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Modelling the local population dynamics of *Maculinea* and their spatial interactions with their larval foodplant and *Myrmica* ant species

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Maculinea blue butterflies have an intricate relationship with their early larval foodplant and the *Myrmica* ant species on which they depend for survival to adulthood. At the large spatial scale it is important to understand the factors controlling the dynamics of the butterfly within a landscape composed of several populations on various sites. However, most recorded movements and dispersal of *Maculinea* through mark-release-recapture studies are less than 500m (Nowicki *et al.* “this volume”) and many remaining fragmented populations are isolated. It is therefore valid and useful to try to develop models which synthesise our knowledge of the internal local dynamics of individual populations on single sites assuming no emigration or immigration. Estimates of population size inter-annual variability, local persistence rates and growth rates of re-colonisations can also contribute to landscape scale metapopulation studies.

Within the MACMAN project (http://www.macman-project.de), our single-site modelling of *Maculinea* extended two existing approaches, one involving deterministic density-dependent interaction models (Hochberg *et al.* 1992) and the other based on spatially-explicit individual-based stochastic processes (HCET model of Hochberg *et al.* 1994; Clarke *et al.* 1997,1998).

Firstly, a deterministic community module has been developed for *Maculinea alcon* (Mouquet *et al.* “in press (a)”). This model was novel and made realistic by incorporating the life stage (seedling, juvenile, vegetative, reproductive and dormant) dynamics of its larval foodplant *Gentiana pneumonanthe*, including the density-dependent impact of the butterfly damage to seedpods and the effect of increasing heathland successional age on reducing both gentian productivity and the abundance of nests of the dominant host ant, *Myrmica scabrinodis*. Model parameters for gentian and butterfly dynamics were estimated from a mixture of long-term (>20 years) field studies and laboratory experiments. Without management of the heathland or natural fires to reset or prevent succession, the host ant and the gentians and thus *M. alcon* will tend to disappear. Model simulations were used to assess the management effect of burning, grazing, mowing or sod cutting the heathland at various frequencies (2-15 years) and intensities on the three species' persistence and population sizes (Table 1).

Maculinea rebeli and *alcon* act as "cuckoos" within the ant nests, being fed by the ants, which provides a form of "contest" competition. In contrast, *Maculinea arion* predates upon the ant brood, which leads to less efficient "scramble" competition for food such that if too many caterpillars are adopted into a nest, few, if any, survive to adulthood (Thomas & Wardlaw, 1992). We have developed a deterministic model for *M. arion* (Mouquet *et al.* "in press (b)"). In addition to the density-dependent contest competition of larvae on the flower buds of *Thymus* (or *Origanum*), this model includes a form of unimodal density-dependent overall survival of caterpillars within the *Myrmica sabuleti* host ant nests, where the intensity of within-nest competition can be related to the extent of spatial clumping of egg-laying and thus adoption of caterpillars. Estimates of model parameters used field data from sites in the UK, France and Sweden, but especially from one location in south-west England during 1972-2002, leading to two model test scenarios under (i) average and (ii) maximum/optimum observed conditions. Under otherwise average conditions, adult butterfly numbers track closely the simulated long-term (20 year) cyclical variation in the number of ant nests, whereas reductions from high to very low plant densities initially lead to increases then rapid decreases in butterfly numbers followed by rapid recovery when plant density increases again (Figure 1). In contrast, adult population responses to major cyclical variation in (weather-related) adult fecundity or survival on the plant are delayed by 4-5 years (Figure 1(c)).

Survival dynamics operate at different spatial scales over the *Maculinea* life cycle, from egg laying across a site, to larval competition on individual plants, to adoption and development within ant territories and colonies (plus un-modelled occasional migration between sites). We have tried to incorporate this reality by extending and generalising the spatial-explicit HCET model developed for *M. rebeli* to other *Maculinea* and, in particular, for the contrasting predatory species *M. arion* (Table 2). Model parameters for the case of *M. arion* were derived from published and unpublished field studies and other unpublished studies of Myrmica ants.

Table 1. Estimates of optimum frequency (years) of heathland burning, grazing, mowing or sod cutting on average population densities (per hectare in brackets) of *Maculinea alcon*, *Myrmica scabrinodis* and *Gentiana pneumonanthe* using model parameters and results from Mouquet *et al.* "in press (a)").

Management	***Maculinea alcon***	***Myrmica scabrinodis***	***Gentiana pneumonanthe***
Burning	3 (952)	2 (1100)	4-6 (36000)
Grazing (strong)	3 (664)	2 (982)	4 (19800)
Grazing (intermediate)	2 (602)	2 (214)	2-3 (17400)
Grazing (weak)	ant and butterfly do not survive		2 (3000)
Mowing (5cm height)	2 (252)	2 (114)	2-4 (35300)
Mowing (10cm height)	ant and butterfly do not survive		4 (19700)
Sod cutting (5% area)	ant and butterfly do not survive		2 (11500)
Sod cutting (15% area)	2 (260)	2 (102)	2 (18100)
Sod cutting (15% area)	3 (274)	2 (616)	4 (8400)

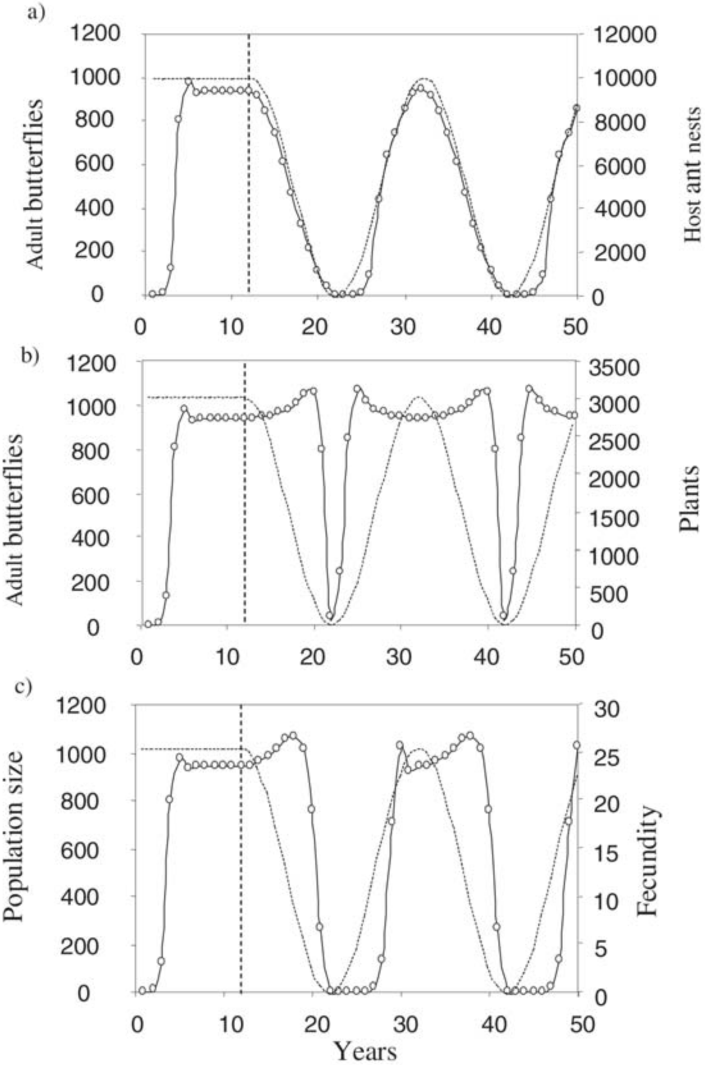

Fig. 1. Effect of temporal variation (dotted sinusoidal line) in (a) the number of host ant nests, (b) the number of larval foodplants and (c) adult fecundity on adult numbers of *M. arion* butterflies (circles with solid line); dashed vertical line indicates start of temporal variation once equilibrium has been reached using constant average site conditions (based on model scenario #1 from Mouquet *et al.* "in press (b)").

M. arion caterpillars can cope with starvation periods and so can exploit multiple ant nests by consuming all of the over-wintering ant brood in a nest, causing the workers to disband, and allowing neighbouring healthy nests to bud into the empty site bringing new brood. Model simulations showed that being less host specific and able to exploit multiple (optimally 3) ant nests increases *M. arion* survival in poor conditions (low plant and host ant density), but can result in over-exploitation of the ants at very high plant densities (Figure 2). As risk of local extinction is

Table 2. Extensions and generalisations of the spatial-explicit individual-based HCET model for *Maculinea* population dynamics within sites.

Stochastic or deterministic temporal variation in habitat quality gradient
- representing effects of inter-annual weather or site management

Extending from 'host'/'non-host' to up to eight competing *Myrmica* ant species

Ant colony distribution extended to 1 colony (territory) per m^2 (i.e. 1 m^2 cells in model)

Territories overlap: ants forage and can adopt caterpillars in neighbouring territories

Some (16%) caterpillar tolerance (and potentially survival) in 'non-host' *Myrmica*
(i.e. degree of non-host specificity)

Scramble competition within individual nests as function of current ant worker and caterpillar numbers

Increased within-year inter-colony dynamics (nest abandonment + budding)
- *M. arion* caterpillars can consume brood from 1-4 immigrant colonies to develop

User friendly interface to change model parameters

Model can be run to simulate effects of:
- different sized with different physical properties or management
- different values of host specificity
- annual or geographical variation in climate
- edge-of-range versus core populations
- functional evolutionary questions

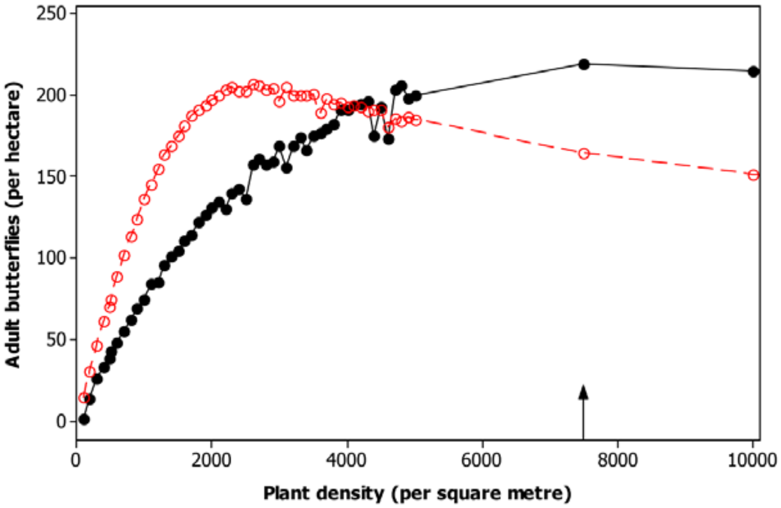

Fig. 2. Example of effect of varying *Thymus* plant density (m^{-2}) on *Maculinea arion* adult density (ha^{-1}) assuming caterpillar scramble competition within nests with either (a) complete host specificity to *Myrmica sabuleti* and only exploiting one colony (solid line, closed circles), or (b) 16% probability of tolerance within non- *M. sabuleti* nests and ability to exploit up to three nests (dotted line, open circles).

greatest in poor conditions, this may explain the evolutionary selection pressure for incomplete host specificity and the ability for caterpillars to starve during temporary periods of colony disbandonment (Thomas *et al.* 1989).

Overall we conclude that conservation strategies for optimal management of *Maculinea* needs to be conducted on a case by case basis.

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