Article

Are individual based models a suitable approach to estimate population vulnerability? - a case study

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Abstract

European populations of the Large Blue Butterfly *Maculinea arion* have experienced severe declines in the last decades, especially in the northern part of the species' range. This endangered lycaenid butterfly needs two resources for development: flower buds of specific plants (*Thymus* spp., *Origanum vulgare*), on which young caterpillars briefly feed, and red ants of the genus *Myrmica*, whose nests support caterpillars during a prolonged final instar. I present an analytically solvable deterministic model to estimate the vulnerability of populations of *M. arion*. Results obtained from the sensitivity analysis of this mathematical model (MM) are contrasted to the respective results that had been derived from a spatially explicit individual based model (IBM) for this butterfly. I demonstrate that details in landscape configuration which are neglected by the MM but are easily taken into consideration by the IBM result in a different degree of intraspecific competition of caterpillars on flower buds and within host ant nests. The resulting differences in mortalities of caterpillars lead to erroneous estimates of the extinction risk of a butterfly population living in habitat with low food plant coverage and low abundance in host ant nests. This observation favors the use of an individual based modeling approach over the deterministic approach at least for the management of this threatened butterfly.

Keywords individual based model; mathematical model; environmental heterogeneity; competition; *Maculinea arion*.

1 Introduction

The last decades have seen an enormous interest in problems related to conservation biology as many species on earth are threatened due to ongoing loss, fragmentation and degradation of habitat (e. g. Shaffer, 1981; Soulé, 1987; Hanski and Gilpin, 1997). To find reliable estimates for the vulnerability of a population associated with the various future scenarios it may face, quantitative models are needed. This is especially important for sound decision making in conservation management.

   The estimation of the risk of population extinction has been approached by different modeling techniques, e.g. by analytically solvable models or Monte-Carlo simulations where the latter are either based on a simple stochastic population model or an individual based model (IBM). Simple deterministic models have gained wide acceptance in conservation biology although they often do not explicitly include mechanistic processes. Deterministic models are relatively simple to produce and easy to interpret and they provide analytical rather than simulation results. For conservation biology, it has been demonstrated that the sensitivity analysis of deterministic models can give insights on which parameters are likely to be most critical for population

survival and thus, may be used to focus research and management efforts (Hochberg et al., 1994; Heppell et al., 2000).

In contrast, individual based models (IBMs) are typically tedious to create. They include many parameters which are difficult to estimate for natural populations and which rely on very detailed knowledge on the species and the spatial structure of its populations. IBMs use information at the level of individual organisms. They derive characteristics of the population as an integral of all individuals constituting the population. In contrast to the deterministic models IBMs are mechanistic in approach and they have also been successfully applied in conservation biology (e.g. Matsinos et al., 2000; Griebeler and Seitz, 2002; DeAngelis and Mooij, 2005; Griebeler and Gottschalk, 2010). Furthermore, in IBMs details on the spatial configuration of the landscape are easy to implement. It has been demonstrated that landscape heterogeneity strongly influences the dynamics of a population and consequently its extinction risk (Matsinos et al., 2000; Gottschalk et al., 2003; Griebeler and Gottschalk, 2010).

In this article, I compare two modeling techniques that are applied in conservation biology, the deterministic approach and the individual based approach. I test whether the assumed high predictive power of both modeling approaches is true. In particular, I present a simple analytically solvable mathematical model (MM) for the Large Blue Butterfly *Maculinea arion*. I contrast results obtained from the sensitivity analysis of the MM to the respective results derived from a spatially explicit IBM for this butterfly (Griebeler and Seitz, 2002).

2 Material and Methods

2.1 Biology of the *Maculinea-Thymus-Myrmica* system

As all *Maculinea* butterflies, *M. arion* is univoltine. Adults usually fly for about 4 weeks in July or August. Each female butterfly lays a clutch of one egg on flower buds of specific plants about 60 times per generation. *Thymus* plants are preferred for oviposition and *Origanum* is frequently used in the absence of thyme. A high proportion of eggs hatch about one week after being laid (Thomas et al., 1991). Young caterpillars feed on buds for about three weeks, although they are cannibalistic during their first instars (Thomas, 1977). Occasionally, within this time, caterpillars are parasitized by *Trichogramma* species (Thomas et al., 1991). Caterpillars acquire only about 1% of their ultimate biomass during their life on plants (Thomas, 1977). They then molt for the third and last time, drop to the ground where they await discovery by *Myrmica* workers, or die within the next 2 days if they are beyond the foraging range of an ant colony (Thomas, 1977; Thomas et al., 1989). Curiously, adult *Maculinea* cannot detect *Myrmica*, and place their eggs more or less randomly on plants growing both beyond and within the foraging range of these ants (Thomas et al., 1989). Even though workers from most species of *Myrmica* take the caterpillar back to their nests with equal success, caterpillars almost exclusively survive within nests of *M. sabuleti* (Elmes et al., 1998). Within the nests, caterpillars mimic an ant larva in its final instar. They are obligate predators of *Myrmica* larvae. It is estimated that 230 of the largest available larvae, and a minimum nest size of 354 *M. sabuleti* workers, is needed to support a single butterfly. Therefore, many caterpillars die in ant nests if nests are too small (Thomas and Wardlaw, 1992). Mortality of caterpillars is 2.8 times higher in nests with queen ants in comparison to queen less nests (Thomas and Wardlaw, 1990). After the caterpillars have exploited ant nests for about 10 months, butterflies finally emerge from pupae.

Based on its life-cycle, the key to conserving *M. arion* is to manage sites to encourage high densities of the host ant to coexist with any initial larval food plant (Thomas et al., 1998). Maintenance or re-establishment of regular grazing or mowing of sites guarantees such conditions (Thomas et al., 1998).

2.2 Mathematical model

In order to assess the power of simple mathematical models for conservation, I developed an analytically solvable deterministic model for *M. arion*. This model is based on the model of Hochberg et al. (1994) which was established for another large blue butterfly, *Maculinea rebeli*. The life-cycle of this species is very similar to the life-cycle of *M. arion*. Both species quickly develop on their food plants and gain the major part of their ultimate biomass in host ant nests. While *M. arion* is an obligate predator of *Myrmica* larvae, caterpillars of *M. rebeli* mimic ant larvae and thus induce *M. schenki* workers to feed them directly with regurgitations, trophic eggs and prey (Elmes et al., 1991). Following the model of Hochberg et al. (1994), I divided the life cycle of *M. arion* into two parts: (1) adult reproduction, survival of eggs and of caterpillars on flower buds of thyme (g_1), and (2) subsequent recruitment and survival of caterpillars in ant nests (g_2). Consequently, the size of the adult butterfly population at generation $t+1$ (N_{t+1}) is given by the equation:

$$N_{t+1} = g_1(N_t, T) \cdot g_2(g_1(N_t, T), A) \qquad (1)$$

where N_t is the population size at generation t, T is the constant population density of thyme and A is the constant population density of host ant nests.

The first life step, modeled by function $g_1(N_t, T)$ starts with oviposition. Each female butterfly lays in total 60 eggs per generation (Thomas, 1989; Thomas et al., 1991). Having an equal sex ratio the model treats each adult butterfly as laying λ (=30) eggs per generation. An amount of 90 percent of eggs hatch ($\Phi_{\text{egg hatching}}$, Thomas et al., 1991) and 5.3 percent of the hatched caterpillars die from parasitism by *Trichogramma* species ($1-\Phi_{\text{Trichogramma}}$, Thomas et al., 1991). Non-parasitized caterpillars continue to develop within the flower buds, with one caterpillar surviving per bud. This competition on flower buds that results from cannibalism of caterpillars is modeled in accordance with Hochberg et al. (1994) by the general intraspecific competition model of Hassell (1975):

$$g_1(N_t, T) = \frac{N_t \lambda \Phi_T}{1 + x_T} \qquad (2)$$

where $\Phi_T = \Phi_{\text{egg hatching}} \cdot (1-\Phi_{\text{Trichogramma}})$ is the proportion of caterpillars surviving from density-independent causes of mortality (hatching rate of eggs, parasitism of caterpillars by *Trichogramma*) and $x_T = \dfrac{N_t \lambda \Phi_T}{\varepsilon_T T}$ is the average number of competing caterpillars per flower bud. Parameter ε_T equals T_B which is the number of flower buds per square meter in field and T gives the total size of the study area that is covered by thyme. T equals ($S \cdot T_C / 100$) where T_C is the percentage of ground covered by *Thymus* plants (Braun-Blanquet, 1951) and S is the size of the habitat.

The second life step ($g_2(g_1(N_t, T), A)$) starts with adoption of caterpillars in host ant nests and depends on the composition of the *Myrmica* fauna in the field. A constant proportion of caterpillars are adopted by other non-host *Myrmica* ants ($\Phi_{\text{other Myrmica}}$). All caterpillars adopted by wrong *Myrmica* ants die within their nests. The proportion of caterpillars recruited in correct host ant nests ($\rho(A)$) is modeled by assuming that host ant nests are randomly distributed with respect to *Thymus* plants:

$$\rho(A) = 1 - e^{-\eta A} \qquad (3)$$

where η (= 0.0009 ha, Griebeler and Seitz, 2002) is the mean potential area of search of workers from a host ant nest and A is the total number of host ant nests in the study area.

To model competition in host ant nests, I applied the general function of Hassell (1975) following Hochberg et al. (1994). This leads to:

$$g_2(g_1(N_t,T),A) = \frac{\rho(A)\Phi_A}{1+x_A} \qquad (4)$$

where $\Phi_A = 1-(\Phi_{\text{other Myrmica}}/100)$ and $x_A = \dfrac{\rho(A)\Phi_A\, g_1(N_t,T)}{\varepsilon_A A}$ is the average number of caterpillars competing per host ant nest. Values of Φ_A and $\Phi_{\text{other Myrmica}}$ depend on the composition of the *Myrmica* fauna of the studied area. $\Phi_{\text{other Myrmica}}$ is the proportion of non-host ant nests in the area and thus Φ_A is the frequency of adoption of caterpillars by correct host ants. Parameter ε_A (= 0.3, Thomas and Wardlaw, 1992) is the number of caterpillars that are expected to develop to butterflies per host ant nest.

2.3 Extinction risk of the butterfly

As suggested by Hochberg et al. (1994) I used the intrinsic growth rate R_0 and the equilibrium level of adult butterflies N^* to assess the extinction risk of a population. R_0 is the average number of offspring that survives to adulthood per parent in the absence of intraspecific competition. It measures the capacity of a species to increase in size after a severe decline in size or a colonization of a new habitat. R_0 depends on habitat conditions. Qualitatively, Hochberg et al. (1994) call populations for which $1 \ll R_0$ 'safe' from extinction, those with $R_0 \approx 1$ as 'in danger' of extinction and those with $R_0 \ll 1$ as 'doomed' to extinction.

For the MM, R_0 is easily found by evaluating N_{t+1}/N_t at the limit $N_t \rightarrow 0$:

$$R_0 = \lambda \cdot \Phi_T \cdot \rho(A) \cdot \Phi_A \qquad (5)$$

The equilibrium level of butterflies N^* is found by setting $N^* = N_{t+1} = N_t$ and solving equation (1) for N^*:

$$N^* = \frac{\rho(A)\Phi_A - \frac{1}{\lambda\Phi_T}}{\frac{1}{\varepsilon_T T} + \frac{\rho(A)\Phi_A}{\varepsilon_A A}} \qquad (6)$$

2.4 Model sensitivity

To compare the MM and the IBM, I repeated the analyses given in Griebeler and Seitz (2002) for the MM. In these new analyses I again assumed an area size of 1 ha. I calculated R_0 and N^* for various model parameter values applying equations (5) and (6).

In the first study, I aimed to assess the errors in the estimated extinction risk of a population which are introduced by errors in model parameter values. Therefore, I systematically varied the value assumed for each of the model parameters λ, $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$, η and ε_A while holding the other parameters constant (Table 1). In this study I set habitat characteristics to A=1300, $\Phi_{\text{other Myrmica}}$=50%, T_C=30% and T_B=150 (Griebeler and Seitz, 2002). For each combination of model parameter values I computed R_0 and N^*.

In the second study, I investigated the influence of habitat characteristics on the extinction risk of a butterfly population based on R_0 and N^*. As in Griebeler and Seitz (2002) habitat characteristics studied were *Thymus* cover T_C, the abundance of host ants A and the proportion of caterpillars that are adopted by other non-host *Myrmica* ant species $\Phi_{\text{other Myrmica}}$. Two analyses were performed for an area of a size of 1 ha. First, *Thymus* cover T_C and the number of host ant nests A were both simultaneously systematically altered, assuming that a constant proportion of 50% of caterpillars are adopted by other *Myrmica* ($\Phi_{\text{other Myrmica}}$). Second, the number of host ant nests A and the proportion of caterpillars that are adopted by other *Myrmica* ($\Phi_{\text{other Myrmica}}$) were

analogously simultaneously changed, assuming a constant *Thymus* cover T_C of 30%. In both analyses, T_B was always set to 150 flower buds per m^2 and the remaining model parameters were chosen as given in Table 1.

Table 1 Model parameters and their values

Parameter	Meaning	Value
S	Area size [ha]	Site dependent
A	Density of host ant nests per ha	Site dependent
T_C	*Thymus*-cover [%]	Site dependent
$T_B = \varepsilon_T$	Number of flower buds per m^2	Site dependent
$\Phi_{\text{other Myrmica}}$	Proportion of adoption of caterpillars by incorrect host ants [%]	Site dependent
λ	Number of eggs laid per adult	$30 = {}^{60}/_2$ (Thomas, 1989)
$\Phi_{\text{egg hatching}}$	Egg survival	0.9 (Thomas et al., 1991)
$\Phi_{\text{Trichogramma}}$	Survival from parasitism by *Trichogramma*	0.947 (=1-0.053, Thomas et al. 1991)
η	Mean potential area of search of workers from an ant nest [ha]	0.0009 (Thomas 1990, Griebeler and Seitz, 2002)
ε_A	Average number of caterpillars competing per host ant nest, nest capacity	0.3 (Thomas and Wardlaw, 1992)

3 Results

For none of model parameters λ, $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$, η and ε_A, I found a parameter value that resulted in R_0 values below one which would indicate that the respective population is 'in danger' or 'doomed' to extinction (Fig. 1). With respect to R_0 and N^* the mean potential search area of workers from a nest η (Fig. 1) was most sensitive to errors. Increasing η values (Fig. 1) exponentially increased R_0 ($R_0 = \lambda \cdot \Phi_T \cdot \rho(A, \eta) \cdot \Phi_A = c \cdot \rho(A, \eta)$, with $c = \lambda \cdot \Phi_T \cdot \Phi_A =$ const; in formulas hereafter sub indices are added to analogous constants c if more than one constant is needed) and hyperbolically increased N* ($N^* = \dfrac{\rho(A, \eta)c_1 - c_2}{c_3 + \rho(A, \eta)c_4}$). In contrast, increasing the number of eggs laid per adult (λ, Fig. 1) linearly increased R_0 ($R_0 = \lambda \cdot \Phi_T \cdot \rho(A, \eta) \cdot \Phi_A = c \cdot \lambda$) and hyperbolically increased N* ($N^* = \dfrac{c_1 - \frac{1}{\lambda c_2}}{c_3}$). For parameters $\Phi_{\text{egg hatching}}$ and $\Phi_{\text{Trichogramma}}$ (Fig. 1), R_0 linearly increased with increasing values ($\Phi_{\text{egg hatching}}$: $R_0 = \lambda \cdot \Phi_T \rho(A) \cdot \Phi_A = \lambda \cdot \Phi_{\text{egg hatching}} \cdot \Phi_{\text{Trichogramma}} \cdot \rho(A) \cdot \Phi_A = c \cdot \Phi_{\text{egg hatching}}$; $\Phi_{\text{Trichogramma}}$: $R_0 = \lambda \cdot \Phi_T \rho(A) \cdot \Phi_A = \lambda \cdot \Phi_{\text{egg hatching}} \cdot \Phi_{\text{Trichogramma}} \cdot \rho(A) \cdot \Phi_A = c \cdot \Phi_{\text{Trichogramma}}$), whereas N^* hyperbolically increased ($\Phi_{\text{egg hatching}}$: $N^* = \dfrac{c_1 - \frac{1}{c_2 \Phi_{\text{egg hatching}}}}{c_3}$; $\Phi_{\text{Trichogramma}}$: $N^* = \dfrac{c_1 - \frac{1}{c_2 \Phi_{\text{Trichogramma}}}}{c_3}$. While R_0 was independent of the average number of caterpillars competing per host ant nest ε_A (see equation (5)), N^* hyperbolically increased ($N^* = \dfrac{c_1}{c_2 + \frac{c_3}{\varepsilon_A}}$) with increasing ε_A values (Fig. 1).
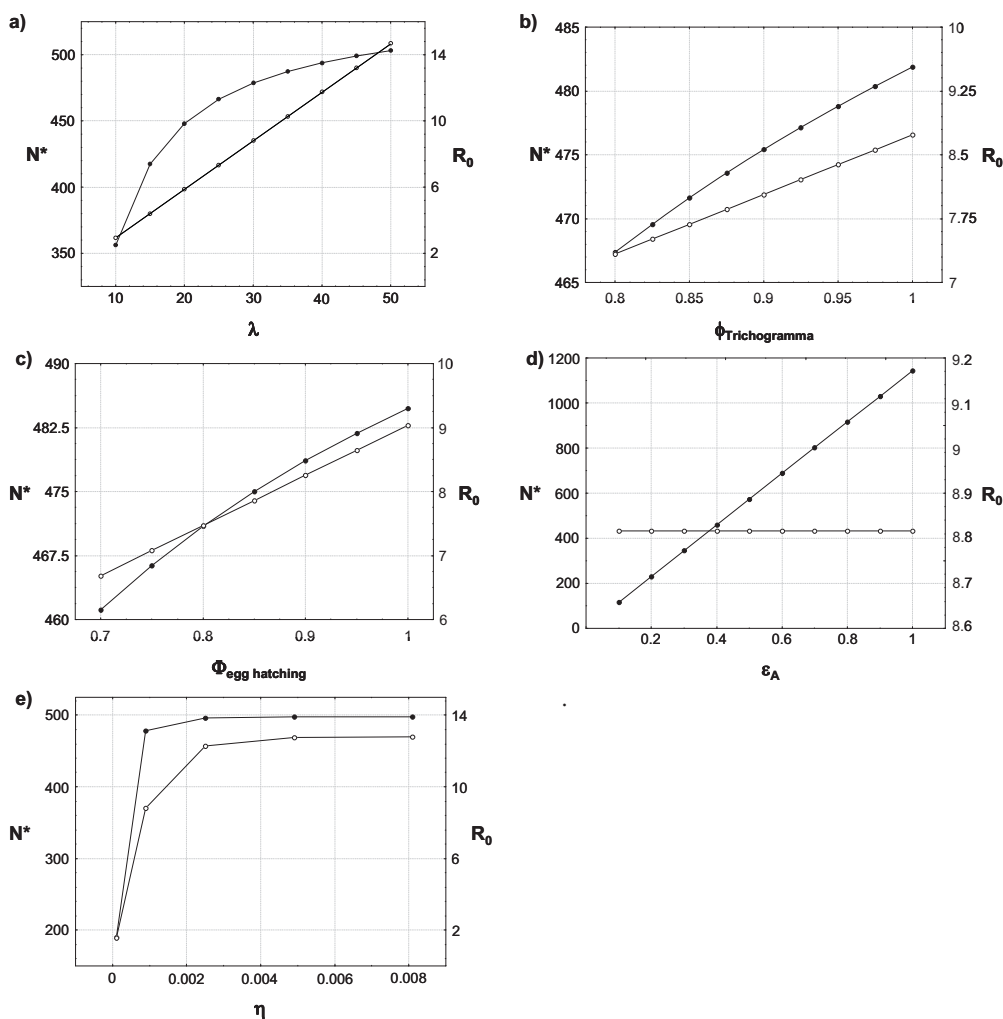
Fig. 1 Sensitivity analysis of model parameters λ, $\Phi_{Trichogramma}$, $\Phi_{egg\ hatching}$, ε_A and η. R_0 (open circles) and N^* (filled circles) are shown in relation to different values that were assumed for a) number of eggs laid per adult λ, b) survival of parasitism by *Trichogramma* $\Phi_{Trichogramma}$, c) egg survival $\Phi_{egg\ hatching}$, d) average number of caterpillars competing per host ant nest ε_A, and e) mean potential area of search of workers from an ant nest η. R_0 and N^* are calculated from equations (5) and (6). Habitat size was 1 ha (*S*), *Thymus* cover (T_C) was 30%, number flower buds per m^2 (T_B) was 150, number of host ant nests (*A*) was 1,300 and non-host adoption of caterpillars ($\Phi_{other\ Myrmica}$) was 50%. For values of λ, $\Phi_{Trichogramma}$, $\Phi_{egg\ hatching}$, ε_A and η see Table 1.

Thymus cover T_C and the number of host ant nests *A* are site dependent and can directly be altered by conservation measures (Thomas, 1990; Thomas et al., 1998; Fig. 2). R_0 did exponentially increase with an increasing number of host ant nests ($R_0 = \lambda \cdot \Phi_T \cdot \rho(A) \cdot \Phi_A = c \cdot \rho(A)$), but this increase was independent of the amount of *Thymus* cover (see equation (5)). A population inhabiting an area with less than 100 ant nests was predicted to be 'in danger' or 'doomed' to extinction. While R_0 did not depend on *Thymus* cover, N^* did

hyperbolically increase with increasing *Thymus* cover for a fixed number of host ant nests ($N^* = \dfrac{c_1}{\frac{1}{c_2 T_c} + c_3}$). For

constant *Thymus* cover, N^* did hyperbolically increase with increasing numbers of host ant nests

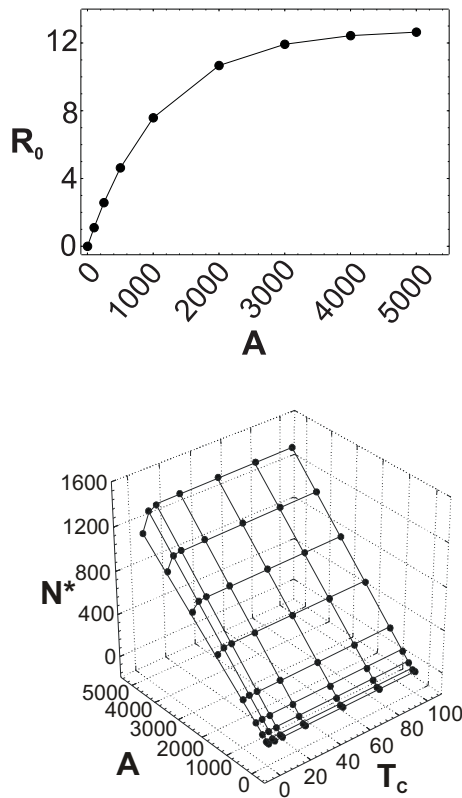($N^* = \dfrac{\rho(A)c_1 - c_2}{c_3 + \rho(A)c_4}$).

Fig. 2 Sensitivity analysis of model parameters T_C and A. Calculated R_0 and N^* values are shown in relation to *Thymus* cover T_C and density of host ant nests per hectare A. The proportion of caterpillars adopted by incorrect host ants $\Phi_{\text{other Myrmica}}$ was 50%. Area size S was one hectare. Site independent parameters were chosen according to Table 1. Note that R_0 is independent of T_C (see equation (5)).
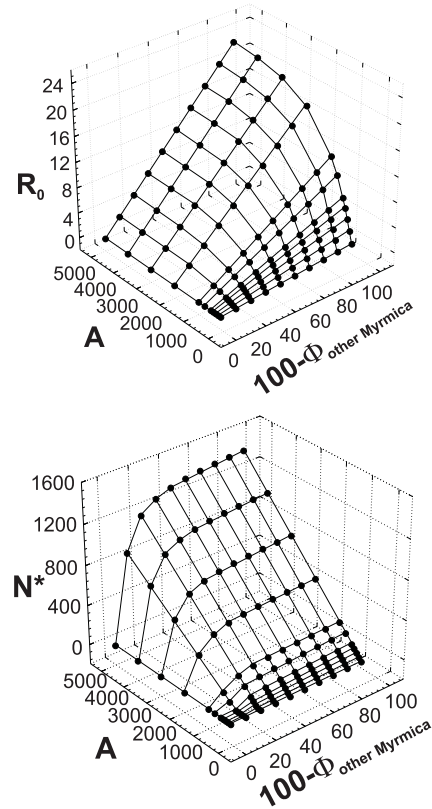
Fig. 3 Sensitivity analyses of model parameters A and $\Phi_{\text{other Myrmica}}$. Calculated R_0 and N^* values are shown in relation to density of host ant nests per hectare A and proportion of adoption of caterpillars by incorrect host ants $\Phi_{\text{other Myrmica}}$. *Thymus* cover T_C was 30%. Area size S was one hectare. Site independent parameters were chosen according to Table 1.

The relation between the number of host ant nests A and the proportion of adoption of caterpillars by correct host ants (100-$\Phi_{\text{other Myrmica}}$) and predicted R_0 and N^* values, respectively is given in Fig. 3. For a fixed number of host ant nests, R_0 did linearly increase ($R_0 = \lambda \cdot \Phi_T \cdot \rho(A) \cdot \Phi_A = c \cdot \Phi_A$) and N^* did hyperbolically increase

($N^* = \dfrac{\Phi_A c_1 - c_2}{c_3 + \Phi_A c_4}$) with increasing proportions of host ant adoption (100-$\Phi_{\text{other Myrmica}}$). In contrast, R_0 did

exponentially increase ($R_0 = \lambda \cdot \Phi_T \cdot \rho(A) \cdot \Phi_A = c \cdot \rho(A)$) and N^* did hyperbolically increase ($N^* = \dfrac{\rho(A) c_1 - c_2}{c_3 + \rho(A) c_4}$)

with increasing numbers of host ant nests for a fixed proportion of host ant adoption (100-$\Phi_{\text{other Myrmica}}$). In particular, there were several situations that assume positive host ant adoption when the population was 'in danger' or 'doomed' to extinction: A=100 and (100-$\Phi_{\text{other Myrmica}}$)≤40%; A=200 and (100-$\Phi_{\text{other Myrmica}}$)≤20%; 300≤$A$≤500 and (100-$\Phi_{\text{other Myrmica}}$)≤10%.

In conclusion, for the MM the sensitivity analysis of habitat characteristics suggested that *Thymus* cover is of very low importance for species survival (minimum 1% cover) but the number of host ant nests and the proportion of host ant adoption are key factors for the survival of the Large Blue Butterfly *M. arion*.

4 Discussion

4.1 Comparison of sensitivity analyses

The sensitivity analysis of the MM revealed that the mean potential search area of workers from an ant nest η, the number of eggs laid per adult butterfly λ, the average number of caterpillars competing in a host ant nest ε_A, the number of host ant nests A and the proportion of caterpillars adopted by incorrect host ants $\Phi_{\text{other Myrmica}}$ are all important with respect to the vulnerability of *M. arion* (Fig. 1). Errors in these parameters may result in wrong estimates of the extinction risk of the population. For example, assuming 0.0001 ha (vs. $\eta = 0.0009$ ha, Table 1) for the mean potential search area of workers from an ant nest would have classified a population as 'in danger' of extinction (R_0=1.1) instead of 'safe' from extinction (R_0=8.4). Moderate errors in egg survival $\Phi_{\text{egg hatching}}$ and survival from parasitism by *Trichogramma* $\Phi_{\text{Trichogramma}}$ did not influence the classification of a population's vulnerability within the range of values studied for each rate. Equation (5) predicts that R_0 is independent of *Thymus* cover T_C and of the average number of caterpillars competing in a host ant nest ε_A. Thus, errors in estimates of T_C and ε_A do not affect the classification of a population's vulnerability in the MM.

There were several consistencies between the predictions of the MM and the IBM (Griebeler and Seitz, 2002), however, also severe differences existed. Both models suggested that parameters λ, η, A and $\Phi_{\text{other Myrmica}}$ are of high importance for the vulnerability of the butterfly whereas both parameters $\Phi_{\text{egg hatching}}$ and $\Phi_{\text{Trichogramma}}$ are of low importance. In contrast, in the MM *Thymus* cover T_C did not affect survival (R_0>1) whereas the IBM predicted that this is only true when more than 500 host ant nests per hectare exist.

The MM predicted for none of the studied values of parameters λ, $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$ and η values of R_0 which were close to or lower than one and which would indicate that the respective population is 'in danger' or 'doomed' to extinction. In contrast, the IBM estimated for λ=10 an extinction probability of 100%. Furthermore, the relation between λ and population size (N^* and mean population size, respectively) differed between the two models. While the MM predicted a hyperbolic increase in size with increasing λ values, the IBM predicted an optimum at λ=30. Predicted relations between the population size and each of the parameters $\Phi_{\text{egg hatching}}$ and $\Phi_{\text{Trichogramma}}$ did also differ between the two models. While the MM predicted a linear increase in size for increasing survival rates, the IBM predicted a hyperbolic increase. Both models suggested a hyperbolic relation between η and population size.

In the IBM habitat characteristics T_C, A and $\Phi_{\text{other Myrmica}}$ were key parameters for the survival of a *M. arion* population. However, the MM only corroborated the importance of A and $\Phi_{\text{other Myrmica}}$. R_0 that measures the persistence of a butterfly population was independent of *Thymus* cover in the MM whereas the IBM suggested that cover should not fall bellow 5% for low numbers of host ant nests (A<750). Both models predicted a hyperbolic relation between population size and *Thymus* cover, but the predicted increase in size was much stronger in the IBM than in the MM. Adding extra *Thymus* when cover was still below 20% tripled the population size in the IBM. In contrast, the MM predicted a saturation level at 10% thyme and the population size increased only about 25%. For the IBM, both an increase in the number of host ant nests and in host ant adoption resulted in a rapid decrease in the extinction probability. In this model, a population was not endangered if more than 20% caterpillars were adopted by the correct host ant and the nest density of host ants was higher than 500 nests per ha. For the MM, however, this limit was much weaker. If nest density of host ants was greater than 500 nests per ha the model only asked for positive host ant adoption. For the IBM, there was a linear increase in population size for an increasing number of host ant nests under a fixed *Thymus* cover.

The MM found a hyperbolic increase, but a linear fit worked also very well (Fig. 2, worst fitting found for T_C=1, in this case R=0.998). In contrast, predicted relations between the proportion of host ant adoption and population size strongly differed between the two models. While the MM predicted a hyperbolic increase in size for increasing proportions of host ant adoption, the IBM revealed a curve with an optimum.

In general, population sizes predicted by the MM were much higher than those predicted by the IBM and estimated sizes are unrealistic for the species. Thomas (1990) stated that a 'safe' population of 400-1,000 adult butterflies could theoretically be supported by one hectare sized ideal habitat (at least 2,500 *M. sabuleti* nests). The IBM corroborated his field observations whereas the MM did not. The IBM predicted approximately 400 adults for a habitat of 1 ha size, 30% *Thymus* cover, 2,500 *M. sabuleti* nests and at least 20 % host ant adoption whereas the MM estimated about 600 butterflies.

4.2 Implications for population viability

The sensitivity analysis of the MM revealed several results that differed from those obtained for the IBM. I found several situations where the extinction risk of the population was lower in the MM than in the IBM and where the estimated population sizes (N^*) were clearly higher in the MM than in the IBM. While the number of host ant nests A and the proportion of caterpillars adopted by non-host *Myrmica* $\Phi_{\text{other Myrmica}}$ were detected as key factors for survival by both models, a third factor *Thymus* cover, which was discovered by the IBM, was insignificant in the MM. Such potential errors may result in wrong estimates of the viability of a natural *M. arion* population, especially in those cases where habitat quality is poor (low abundance of thyme and host ants, high abundance of non-host *Myrmica* ants) but reliable estimates for the extinction risk are needed. This potential inaccuracy of the MM may severely limit its application in conservation and favor the use of the IBM, as the latter model revealed more conservative estimates of the extinction risk.

The MM, however, does not explicitly include the mechanistic processes which underlie the interaction between *M. arion*, *Thymus*, *Myrmica* host ants and non-host *Myrmica* ants, whereas these are included in the IBM. In the MM I assumed the general interspecific competition model of Hassell (1975) for modeling competition of caterpillars on plants and in host ant nests. One known limitation of this competition model is that it is unable to explicitly account for possible heterogeneities in intraspecific competition (Hochberg et al., 1994). Such heterogeneities in competition arise on *Thymus* plants and in host ant nests. *Thymus* plants grow in small groups that are more or less randomly distributed in the natural habitat of *M. arion*. This patchy distribution of flower buds was included in the habitat model of the IBM but was neglected by the MM. In the IBM, the habitat was modeled as a grid of square cells, with each covering an area of 1 m^2. According to the natural degree of *Thymus* cover a proportion of cells was randomly selected where the host plant was abundant and the number of flower buds was T_B in each of the cell with host plants. The MM, however, assumed that flower buds were randomly distributed within the habitat. If caterpillars are clumped in field due to clumping of *Thymus* this will result in a higher competition of caterpillars in host ant nests and in overall lower population sizes than predicted by the MM due to the resulting higher mortalities in host ant nests. Analogously, an increase in the number of eggs per adult (λ) will also increase the clumping of caterpillars in host ant nests, due to the clumping of eggs on thyme. The resulting higher mortalities in host ant nests did also cause the decline in population size observed in the IBM when the number of eggs laid per adult exceeded 30 eggs. These increasing mortalities with an increasing clumping of eggs were not observed in the MM.

Another striking difference between the results of the MM and the IBM is that a maximal population size is reached at 50% host ant adoption in the IBM which was absent in the MM (Fig. 3). This maximum results from scramble competition of caterpillars in host ant nests (Clarke et al., 1998), causing a decrease in the survival probability of a caterpillar with an increasing number of caterpillars within the nest. If the proportion of adoption by the correct host ant is low, only a few caterpillars are adopted and mean survival rate of these

adopted individuals is high. With an increasing proportion of adopted caterpillars the mean number of caterpillars adopted per nest will exceed one and thus, the survival probability of each caterpillar will decrease. These results in an overall smaller output of each nest with increasing numbers of caterpillars adopted, consequently resulting in a decrease in the mean population size for high proportions of host ant adoption. However, this strong competition of caterpillars in nests resulting in exponentially decreasing survival rates (Thomas and Wardlaw, 1992) was only observed in the IBM. It was absent in the MM which assumed Hassell's competition function (Hassell, 1975) that caused a hyperbolical decrease in survival rates.

In conclusion based on this study, I cannot fully corroborate the wide acceptance that simple deterministic models are able to reveal important insights on which parameters are likely to be most critical for the survival of a species. My evaluation is mainly based on the observation that mathematical models often neglect important details in landscape configuration and in the interaction of species with the landscape. In this study such details have resulted in a lower intraspecific competition of caterpillars on host plants and in host ant nests in the MM than in the IBM. Landscape heterogeneity, however, is easy to model when applying the individual based modeling approach and this advantage may favor the use of this modeling technique over mathematical modeling at least if heterogeneity of the environment could be of high importance for population dynamics as in the case of *M. arion*.

References

Braun-Blanquet J. 1951. Pflanzensoziologie, Grundzüge der Vegetationskunde. Springer, Wien

Clarke RT, Thomas JA, Elmes GW, Wardlaw JC, Munguira ML, Hochberg ME. 1998. Population modelling of the spatial interactions between *Maculinea rebeli* their initial foodplant *Gentiana cruciata* and *Myrmica* ant hosts. Journal of Insect Conservation, 2: 29-37

DeAngelis DL, Mooij WM. 2005. Individual-based modeling of ecological and evolutionary processes. Annual Reviews in. Ecology, Evolution and Systematics, 36: 147-168

Elmes GW, Thomas JA, Wardlaw JC, Hochberg ME, Clarke RT, Simcox DJ. 1998. The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. Journal of Insect Conservation, 2: 67-78

Elmes GW, Wardlaw JC, Thomas JA. 1991. Larvae of *Maculinea rebeli*, a large-blue butterfly, and their *Myrmica* host ants: patterns of caterpillar growth and survival. Journal of Zoology, 224: 79-92

Gottschalk E, Griebeler EM, Waltert M, Mühlenberg, M. 2003. Population dynamics of the Grey Bush Cricket *Platycleis albopunctata* (Orthoptera: Tettigonidae) – what causes interpopulation differences? Journal of Insect Conservation, 7: 45-58

Griebeler EM, Gottschalk E. 2010. Conservation of the Grey Bush Cricket *Platycleis albopunctata* (Orthoptera: Tettigonidae) under differing habitat conditions: implications from an individual-based model. In: Relict Species: Phylogeography and Conservation Biology (Eds. JC Habel and T Assmann). Springer-Verlag, Berlin, Heidelberg, 385-399

Griebeler EM, Seitz A. 2002. An individual based model for the conservation of the endangered Large Blue Butterfly, *Maculinea arion* (Lepidoptera: Lycaenidae). Ecological Modelling, 156: 43-60

Hanski I, Gilpin M. 1997. Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, San Diego

Hassell MP. 1975. Density dependence in single-species populations. Journal of Animal Ecology, 44: 283-295

Heppell SS, Crouse DT, Crowder LB. 2000. Using matrix models to focus research and management efforts in conservation. In: Quantitative Methods for Conservation Biology (Eds. S Ferson and M Burgman). Springer, New York, 148-168

Hochberg ME, Clarke RT, Elmes GW, Thomas JA. 1994. Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant hosts. Journal of Animal Ecology, 63: 375-391

Matsinos YG, Wolff WF, DeAngelis DL. 2000. Can individual-based models yield better assessment of population variability? In: In: Quantitative Methods for Conservation Biology (Eds. S Ferson and M Burgman). Springer, New York, 188-198

Shaffer ML. 1981. Minimum population sizes for species conservation. Bioscience, 31: 131-134

Soulé ME. 1987. Viable Populations for Conservation. Cambridge University Press, Cambridge

Thomas JA. 1977. Second Report on the Conservation of the Large Blue butterfly. Institute of Terrestrial Ecology, UK

Thomas JA. 1989. Return of the Large Blue butterfly. British Wildlife, 1: 2-13

Thomas JA. 1990. Rare species conservation: case studies of European butterflies. In: The Scientific Management of Temperate Communities for Conservation (Eds. IF Spellerberg, FB Goldsmith and MG Morris). Blackwell, Oxford, 149-197

Thomas JA, Elmes GW, Wardlaw JC, Woyciechowski M. 1989. Host specificity among Maculinea butterflies in *Myrmica* ant nests. Oecologia, 79: 452-457.

Thomas JA, Munguira ML, Martin J, Elmes GW. 1991. Basal hatching by *Maculinea* butterfly eggs: a consequence of advanced myrmecophily? Biological Journal of the Linnean Society, 44: 175-184

Thomas JA, Simcox DJ, Wardlaw JC, Elmes GW, Hochberg ME, Clarke RT. 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. Journal of Insect Conservation, 2: 39-46

Thomas JA, Wardlaw JC. 1990. The effect of queen ants on the survival of *Maculinea arion* larvae in *Myrmica* ant nests. Oecologia, 85: 87-91

Thomas JA, Wardlaw JC. 1992. The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. Oecologia, 91: 101-109