	133.0
M7	7,10,11,12,13,14,15,18	Close sites	2.35	134.6
M8	15,16,17,22,23,24,25	In line close sites	2.46	123.1
M9	17,22,23,26,27,28,29,31	In line close sites	2.67	120.4
High level (~50% of the total area)				
H1	1,4,9,14,16,22,24,30,31,32	Scattered sites	4.09	131.7
H2	1,4,9,11,15,16,18,21,24,27,30,32	Scattered sites	4.28	133.7
H3	9,16,18,25,31	Scattered sites	4.31	136.2
H4	2,5,9,11,18,21,22,25,31	Scattered sites	4.22	137.3
H5	7,9,10,11,12,13,14,15,16,17,18,19,20,21	Close sites	4.33	81.3
H6	7,8,9,10,11,12,13,14,15,17,18,19,20,21	Close sites	3.75	77.2
H7	17,19,20,21,22,23,24,25,26,27,28,29,30, 31,32	In line, close sites	4.23	96.1
H8	1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,17,18	In line sites (upper edge)	4.34	82.7
H9	16,22,23,24,25,26,27,28,29,30,31,32	In line sites (lower edge)	4.05	94.2

The strategy $S_0 = \{ \}$ meaning no treatment for any patch has been considered as a reference level as well.

2.5. Kullback–Leibler criterion

Pest management strategies are ordered according to an index measuring how far the metapopulation state resulting after the intervention is from the theoretical reference state of populations in all patches being below the threshold. At time T , we evaluate the ‘global’ metapopulation status by comparing the probability distribution P of the random vector of presence/absence $\delta(T) = (\delta_1(T), \dots, \delta_n(T))$ predicted by any stochastic metapopulation model, with the probability distribution P_0 indicating that populations in all patches are certainly below the threshold: $P_0(\delta_1(T) = 0, \dots, \delta_n(T) = 0) = 1$. The distance of P from P_0 is measured by the Kullback–Leibler divergence, defined as $KL(P) = -\log P(\delta_1(T) = 0, \dots, \delta_n(T) = 0)$.

In the case of the multivariate IFM considered here, $KL(P)$ can not be explicitly obtained, but it can be easily approximated by simulations. The chain rule:

$$\begin{aligned}
 &P(\delta_1(t+1), \dots, \delta_n(t+1)) \\
 &= P(\delta_1(t+1), \dots, \delta_n(t+1) | \delta_1(t), \dots, \delta_n(t)) P(\delta_1(t), \dots, \delta_n(t)) \\
 &= P(\delta_1(t), \dots, \delta_n(t)) \\
 &\times \prod_i P(\delta_i(t+1) | \delta_1(t), \dots, \delta_{i-1}(t), \delta_{i+1}(t), \dots, \delta_n(t)) \quad (5)
 \end{aligned}$$

allows the approximation of $KL(P)$ by iterating formula (5) up to an initial probability $P(\delta_1(1), \dots, \delta_n(1))$ and by using formulas (3) and (4) for the transition probabilities

$$\begin{aligned}
 &P(\delta_i(t+1) | \delta_1(t), \dots, \delta_{i-1}(t), \delta_{i+1}(t), \dots, \delta_n(t)) \\
 &= \begin{bmatrix} C_i(t) & \text{if } \delta_i(t+1) = 1 \ \& \ \delta_i(t) = 0 \\ 1 - C_i(t) & \text{if } \delta_i(t+1) = 0 \ \& \ \delta_i(t) = 0 \\ E_i & \text{if } \delta_i(t+1) = 0 \ \& \ \delta_i(t) = 1 \\ 1 - E_i & \text{if } \delta_i(t+1) = 1 \ \& \ \delta_i(t) = 1 \end{bmatrix} .
 \end{aligned}$$

For the estimated parameters set, start the simulation from an initial vector $(\delta_1(1), \dots, \delta_n(1))$ of states (either 0 or 1) of the n local populations (the choice of the initial distribution will become clearer later on in the text). For each time $t = 1, \dots, T - 1$, calculate $S_i(t)$ and $C_i(t)$, and generate a random number U according to a uniform distribution on $(0,1)$. Finally, determine $\delta_i(t+1)$ by comparing E_i and $C_i(t)$ to U :

$$\delta_i(t+1) = \begin{bmatrix} 1 & \text{if } \delta_i(t) = 0 \ \& \ U \leq C_i(t) \\ 0 & \text{if } \delta_i(t) = 0 \ \& \ U > C_i(t) \\ 0 & \text{if } \delta_i(t) = 1 \ \& \ U \leq E_i \\ 1 & \text{if } \delta_i(t) = 1 \ \& \ U > E_i \end{bmatrix} .$$

Repeat this procedure many times (here, 100,000) and calculate the fraction of simulated dynamics ending in pattern $(0, \dots, 0)$ to obtain $P(\delta_1(T) = 0, \dots, \delta_n(T) = 0)$. As this probability is usually vanishingly small, a better approximation can be obtained by simulating the metapopulation for $T - 1$ years to estimate $P(\delta_1(T - 1), \dots, \delta_n(T - 1))$ in accordance with the previously described procedure, and then multiplying this estimated value by the exact probability of the final transition (either E_i or $1 - C_i(T - 1)$). For further details see Moilanen (1999).

The framework described in Section 2.4. allows the description of each strategy in terms of the state of the local populations. The

patches occupancy is simulated, and at the treatment times the state of the treating patches is forced to be 0 if they are occupied (Step 2 in Fig. 1). We assume as initial vector in all the simulations the last observed metapopulation state (year 2005, see Table 1). Finally, for each strategy the corresponding value $KL(P)$ is computed (Step 3 in Fig. 1). Among a given set of strategies, the ones with lower KL values are those making the metapopulation state closer to the reference state (Step 4 in Fig. 1).

2.6. Sensitivity analysis

We first assess the robustness of the obtained ranking with respect to independent variations in the estimates of the critical patch area A_0 and of the survival rate of migrants α . Two alternative values for A_0 are 40 m² and 4000 m², corresponding to 0.1 and 10 times the adopted value for A_0 respectively. Regarding α , two alternative values are 3.9 and 0.7, corresponding to a 2% and 50% survival at 1 km distance.

We also analyse the effect of sampling errors on strategy ranking, by considering possible under/overestimation of the true value. Let m_i be the sampled value at patch i and m_i^* the true value: we suppose $m_i = 0.75m_i^*$ in the case of underestimation, while $m_i = 1.25m_i^*$ in the case of overestimation.

Summing up, six more complete analyses are carried out (Step 5 in Fig. 1) by considering the original data and four alternative parameter sets: ($A_0 = 400$ m², $\alpha = 3.9$), ($A_0 = 400$ m², $\alpha = 0.7$), ($A_0 = 4000$ m², $\alpha = 2.3$) and ($A_0 = 40$ m², $\alpha = 2.3$), and the two new data sets with the original parameters set ($A_0 = 400$ m², $\alpha = 2.3$).

3. Results

3.1. Testing criteria for metapopulation definition

Local population abundance has a very low correlation with patch area, varying from -0.16 in 2003 to 0.09 in 2004 and 2005. Randomization tests based on at least 4999 randomizations are used to test the significance of the uni- and bivariate Moran's I and of the Mantel correlograms (Legendre and Legendre, 1998). The Mantel correlogram is computed for different distance matrices. All the correlograms are interpreted for distances $\leq 15,000$ m. None of the tests highlights any significant autocorrelation (probability level equal to 0.01) of and between PPM pest abundance. The obtained results partially agree with Samalens and Rossi (2011) who, unlike us, considered a spatially homogeneous landscape. Fig. 3 shows the correlograms based on equal distance classes. Analogous results are obtained by considering equal sized classes. Thus, the criterion (d) of asynchronous fluctuations of local populations (see Section 2.2) can be considered as satisfied and the prerequisite for the analysis (see Fig. 1) as well.

3.2. IFM parameterization

The estimated values for parameters x and y are 0.77724 and 0.00314, respectively. The 95% confidence intervals, computed by pseudo-likelihood (see Moilanen, 1999), are (0.46, 1.55) and (0.0011, 0.0783) for x and y , respectively. The goodness of fit (see Step 1 in Fig. 1) is checked by starting 100,000 simulations from the first year of data (2003, see Table 1) and simulating the presence/absence for the two consecutive years (2004 and 2005). From these simulations, we compute the 95% confidence interval for the fraction of occupied sites in 2004 and 2005. Fig. 4 shows that in 2004 the observed mean occupancy is close to the upper bound of the confidence interval, while in 2005 it almost coincides with the interval centre.

Table 2 compares the obtained parameters values to the values estimated under the different hypotheses considered for sensitivity

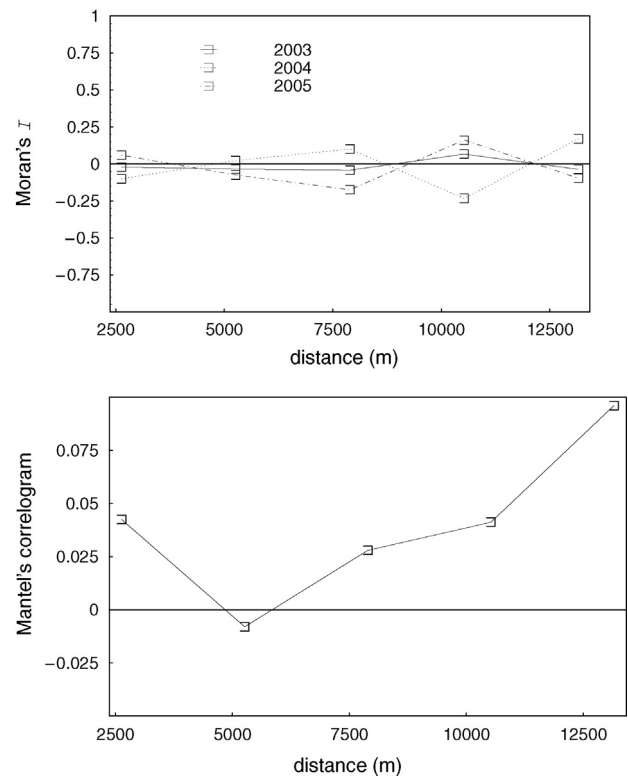


Fig. 3. Univariate Moran's I correlogram for the pest density of the Pine processionary moth on the three years of data (top). Mantel's correlogram based on the Euclidean distance for the pest densities of the Pine processionary moth (down). Spatial autocorrelation is never significant, according to the permutations test (4999 permutations) and the Holm's correction method.

analysis in Section 2.6. Sensitivity is assessed independently for each parameter. Changes in the value of α affect parameter y , because connectivity only is modified (see formula (4)). Changes in the value of A_0 affect parameter x , because extinction only is modified (see formula (2)). Sensitivity analysis with respect to sampling errors is carried out by considering $\alpha = 2.3$ and $A_0 = 400$ m². The hypothesis of underestimation of the true nest abundance can not be analysed because this hypothesis produces the absence of turnover (i.e., extinction is not observed) and, therefore, prevents the estimation of x . Under the hypothesis of overestimation of the true nest abundance we obtain $x = 0.74035$ and $y = 0.00331$, which are close to the estimated values from the observed data.

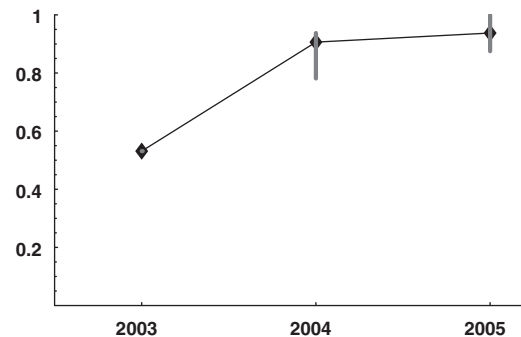


Fig. 4. The goodness of fit estimated IFM for the Pine processionary moth in the Aspromonte (Calabria, Italy) is checked by comparing the fraction of occupied sites at years 2004 and 2005 (black diamonds) to their 95% confidence intervals (gray vertical bars). The 95% confidence intervals were obtained from 100,000 simulations of occupancy, starting from the first year of data, 2003.

Table 4

Sensitivity analysis. Values of the index KL for the control strategies of the Pine processionary moth metapopulation in the national park of Aspromonte (Calabria, Italy) described in Table 3 for the different parameter sets defined in Section 2.6. The last column refers to the hypothesis that the true nest density is overestimated by a factor of 1.25, according to Section 2.6. Bold type denotes the lowest KL value (the best strategy).

Strategy	KL $\alpha = 2.3$ $A_0 = 400 \text{ m}^2$	KL $\alpha = 2.3$ $A_0 = 40 \text{ m}^2$	KL $\alpha = 2.3$ $A_0 = 4000 \text{ m}^2$	KL $\alpha = 3.9$ $A_0 = 400 \text{ m}^2$	KL $\alpha = 0.7$ $A_0 = 400 \text{ m}^2$	KL Overest. $\alpha = 2.3$ $A_0 = 400 \text{ m}^2$
S_0	144.3	135.5	183.7	148.2	141.8	135.9
Low level (15% of the total area)						
L1	142.4	131.7	181.3	143.2	139.6	135.3
L2	142.5	133.8	182.3	143.1	136.7	134.4
L3	141.4	133.4	183.2	143.1	141.7	135.6
L4	129.9	117.6	171.9	131.1	126.6	120.7
L5	139.6	133.7	181.2	142.8	140.6	135.3
L6	140.9	132.6	178.7	140.4	140.9	134.1
L7	142.9	134.5	183.5	144.1	141.5	135.9
L8	119.5	110.4	156.5	121.4	122.9	114.5
L9	118.6	105.7	153.1	111.9	111.9	113.0
Medium level (30% of the total area)						
M1	130.8	120.8	166.2	134.9	125.9	123.2
M2	132.7	125.2	166.4	134.6	128.7	125.9
M3	133.6	126.5	169.8	132.2	130.1	127.6
M4	128.1	124.2	167.3	136.0	123.6	125.6
M5	140.6	133.7	179.4	142.4	140.0	135.3
M6	133.0	115.9	164.8	131.0	133.2	119.9
M7	134.6	135.0	180.7	147.3	130.0	134.1
M8	123.1	116.4	154.3	124.5	126.6	117.2
M9	120.4	111.5	152.0	120.1	122.4	113.5
High level (50% of the total area)						
H1	131.8	123.2	165.5	132.7	122.8	124.6
H2	133.2	123.3	168.0	132.3	124.6	125.8
H3	135.0	129.3	172.3	138.1	133.2	129.7
H4	136.8	128.0	174.9	137.6	130.0	130.4
H5	80.3	76.4	100.1	85.4	73.5	77.9
H6	68.9	74.2	100.6	79.0	76.8	75.1
H7	96.5	91.5	119.7	97.4	97.4	91.9
H8	82.7	77.6	112.3	87.5	78.1	74.1
H9	94.3	89.6	116.3	126.5	95.4	90.0

The computation time to carry out 100,000 simulations of a 1-year metapopulation occupancy by *Mathematica* 5.0 is 123 s, Intel® Core™ i7-2720QM processor.

3.3. Strategy ranking

The KL values calculated in 2008 for the three kinds of strategies defined by allocating in space one only treatment in 2006 (see Section 2.4) are presented in Table 3. Results are grouped according to the intervention level, from low to high. Strategy S_0 has the highest Kullback–Leibler value (144.3), indicating that all the strategies turn out to be effective in pest reduction. All but one scattered strategies have higher KL values in all the three intervention levels. For the low intervention level, these values are not significantly different from $KL(S_0)$. For low and medium intervention levels, the lowest KL values are reached by the in-line strategies. Both close and in-line strategies show low KL values at the high intervention level. Within this latter level, the best strategy is the close-type strategy H6 forming like a clump, clearly splitting the remaining patches in two parts. The fact that as the intervention level (i.e., the treated area) increases, close and in-line strategies provide close KL values is an evident effect of both the spatial network shape and the limited number of patches (see Fig. 2). The ranking does not show any specific role of the number of treated sites and of the area (see Table 3). This can be clearly seen within each level and across the levels as well.

The obtained results indicate that the most effective strategies are the ones reducing patch connectivity. This might also be due to the specific feature of the IFM, a model essentially based on

patch connectivity. This interpretation is confirmed by the results of the sensitivity analysis, shown in Table 4. The fact that for the high intervention level both strategies H5 and H6 can be optimal, according to the parameter set, is due to the fact that the two strategies are very similar and differ by a small area only.

The role of the temporal pattern of the intervention is evaluated under the hypothesis of a fixed but differently distributed on time control effort. Efficacy of the strategies is assessed at a fixed time interval after the last observed year (2005, see Table 1). The results shown in Table 5 reveal the importance of the time lag between the last treatment and the time of evaluation. For the two assessed strategies, H7 and H8, the most effective temporal pattern is the one with treatment in 2006 and 2008. As general insight, it might be considered that pest control intervention in metapopulation systems like the one under study does not have long lasting effect.

Finally, an example of how to combine spatial and temporal patterns of intervention is provided. The lowest value of KL is obtained for H8c (see Table 5), a strategy combining the effect of concentrating the major control effort (i.e. the treated area) close to the assessment time with the advantages offered by a clump strategy.

Analogous results are obtained by carrying out the sensitivity analysis of temporal and spatio-temporal strategies (not shown here to save space).

4. Discussion

For area-wide pest management monitoring population dynamics and realistic models able to forecast variation of

Table 5
Values of the index *KL* for different the temporal and spatio-temporal control strategies of the Pine processionary moth metapopulation in the national park of Aspromonte (Calabria, Italy). In model simulations the strategies are applied at different point in times from 2006 to 2009 and evaluated at year $T=2010$. For each year, the treated area is indicated by using the same notations of Table 3 Bold type denotes the lowest value (the best strategy) for the two types of intervention. Parameters: $A_0 = 400 \text{ m}^2$, $\alpha = 2.3$, $x = 0.77724$ and $y = 0.00314$.

Short description	2006	2007	2008	2009	<i>KL</i>
Temporal treatment allocation					
H7		H7	–	–	99.4
H7		–	H7	–	96.1
H8		H8	–	–	91.5
H8		–	H8	–	83.0
Spatio-temporal treatment allocation					
H7a	17,19,20,21,22, 23,24,25,26,27	28,29, 30,31,32	17,19,20,21,22, 23,24,25,26,27	28,29, 30,31,32	97.2
H7b	28,29,30,31,32	17,19,20,21,22,23,24,25,26,27	28,29,30,31,32	17,19,20,21,22,23,24,25,26,27	91.5
H7c	19,20,21,26,28,31	17,22,23,24,25,27,29,30,32	19,20,21,26,28,31	17,22,23,24,25,27,29,30,32	98.2
H7d	17,22,23,24,25,27,29,30,32	19,20,21,26,28,31	17,22,23,24,25,27,29,30,32	19,20,21,26,28,31	102.1
H8a	7,11,17,18	1,2,3,4,5,6,8,9,10,12,13,14,15	7,11,17,18	1,2,3,4,5,6,8,9,10,12,13,14,15	112.4
H8b	1,2,3,4,5,6,8,9,10,12,13,14,15	7,11,17,18	1,2,3,4,5,6,8,9,10,12,13,14,15	7,11,17,18	117.3
H8c	1,2,3,4,5,6	7,8,9,10,11,12,13,14,15,17,18	1,2,3,4,5,6	7,8,9,10,11,12,13,14,15,17,18	69.5
H8d	7,8,9,10,11,12,13,14,15,17,18	1,2,3,4,5,6	7,8,9,10,11,12,13,14,15,17,18	1,2,3,4,5,6	82.7

population abundance by taking into account habitat fragmentation (Tschamtké and Brandl, 2004) are required. Spatially explicit metapopulation models can incorporate complex details on landscape structure and connectivity, providing insight into the role of habitat fragmentation on pest population dynamics. In particular, the Incidence Function Model takes advantage of using only a few parameters and some plausible assumptions on population processes that are satisfied for most pest populations. The disadvantage of possible simplifications introduced by this metapopulation model (Baguette, 2004) is outweighed by the advantage of enabling to deal with complex systems in a cost-efficient manner with simple modelling tools (Bodini et al., 2008). Metapopulation model parameters can be estimated from snapshot data or limited time series data across the metapopulation. Subsequently, the parameters can be used to iterate the model using different scenarios of the spatial and temporal distribution of treatments for a given set of patches. The modelling approach we used is particularly relevant if other modelling approaches can not be applied due to scarce data on the pest biology (e.g., the biodemographic rate functions and between-patches movement), as in the case of the Pine processionary moth (Netherer and Schopf, 2009).

The outcomes of metapopulation modelling can suggest general management recommendations. However, conservation literature warns us that to help managers in achieving the best results with limited resources, population ecology should be merged with decision theory (Possingham et al., 2001). Our work shows the usefulness of linking metapopulation models and the Kullback–Leibler divergence to represent the regional dynamics of pest populations and evaluate the consequences of short-term control techniques application at the regional level. The proposed method requires rather simple and fast computations, and allows to efficiently use data on pest population dynamics to predict the outcomes of control interventions under condition of limited knowledge. The method has been applied to pest management strategy evaluation for the Pine processionary moth populations in the Calabrian forests inhabiting spatially separated patches. We preliminarily proved by using tools from spatial statistics (Liebold and Gurevitch, 2002) that Pine processionary moth populations undergo asynchronous fluctuations. This enables to apply a metapopulation approach (Hanski, 1997). The method allows a comparative assessment of the efficacy of different predefined types of strategy defined in terms of spatial and temporal pattern of

allocation of the interventions. Within each type of control strategies the method allows a clear identification of the best one. The results we obtained for the Pine processionary moth populations in the Calabrian forests indicate that the best strategies are the ones reducing metapopulation connectivity. The importance of regular application of the intervention and the difficulty in achieving a long lasting control effect emerged as a general result as well. There are also indications that an asynchronous distribution of the treatment could contribute to the control of the moth. At least in the case extensively studied here of purely spatial treatment allocation, sensitivity analysis indicates that the best strategy in each intervention level is invariant with respect to parameters variations. Consistent results like those obtained for the PPM in Aspromonte mean that the method is able to provide a robust indication to managers. Nevertheless, management programmes are often vulnerable to naively using mathematical and simulation models inappropriately (Walsh et al., 2012; Peck and Bouyer, 2012). Testing the metapopulation hypothesis and verifying the goodness of fit of the selected model (the IFM) are fundamental steps of the decision process we propose here. Moreover, as we analysed a real system with a limited number of sites and a specific patches geometry along a transect, the possibility of deriving completely general indications for managers on the comparative efficacy of the tested patterns is limited. The performances of the *KL* divergence on more general networks will be part of future researches, together with improvements of the approximation method for *KL* computation.

Though focusing on threshold based control, the more general assumptions considered in this paper allow to extend the method to a more comprehensive system of compatible control techniques as used in Integrated Pest Management programmes (Kogan et al., 1999) for the evaluation of metapopulation management scenarios. The IFM is suitable for representing global dynamics with respect to a threshold density rather than within-patch dynamics. Consequently, the *KL* values obtained from the evaluation of IFM scenarios are useful for quantifying the benefits resulting from the application of management strategies at the global rather than the local level.

In pest management, decision makers are faced with different type of uncertainties about biological and environmental processes, and observational uncertainty (Shea et al., 2002). In fact, sampling methodology and techniques produce both random and systematic errors in the estimates of population density (e.g., Schaub

et al., 1988) and different types of errors can occur in metapopulation data, affecting parameter estimation (Moilanen, 2002). This produces uncertainties in the outcome of interventions and exposes the decision maker to risk (e.g., Roux and Baumgärtner, 1988). The sensitivity analysis applied in our study shows how to account for variability of both model parameters and population abundance estimates in the evaluation of pest control strategies (Drechsler, 2004). Sensitivity analysis is also important because it may show possible restrictions to the applicability of the adopted model, and indicate different ranking of control strategies.

A formal cost-benefit analysis certainly provides a better support to management strategy evaluation with respect to multiple criteria. A preliminary extension of the proposed methodology to include a cost function related to the treated area has been proposed in Bodini and Gilioli (2009). The method can be extended to consider the optimal selection of a sequence of strategies under constraints like costs, maximum intervening area and protected (i.e., pest-free) areas creation, for instance. This also allows to consider long-term control strategies that assume particular importance in area-wide pest management. However, this extension is not straightforward as the minimizing function is not linear and therefore ad hoc algorithms should be developed.

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