A generalization of the Incidence Function Model for metapopulations with fluctuating behaviour:an application to *Lymantria dispar* (L.) in Sardinia.

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Abstract: Most of the analysis and modeling approaches on gypsy moth population dynamics have been applied to a continuous spatial dimension, and therefore they do not account for the possible role of highly fragmented forest stands on pest dynamics. Spatially explicit metapopulation models show some advantages in representing the spatio-temporal metapopulation dynamics in fragmented habitats. In this work, the most popular of these models has been extended to take into account periodicity in the pest dynamics. Data on the gypsy moth *Lymantria dispar* (L.) (Lepidoptera Lymantriidae), one of the main oak forest defoliators in the Holarctic Region, referring to the period 1980-2010 in Sardinia (Italy) are analyzed.

Keywords: Spatially explicit metapopulation models, Incidence Function Model, *Lymantria dispar* (L.) (Lepidoptera Lymantriidae)

1. Introduction

The gypsy moth *Lymantria dispar* (L.) (Lepidoptera Lymantriidae) population dynamics modeling has a long history. Models developed range in complexity and approaches that have been used, from statistical models (Zhou & Liebhold, 1995; Cocco *et al*., 2010) to simulation models based on complex assumptions on ecological processes (Sharov & Colbert, 1996). In many situations, especially in the oak forests of the Mediterranean basin, the host plants for the gypsy moth are not continuous. However, the role of habitat fragmentation in determining the pattern of gypsy moth population dynamics has not been carefully addressed. Analyses of spatial heterogeneity are either based on correlations that take into account details of landscapes and their effect on population processes (Hunter, 2002) or on metapopulation models that deal with the occurrence of individual populations in an ensemble of habitat fragments (Tscharntke & Brandl, 2004). Spatially explicit metapopulation models could be of great importance to pest managers for their contribution to a better understanding of how the spatial arrangements of fields or forest stands can influence the population dynamics. Despite these promises and the fact that metapopulation models have been originally proposed for pests, they remain a widely used tool in conservation biology but receive little attention in pest control (Hunter, 2002).

In this paper, we propose a modelling approach to *L. dispar* metapopulation dynamics and apply it to a dataset of gypsy moth abundance recorded in Sardinia (Italy). Model simulations are performed and the obtained dynamics are evaluated in their capability to capture the most significant properties of spatio-temporal population dynamics patterns. The proposed model significantly improves the results obtained by Gilioli *et al.* (2011a).

2. Materials and Methods

Data. Gypsy moth population dynamics were recorded in the period 1980-2010 in the main cork, holm and pubescent oak areas of Sardinia based on 282 monitoring sites (Luciano, 1989; Cocco *et al*., 2010). Each monitoring site has been considered as the centroid of a patch, the basic environmental unit in which the local dynamics of colonization and extinction occur. Patches connected by fluxes of migrant larvae are considered belonging to the same macroarea (MA). MAs are separated by physical or ecological barriers, and fluxes among MAs can be considered negligible. Five MAs were identified: the results on MA 2 are presented here.

Model description. The Incidence Function Model (IFM; Hanski 1994) is based on presence/absence data of a species in a highly fragmented landscape. The process of occupancy of patch *i* is described by a first-order Markov chain with two states, {0, 1} (empty and occupied, respectively). Following Hanski, the colonization probability of patch *i* at time *t*, $C_i(t)$, is defined to be a sigmoidal function increasing with connectivity

$$C_i(t) = \Delta_i^2(t) \,/\, (\Delta_i^2(t) + y^2) \qquad (1)$$

where $\Delta_i(t) = \Sigma \,\{o_j\,(t) \exp(-\,\alpha \times r_{ij} \times d_{ij})A_j : \; j \neq i\}$ is the connectivity of patch *i* at time *t*, A_j is the area of patch *j*; d_{ij} is the centroid-to-centroid (Euclidean) distance between patches *i* and *j*; r_{ij} corrects the Euclidean distance by taking into account possible disturbances (presence of a different host species, grazing, etc.); *y* describes the colonization ability of the species, α is a positive constant setting the survival rate of migrants over the distance.

In this paper, the extinction probability of a population in patch *i* at time *t* is assumed to be a sigmoidal function increasing with the recent history of the patch

$$E_i\,(t\,;K) = h_i^2(t\,;K) \,/\, (h_i^2(t;K) + x(t)^2) \qquad (2)$$

where $h_i(t\,;K) = \Sigma\{o_i(k) : k = t, t\text{-}1, \dots, t\text{-}K\}$, $o_i(k) = 1$ if at time *t* patch *i* is occupied and $o_i(k) = 0$ otherwise; $x(t) = \gamma + \beta\,\mathrm{Sin}^2\,(\theta t + \pi\, s/\theta)$ is a sinusoidal function accounting for periodicity in local dynamics, which is common to all the patches in the same MA.

Parameters α, γ, β, θ, *s* and *y* are estimated by maximization of the pseudo-likelihood corresponding to the initial distribution given by the first observed metapopulation state (Moilanen, 1999).

3. Results

Figure 1 clearly shows the periodic behavior of the observed proportion of occupied patches (green line). Data of the period 1980-1983 have been discarded due to the high number of missing data. The first population peak is reported in 1990, the other population outbreak occurs in 1997. After 2000, the pattern of fluctuations displays less regularity, which can be partially explained by pest control treatments carried out to reduce the impact of gypsy moth infestation in the sites where outbreaks started (foci).

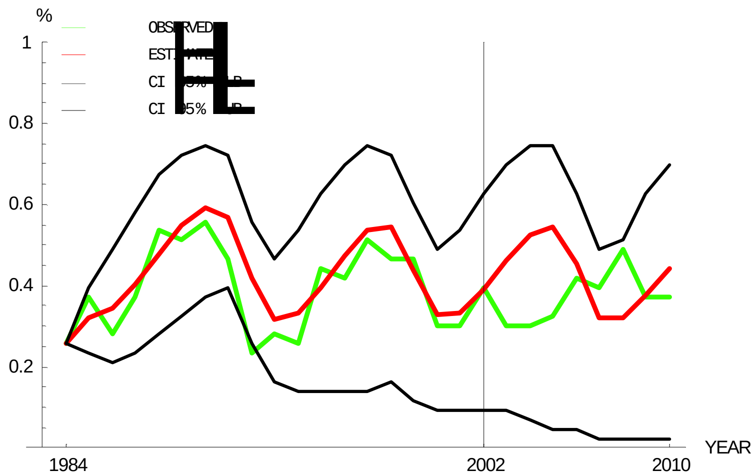

Figure 1: Observed and mean estimated proportion of occupied patches. Data of the period 1984-2002 have been used for estimation. After 2002, groups of patches received pest control treatments.

The estimated period is 7.1 years (θ = 0.44), K=5, α=0.01767, β=10.405, γ=3.031, s=0.98 and y=86.1. To compare model outputs and observed incidences, 10,000 simulations have been carried out, starting from the first year of data (1984).
Figure 1 compares the observed fraction of occupied sites and the mean estimated fraction, obtained from simulations. Confidence intervals have been obtained by computing the symmetric percentiles (0.025, 0.975) of the simulated values, for each time t. Before 2002, the observed data seem to be well represented by the model. The model behaviour after 2002 differs from observations as the populations dynamics are influenced by the pest control treatments. According to a few preliminary results, the estimated model seems to be able to adapt to the implementation of pest management strategies.

4. Concluding remarks

The major advantage offered by the metapopulation model developed here is the possibility of describing temporal trends of population dynamics in phase with observations. In particular, the increase in the incidence at MA-level for population following a latency period, is well described by the model. This has important implications for sampling strategies as well, leading to the possibility of using a binomial sample design for management purposes, by defining the state of presence/absence of gypsy moth population abundance instead of counting egg masses. The description of variation in population incidence could allow to obtain a descriptor of the increase in the risk of population outbreaks. Different management strategies could be evaluated according to the approach proposed by Gilioli *et* al. (2008) and Gilioli *et al*. (2011b) and based on the IFM and the Kullback-Leibler divergence (Kullback and Leibler, 1951).

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