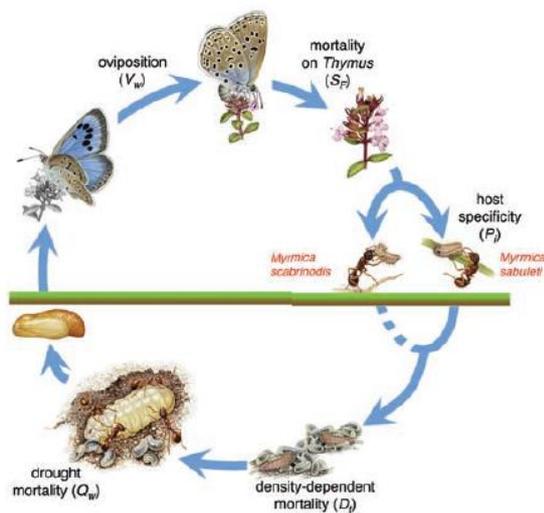


OLM 10.3. The *Maculinea* story

The Large Blue butterfly (*Maculinea arion*) is a model species of the evidence-based conservation of butterflies. The research project preceding its successful reintroduction to England is a nice illustration of the efficient integration of research on different fields of ecology using very different methodologies by combining them into a coherent framework.

M. arion is found all over Europe. It is a near-threatened species according to IUCN classification, known to be present in England since 1795 (Thomas et. al. 2009). Its life cycle depends on the presence of thyme (*Thymus*) species and the ant *Myrmica sabuleti* (Figure 10.3.1).



	Description
V_w	# eggs per adult, dependent on weather
S_F	mean survival of eggs and early larval instars on <i>Thymus</i>
P_i	proportion of instar IV larvae adopted by <i>Myrmica</i> ants in year t , dependent on <i>Myrmica</i> species
D_t	density-dependent survival within <i>Myrmica</i> nests
Q_w	reduction in larval survival in <i>Myrmica</i> nests in drought years

Figure 10.3.1: The life cycle of *Maculinea arion* and the estimated parameters of the life cycle model.

Adult butterflies lay their eggs on *Thymus* flowers (V_w). Larvae feed on the flowers; their survival is affected by predation, parasitism and cannibalism (S_F). Phase-IV larvae leave the plant and are carried to a *Myrmica* colony by the first ant worker encountered. Its chance of survival (P_i) depends on the actual *Myrmica* species; *M. sabuleti* is the optimal host. Larvae acquire ~98% of their final biomass eating ant brood. Their survival probability in ant colonies hosting more than one larva is density dependent (D_t), with the effect being even more pronounced in dry years (Q_w). Larvae pupate within the ant colony which they leave as adults (after Thomas et al. 2009).

By the end of the 1970s the last colony of *M. arion* was extinct in England. The attempt of its reintroduction was prepared carefully, by searching for the factors determining the size of the population at different stages of its life cycle. One of the first questions to answer was if it was the plant or the ant host that regulated the dynamics of the butterfly population. In a series of studies, a total of 18 life cycle parameters were measured, ranging from the dispersal of adults through the choice of location for laying eggs to larval mortality (Thomas

et al. 2009). Since fourth-phase larvae parasitize ant colonies, the specific details of this interaction were explored, by estimating the probability of different ant species to accept the larvae, and by measuring the density dependent mortality of the larvae within colonies of different ant species. In some cases, the data were obtained from field observation (e.g., for dispersal and for host specificity), in other cases (like for estimating the carrying capacity of ant colonies) field and lab experiments were carried out.

Studies of similar *Maculinea-Myrmica* systems revealed, that the size of the butterfly populations does not depend on the density of the plant host (see Figure 10.3.2.a for an example), but is influenced to a large extent by the density of the ant colonies (Figure 10.3.2.b). This means that attention should be focused on the ecological tolerance of the host ant species.

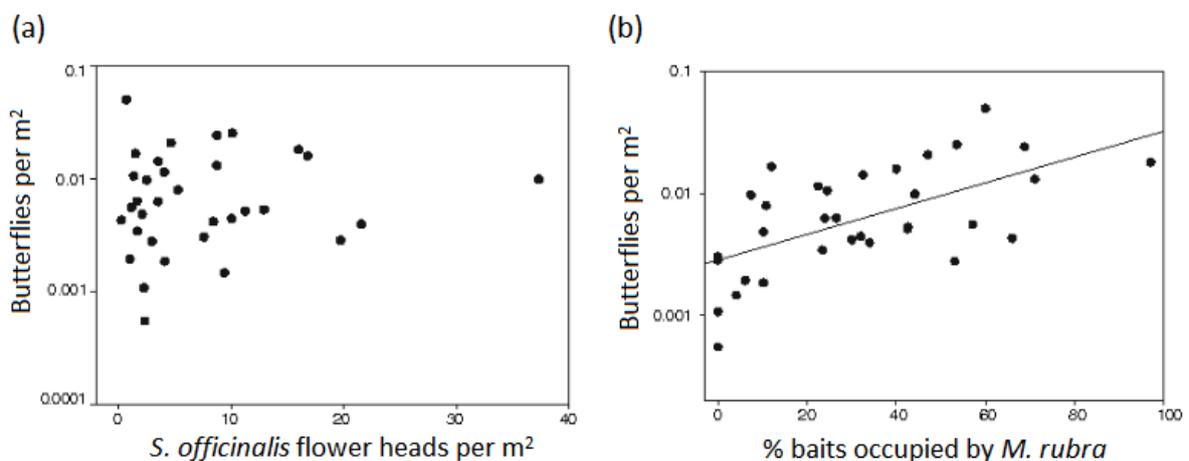


Figure 10.3.2: Ant host abundance influence the density of *Maculinea nausithous* the most

An investigation of 30 local *Maculinea nausithous-Myrmica rubra* communities suggests that a) the plant host does not substantially affect the density of the butterfly population, b) but *Maculinea* density increases with the density of the ant host ($r^2 = 0.23$, $p = 0.005$, after Anton et al. 2008).

The specific model used for predicting the dynamics of *M. arion* populations concluded (Hochberg et al. 1992; Mouguet et al. 2005) that a high proportion of *Myrmica sabuleti* colonies is necessary on areas covered with *Thymus* for the persistence of the butterfly, because, even though the larvae are accepted also by other ant species, larval mortality is high in their colonies. The outcome of the competition among different *Myrmica* species depends on soil temperature, which in turn is determined by turf height (Figure 10.3.3). The habitat survey of the *Maculinea* populations in England revealed that the most likely cause of the local extinction of the species was the extinction of its optimal ant host, which was a direct consequence of the decrease of short-grass thyme fields, the optimal habitat of the thermophile ant host. Therefore, the key to the reintroduction of *M. arion* to England was

the reconstruction of short-grass pastures (Thomas et al. 2009). The main controlling factor in this success story proved to be one that has not been previously considered at all.

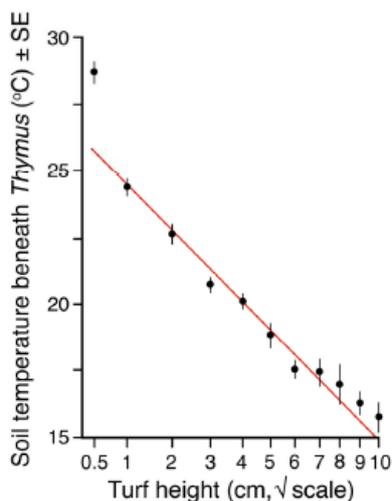


Figure 10.3.3: Soil temperature under *Thymus* as a function of turf height (Supporting Online Material for Thomas et al. 2009).

Modelling accompanied the whole process of solution of the problem (Hochberg et al. 1992; Hochberg et al. 1994; Mouquet et al. 2005). The first step of modelling is setting up the flow diagram, based on the life-cycle of the butterfly (Figure 10.3.4) complemented by mathematical equations describing the transitions. It is at this stage at which inclusion or omission of different dynamical complications and the forms of the functions are decided. These decisions are based on prior expert knowledge of the system.

The model of Mouquet et al. (2005) is based on a flow diagram that consists of two paths associated with the two hosts species playing a role in the life-cycle of *M. arion*.

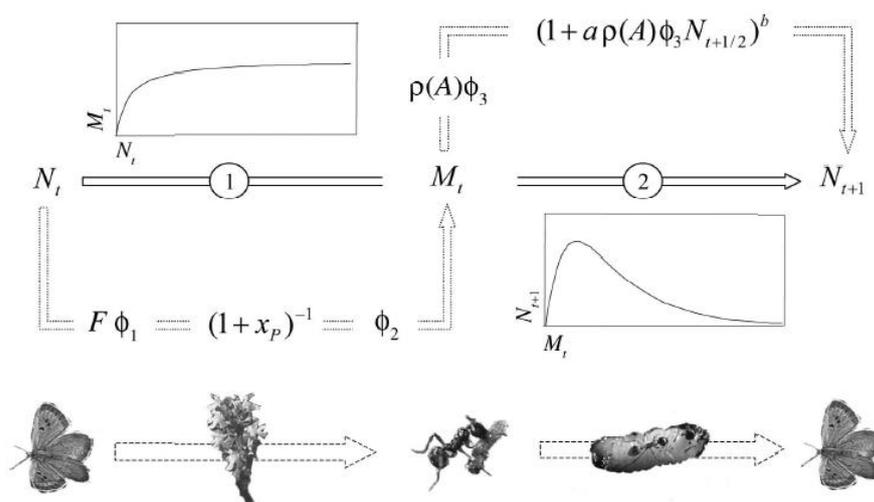


Figure 10.3.4. Flow diagram explaining the structure of the model of the dynamics of a *Maculinea arion* population (see notations in Table 10.3.1. and explanation in the text; Mouquet et al. 2005).

It is assumed that there is contest competition among the larvae on the host plant but it is scramble in the ant nests. (See the forms of the $M_t(N_t)$ and the $N_{t+1}(M_t)$ functions in Figure 10.3.4. The variables and parameters of the model are listed in Table 10.3.1.)

Table 10.3.1. Definitions of the parameters used in the model (Mouquet et. al. 2005).

Parameter	Definition	Units
N_t	Adult butterfly population at time t (Eq. 9)	no. adults/ha
M_t	Number of caterpillars surviving on the plants	no. caterpillars/ha
F	Total number of eggs laid per female butterfly $\div 2$ (1:1 sex ratio)	no. eggs/female
A	Population of ant nests	no. nests/ha
ϕ_1	Proportion of eggs surviving on the plant, from density-independent mortality	none
ϕ_2	Proportion of young caterpillars (after first instar) surviving on the plant, from density-independent mortality	none
ϕ_3	Proportion of caterpillars surviving in the first few weeks following recruitment into ant nests	none
η	Mean potential area of search of the worker from a <i>Myrmica sabuleti</i> nest	ha
P	Number of plants (<i>Thymus</i> or <i>Origanum</i>)	no. adults/ha
x_P	Average number of competing caterpillars per flowering bud (Eq. 3)	no. caterpillars/bud
x_A	Number of competing caterpillars among ant nests (Eq. 6)	no. caterpillars/ha
ε_P	Average number of flower buds per plant	no. buds/plant
ε_A	Carrying capacity of the average nest, a mean weighted by proportion of nests containing caterpillars	no. caterpillars/nest
$\rho(A)$	Proportion of caterpillars recruited into nests (Eq. 8)	none
b	Spatial distribution of the caterpillars among ant nests	none
a	Scaling parameter (Eq. 7)	none

According to the flow diagram, adult population size N is the product of density-dependent recruitment on the plants described by the g_1 function and in the ant nests described by the g_2 function:

$$N_{t+1} = g_1(N_t, P)g_2(g_1(N_t, P), A). \quad (10.3.1)$$

Thus, this model works with two regulating variables and two feed-backs. The distribution of the number of larvae is vital in this system as it can be assumed that more than a single larva in an ant nest is fatal for all the larvae in that nest – a typical outcome of scramble competition (Figure 10.3.5).

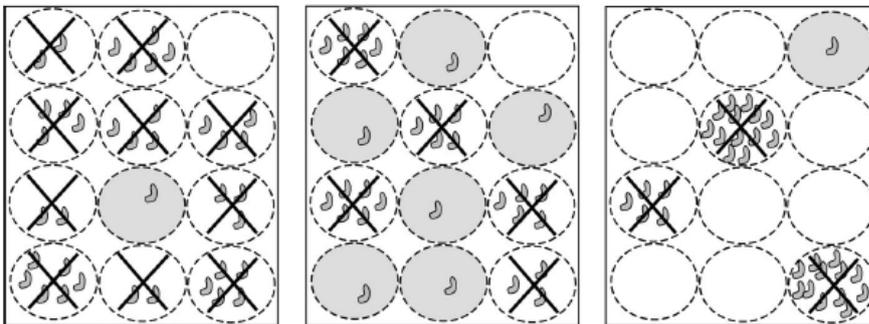


Figure 10.3.5. Effect of spatial distribution of butterfly larvae on their survival in the ants' nests.

Ant nests are considered as patches. If more than one larvae compete in a patch, they all die (scramble competition). In the left panel the distribution of larvae is random; in the other two panels it is increasingly aggregated (after Mouquet et. al. 2005).

The aim of modelling was to determine the set of environmental conditions ensuring the maintenance of the populations. This can be done by a sensitivity analysis. Scanning the plausible range of the parameter space by numerical simulations revealed the sensitivity of model predictions to each of the parameters. Changing parameters may not only shift the equilibrium population density but may lead to complex population dynamics as well. An important lesson to learn from the thorough modelling study by Mouquet et. al. (2005) is that there is no general rule for the management of an area or a species: detailed information on the actual context and the local conditions are indispensable. Viable options depend on local conditions. In the *Maculinea* case these are related to the growth potential of the local butterfly population, the density and spatial distribution of the host plants and of the ant nests.

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