Ecological Monographs, 75(4), 2005, pp. 525–542
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POPULATION DYNAMICS AND CONSERVATION OF A SPECIALIZED PREDATOR: A CASE STUDY OF *MACULINEA ARION*

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Abstract. We employ an empirically motivated ''case model'' approach to investigate the theoretical foundations for the conservation of the endangered butterfly *Maculinea arion*. *Maculinea* butterflies have highly specialized larvae that sequentially exploit a plant and an ant species. Our study establishes that *M. arion*'s specialized life cycle, including scramble competition for limiting resources, and the spatially discrete nature of its resources, make it more sensitive to environmental variation and more prone to local extinction than other univoltine phytophagous species. We find that the number and spatial distribution of the butterfly's resources are key factors in their population dynamics, especially for *M. arion* populations in habitats associated with high larval survival and high adult fecundity. Factors that increase juvenile competition have first a positive effect on adult population size, but beyond a threshold this effect becomes negative. In general, oscillatory dynamics emerge for high potential growth rates and spatially homogeneous juvenile competition. We discuss the relevance of our results to population management, investigate the consequences of environmental variation, and consider different scenarios of conservation. Our model, although based on the *Maculinea* genus, should apply to a broad range of species for which the form of competitive interactions changes predictably at distinct points in the life cycle. Complex life cycles can lead to negative feedbacks involving parameters that are usually thought to optimize population size. We suggest that conservation strategies are neither generalizable for the *Maculinea* genus nor for disparate populations of each species of *Maculinea*, and rather that management should be conducted on a case-by-case basis.

Key words: butterflies; case model; complex life cycle; conservation; Maculinea arion; *management; nested density dependence; population dynamics; spatial distribution.*

INTRODUCTION

It is becoming increasingly clear that exogenous and endogenous drivers of population dynamics can play important roles in population regulation and persistence (Hassell 1975, Murdoch 1994, Den Boer and Reddingius 1996, Lewellen and Vessey 1998), yet the relative importance of these forces is largely unknown. Given the long time scales necessary to assess these issues, theoretical approaches have an important role to play in untangling the relative contribution of each driver. Unfortunately, most theoretical approaches to conservation biology are still too general to be predictive (With 1997), and some authors question their utility in conservation (Doak and Mills 1994). In contrast, empirically motivated theoretical approaches, or so-called ''case models'' (Hochberg et al. 1996, Turchin 2003), have been employed to test general theory within the constraints of specific systems.

The case model approach has been employed to investigate the theoretical foundations of conservation for the butterfly *Maculinea rebeli* (Hochberg et al. 1992, 1994, Elmes et al. 1996, Hochberg et al. 1996, Clarke et al. 1997, 1998). All *Maculinea* species are listed as globally ''endangered'' or ''vulnerable'' (International Union for the Conservation of Nature and Natural Resources 1990), but their status may be even more threatened following recent analyses that show that certain morpho-species (including *M. arion*) consist of clusters of cryptic species (Als et al. 2004, Thomas and Settele 2004). In Europe, *Maculinea* populations have experienced many extinctions at local or national scales (Thomas 1980, 1995), and their conservation has become doubly important because their habitats also support endangered Palearctic landscape biodiversity (Elmes and Thomas 1992, Maes et al. 2003). *Maculinea* butterflies have highly specialized life cycles that involve the exploitation of two different host species. Each *Maculinea* species lays its eggs on specific food plants, where the caterpillars develop as competing herbivores through three larval instars. After the molt to the fourth instar, they drop off their plant and are potentially adopted by red ants of the genus *Myrmica*. Within the ant nest, caterpillars either induce ant workers to feed them (cuckoo species: *Maculinea*

Manuscript received 24 February 2005; accepted 29 April 2005. Corresponding Editor: W. S. C. Gurney.

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rebeli, *M. alcon*) or they are predators of ant larvae (predatory species: *M. arion*, *M. teleius*, and *M. nausithous*).

We have already employed models of *M. rebeli* to show that butterfly survival in ant nests is disproportionately more important to its population dynamics than is competition on the plant (Hochberg et al. 1992), and that apparent competition between the ants and the plants via the butterfly lead to higher butterfly populations at intermediate plant densities (Hochberg et al. 1994, Clarke et al. 1998). However, it is unclear that they accurately represent a predaceous species' dynamics. While cuckoo species show contest competition when vying for resources within ant colonies (Thomas et al. 1993), the predacious species (e.g., *M. arion*) show scramble competition, whereby overcrowding results in the annihilation of the ant colony and the death of all caterpillars (Thomas and Wardlaw 1992). Theory suggests that strong scramble competition produces more erratic dynamics than contest competition (Hassell 1975, May and Oster 1976). Given the propensity for the former interaction to produce cycles, it must be studied in depth before accurate recommendations for the conservation of these endangered species can be made. Population fluctuations of the predacious *M. arion* are among the most variable amongst U.K. univoltine phytophagous species (Thomas et al. 1998, Table 11.2), and although variation in rainfall may explain some observed cycles (Thomas et al. 1998, Roy et al. 2001), an alternative hypothesis addresses the effect of scramble competition for ant prey, perhaps amplified by the spatial distribution of the ant nests (Hassell and May 1985).

The objective of this study is to establish how biological and spatial aspects of competition in the predacious *Maculinea* may impact their population dynamics and vulnerability to local extinction. We evaluate how endogenous (sequential contest and scramble density dependence) and exogenous (climatic) factors both contribute to population dynamics. We also consider how different conservation strategies could be employed, given the relative importance of each type of factor. The predacious *Maculinea* scarcely have been considered in the theoretical literature apart from Griebeler and Seitz's (2002) study, which explored some relationships between habitat characteristics and the persistence of *M. arion*, but did not consider instabilities resulting from density dependence within ant nests, the phase that we hypothesize is pivotal to butterfly population dynamics. Here we modify the Hochberg et al. (1992) model for *M. rebeli*, by integrating scramble competition during the ant phase and explicit consideration of the spatial distribution of ant nests. We also draw upon 30 years of empirical studies of the *M. arion* system (e.g., Thomas 1995, 1998; J. A. Thomas, *unpublished data*) to parameterize the model.

BIOLOGY OF *MACULINEA ARION*

Maculinea arion is a lycaenid butterfly that exploits two sequential larval resources: a plant, *Thymus* spp. or *Origanum vulgare*, followed by *Myrmica sabuleti* ant colonies. The adults emerge in summer, and populations occupy sites of typically 5–20 ha, within which they fly freely but from which they seldom emigrate. Females oviposit on the young flower heads of *Thymus* or *Origanum*. *Maculinea arion* eggs are hidden between flower buds (Thomas et al. 1991) and experience low levels of mortality, e.g., from the generalist parasitoid *Trichogamma evanescens*. The first three larval instars feed on developing flowers, with the first instar also being cannibalistic, causing contest competition. After the third and final molt, the 1–2 mg caterpillar drops to the ground to await discovery by any species of *Myrmica* ant (Thomas 2002). If found, a complex behavioral interaction ensues, during which the larva mimics the worker's grubs, resulting in the ant carrying it back to the nest (Thomas 2002). Inside the *Myrmica* nest, *Maculinea arion* is an obligate predator of the ant brood. *Myrmica* colonies are small compared to those of many ants, but caterpillars use this resource efficiently by selecting the largest available prey, allowing the fixed cohort of smaller ant larvae to continue their growth (Thomas and Wardlaw 1992). Nevertheless, overcrowding is a major cause of mortality in *Maculinea arion*, which generally experiences strong scramble competition, almost invariably resulting in 100% mortality when more than four caterpillars are adopted into a single *Myrmica* nest (Thomas and Wardlaw 1992). The third major cause of mortality of *Maculinea arion* larvae in *Myrmica* nests involves host specificity (Thomas et al. 1989). Although oviposition is apparently indiscriminate and caterpillars are adopted with equal facility by any of up to five *Myrmica* species that may forage beneath the initial food plant, the mean survival of *Maculinea arion* in the field is more than six times higher in colonies of *Myrmica sabuleti* than with any other *Myrmica* species (Thomas 1980, Thomas et al. 1998, Thomas 2002). Finally, *M. arion* may be parasitized by an apparently species-specific ichneumonid parasitoid *Neotypus correensis*, but known infestation levels are low compared to other *Maculinea* species (Hochberg et al. 1996, Thomas 2002).

THE MODEL

The developments below are based on a previous model for *Maculinea rebeli* (Hochberg et al. 1992). Density dependence in population growth rates is encapsulated in two different, sequentially acting functions, each corresponding to competition between *Maculinea* caterpillars for one of their two resources. Unlike the *M. rebeli* model, which had contest competition on plants and again in ant nests, our model for *M. arion* includes strong contest competition on plants followed by severe scramble competition within ant nests. We

TABLE 1. Definitions of the parameters used in the model.

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 ÷ 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 *Myrmica sabuleti* nest	ha
P	Number of plants (*Thymus* or *Origanum*)	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

also go beyond this previous model to include spatial aspects of density dependence. Adult population size N_t is the product of recruitment and competition on the plant g_1 and in ant nests g_2 such that

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

Parameters are specified in Table 1. We present the different model functions encapsulated in Eq. 1 and descriptions of parameters for *Maculinea arion*. (See also Fig. 1.)

Recruitment and competition on the plant

In generation t, the population of N_t adult butterflies lays FN_t eggs over the plant population. A proportion ϕ_1 of the eggs and the first instar caterpillars survive density-independent mortality; older caterpillars suffer contest competition and survive density-independent mortality (ϕ_2). The number of caterpillars M_t surviving on the plants is defined by the survival function g_1, where:

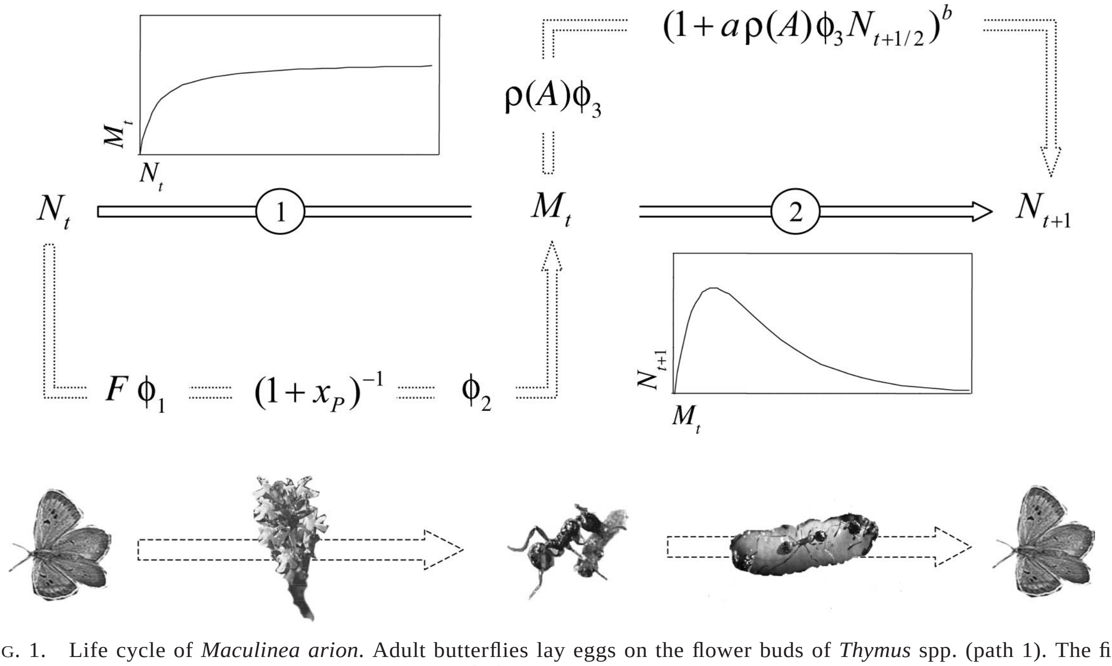

FIG. 1. Life cycle of *Maculinea arion*. Adult butterflies lay eggs on the flower buds of *Thymus* spp. (path 1). The first-instar larvae are then adopted by the ant *Myrmica sabuleti* and parasitize the ant nest (path 2). The two curves correspond to the density-dependence functions (M_t vs. N_t and N_{t+1} vs. M_t) representing contest competition on the plant (left) and scramble competition within ant nests (right). Symbols are defined in Table 1.

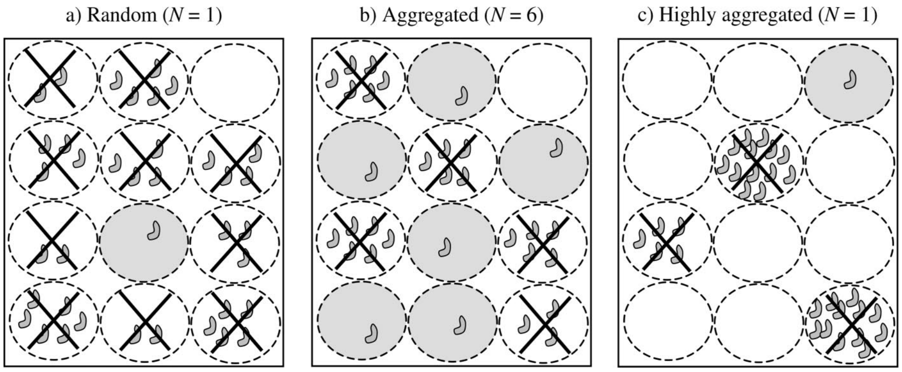

FIG. 2. Consequences of varying the spatial distribution of larvae (caterpillars) among patches (ant nests) on survival of larvae to the episode of scramble competition within patches. In this simple example, the maximal larval density that a patch can hold is 1; if >1 larva competes in a patch, then they all die (i.e., the nest disbands).

$$M_t = g_1(N,P) = N_t F \phi_1 (1 + x_P)^{-1} \phi_2 \qquad (2)$$

with x_P being the mean number of competing caterpillars per flowering bud, whence

$$x_P = N_t F \phi_1 / \varepsilon_P P \qquad (3)$$

with P being the number of plants and ε_P the number of flower buds per plant. The density-dependent mortality function $(1 + x_P)^{-1}$ is characteristic of contest competition models (e.g., Bellows 1981), such that M_t approaches the total number of buds when there are many times more caterpillars than buds.

Recruitment and competition within the ant nest

Our model of density dependence within ant nests was developed from Hassell (1975). It has the interesting property of differentiating microscopic and macroscopic parameters and taking into consideration the spatial nature of density dependence (De Jong 1979, Hassell and May 1985). Hassell's model assumes that the environment contains patches where adults lay eggs. The young larvae then suffer density-dependent mortality within patches. Population change from generation t to $t + 1$ is given by

$$N_{t+1} = \lambda\, N_t (1 + aN_t)^{-b}. \qquad (4)$$

The parameter λ is the finite net rate of increase per adult. The scaling parameter a determines the amplitude of the equilibrium and b measures the severity of density dependence. De Jong (1979) and Hassell and May (1985) showed that the density-dependence parameter b of Eq. (4) could sometimes be interpreted as a spatial form of density dependence. Here the spatial distribution of larvae among patches follows a negative binomial distribution (unevenness in the distribution of eggs among patches) with clumping index k (see Appendix A). An important assumption permitting the spatial interpretation in our system is that larvae suffer scramble competition within patches (i.e., ant nests). Under these conditions, the above studies show that $b = k + 1$.

This transformation enables one to infer, using macroscopic parameters (the total number and distribution of larvae), the consequences of microscopic process (the competition between the larvae within a patch). Fig. 2 illustrates how the spatial distribution and intensity of density dependence can be related in such a context. When larval distribution among patches is random (Fig. 2a), most individuals suffer scramble competition at the microscale (within a patch). The consequence at the macroscale (from patch to patch) is the same as if there were scramble competition between all larvae: mortality increases suddenly and exponentially at the higher densities. When the distribution is aggregated (Fig. 2b), even if there is scramble competition at the microscale, it is effectively equivalent to contest competition at the macroscale because some patches have low larval densities. Competition is fierce in a few high-density patches, and this translates into reduced overall mortality compared to cases where larvae are randomly distributed. Interestingly, when the larvae are extremely aggregated, they effectively experience pronounced competition in a very small number of patches and go extinct (Fig. 2c). Thus larval survival is potentially highest at intermediate levels of aggregation.

These considerations are useful since spatial distributions can be readily estimated in the field, whereas the severity of density dependence is more difficult to measure. We adapted Hassell's (1975) approach to *Maculinea arion* by taking λ (of Eq. 4) to be a function of M_t and of the probability that a caterpillar enters a *Myrmica sabuleti* nest and survives to adulthood. The events are (1) caterpillars are adopted into *M. sabuleti* colonies with probability $\rho(A)$; and (2) a proportion ϕ_3 survive density-independent mortalities within the first weeks of adoption, followed by density-dependent scramble mortality during the next eight months prior to pupation. The model is

$$g_2(M_t, A) = \rho(A) \phi_3 (1 + ax_A)^{-b} \qquad (5)$$

TABLE 2. Parameters observed in the field for *Maculinea arion*.

Parameter	Site	*M. arion* field values†	Scenario 1	Scenario 2
F	X	25.5 ± 7.7 eggs/adult	25.5	**75**
A	X	6800 ant nests/ha	10 000	10 000
	Green Down	30 100 ± 981 ant nests/ha	⋯	⋯
ϕ_1	X	0.911 ± 0.048 eggs surviving	0.91	0.91
ϕ_2	X	0.638 ± 0.109 caterpillars surviving (post–first instar)	0.638	**1**
ϕ_3	X	0.65 caterpillars surviving post-recruitment	0.8	0.8
	Green Down	0.86 caterpillars surviving post-recruitment	⋯	⋯
η	X	0.00041 ha	0.00041	0.00041
P	X	482 ± 79.8/ha	3500	3500
	Green Down	7500/ha	⋯	⋯
ε_P	X	30.9 ± 57.5 flower buds/plant	30.9	30.9
ε_A	X	0.428	0.428	0.428
b	X		2	**6**

Notes: Some parameters are derived from a site (called ''X'') with rather poor but suitable source habitat, and from another site (Green Down) where the habitat is optimum. We considered two scenarios. Scenario 1 is close to the mean values measured in the field. Scenario 2 approximates to the highest recorded values of annual fecundity, density-independent survival on the plant, and a more random distribution of caterpillars among ant nests. The parameters that change from one scenario to the other are in boldface type in the column for Scenario 2.

† Variation around the mean is ±SE.

with x_A being the total number of competing caterpillars among ant nests:

$$x_A = M_t\rho(A)\phi_3. \quad (6)$$

The parameter a is modified from Hassell and May (1985),

$$a = \frac{1 - \exp(-x_A)}{A\varepsilon_a(b - 1)} \quad (7)$$

and $\rho(A)$ is the probability for a caterpillar to be found by an ant; $\rho(A)$ is assumed to obey a Poisson distribution of ant searching area η and ant nest numbers A, such that

$$\rho(A) = 1 - \exp(-\eta A). \quad (8)$$

The general model (Eq. 1) now reads

$$N_{t+1} = N_tF\phi_1(1 + x_P)^{-1}\phi_2\rho(A)\phi_3(1 + ax_A)^{-b}. \quad (9)$$

Unlike previous models of *Maculinea* (Hochberg et al. 1992, Griebeler and Seitz 2002) we omit caterpillar mortality by *Ichneumon* or *Neotypus* parasitoids due to their very low incidence in *M. arion* populations (J. Thomas, *unpublished data*).

PARAMETER ESTIMATION

Details of parameter estimation are given in Appendix A, with values given in Table 2. Model parameters were estimated in the field, supplemented by laboratory experiments. Field sites were located in the United Kingdom (four populations), France (three populations), and Sweden (four populations), but most values were derived from one location in Devon, United Kingdom. Based on these field measures we considered two scenarios to explore the model properties. Scenario 1 represents the mean values measured in the field (Table 2); Scenario 2 corresponds to maximum values recorded in 1972–2002 and has higher butterfly finite rates of increase (high realized fecundity, $F = 75$; high density-independent survival on the plant, $\phi_2 = 1$) and more random distributions of caterpillars among ant nests, which is probably the case when the number of eggs is important (see *Discussion* for more details).

GENERAL MODEL PROPERTIES

Although the mathematical model is conceptually simple, the nested density-dependence functions obviate transparent analytical solutions. We show the results of mathematical analysis and numerical simulations to illustrate the population dynamic and equilibrium properties of the *Maculinea arion* model.

Persistence at low density

The propensity for the population to persist can be obtained by evaluating the maximum population growth rate, or N_{t+1}/N_t at the limit $N_t \to 0$. The main parameter reflecting persistence is the basic reproductive rate R_0, which must be greater than one if the population is to deterministically grow when rare (e.g., at the bottom of an intrinsic population cycle, or after a colonization event or a catastrophic environmental perturbation):

$$R_0 = F\phi_1\phi_2\rho(A)\phi_3. \quad (10)$$

The product $\phi_1\phi_2\rho(A)\phi_3$ encapsulates all forms of density independence: on the plant ($\phi_1\phi_2$), between the plant and the ant nest ($\rho(A)$), and in ant nests (ϕ_3). For the equilibrium to be feasible, the number of caterpillars surviving density-independent mortality must obviously exceed one. $R_0 > 1$ implies a minimum adult fecundity and a minimum number of ant nests, as well as sufficiently low mortalities, such that

$$F > F_{\mathrm{Min}} = \frac{1}{\phi_1\phi_2\phi_3[1 - \exp(-\eta A)]}. \quad (11)$$

Intuitively, if survival is near 100% and ant nests are abundant, then $F_{\mathrm{Min}} \to 1$. Otherwise expressed, for per-

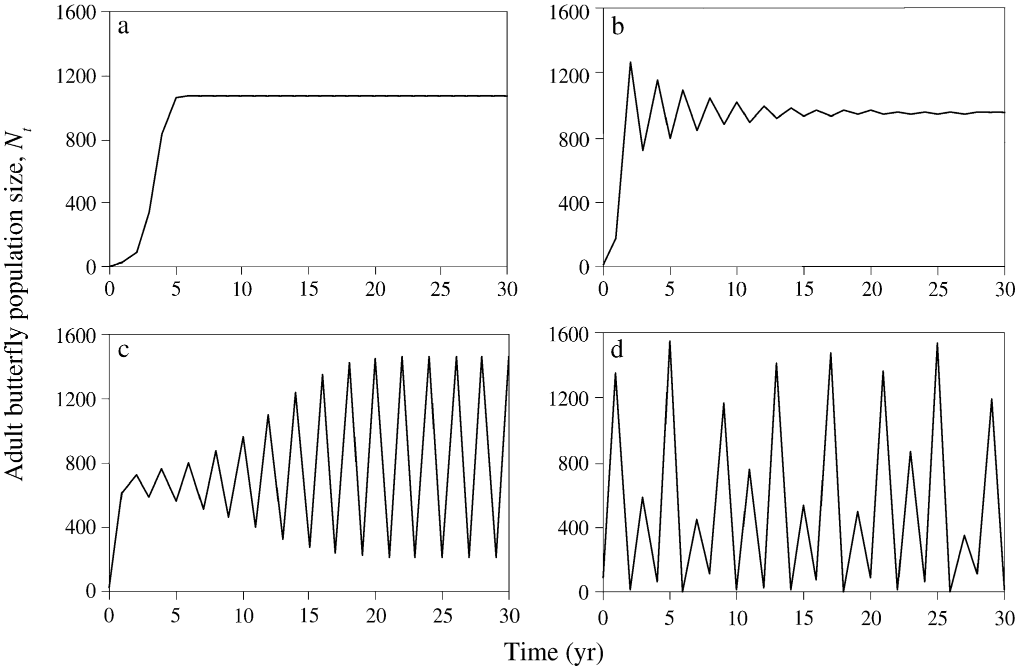

FIG. 3. Example of time series obtained for *M. arion*. We varied species fecundity F and the density-dependence parameter b to generate four different dynamics: (a) monotonic approach ($F = 10$, $b = 2$), (b) oscillatory damping ($F = 28$, $b = 10$), (c) cycles ($F = 40$, $b = 15$), and (d) chaos ($F = 500$, $b = 150$). Other parameters are as for Scenario 1 (Table 2).

sistence, the number of ant nests must be greater than a threshold given by

$$A > A_{\mathrm{Min}} = \frac{-\ln\left(1 - \dfrac{1}{F\phi_1\phi_2\phi_3}\right)}{\eta}. \qquad (12)$$

This is a decreasing function of fecundity, the different density-independent survivals ϕ, as well as the mean potential search of *Myrmica sabuleti* workers η.

Note that R_0 is independent of the number of host plants P on the assumption that, at very small butterfly population sizes, the number of competing caterpillars per plant bud is small ($x_P \ll 1$ in Eqs. 3 and 9). Obviously *Maculinea arion* needs plants to persist, but in this simplistic model, one plant is sufficient.

Basic model properties

We investigate both a limiting case and a more general situation of how density dependence impinges on basic population parameters.

A simple case.—The case $b \to 1$ arises in our model if spatial heterogeneity in the intensity of competition across the population of ant nests is effectively infinite (complete aggregation, i.e., $k \to 0$). In this case the equilibrium is given by

$$N^*_{b\to 1} = \frac{P\varepsilon_P(R_0 - 1)}{aP\varepsilon_P R_0 + F\phi_1}. \qquad (13)$$

However, because $b \to 1$ implies $a \to \infty$ (Eq. 7), we find $N^*_{b\to 1} \to 0$. Infinite aggregation leads to the unrealistic scenario where the whole caterpillar population is in the same nest, resulting in the annihilation of the population through scramble competition. In the case where $b \approx 1$, Eq. (13) becomes

$$N^*_{b\approx 1} = a^{-1}\frac{(R_0 - 1)}{R_0}. \qquad (14)$$

As expected, increasing the intensity of density dependence a reduces population size at equilibrium, while increasing the finite rate of increase, R_0, has a positive effect.

General case.—When $b > 1$, analytical results are not obtainable because of the nested nature of density dependence, which introduces delays in the effects of each regulatory loop. The first episode of (contest) competition between larvae of *Maculinea arion* on the food plant should, if acting alone, produce a monotonic increase in population density from low levels toward a locally stable equilibrium point. Some survivors of this episode then compete via scramble competition within ant colonies, which could lead to complex dynamics, such as limit cycles or chaos, depending on the finite rate of increase and the level of density-dependent compensation, b (Hassell 1975). In our case, the finite rate of increase of caterpillars among ant nests (λ in Eq. 4) is obtained from Eqs. 9 and 10:

$$\lambda = N_t R_0(1 + x_P)^{-1}. \qquad (15)$$

In Fig. 3 we illustrate four kinds of dynamics obtained for *M. arion* adult population size (Eq. 9) by varying adult fecundity (an important component of the basic growth rate R_0) and the density-dependence parameter b. Dynamical outcomes range from monotonic damping to oscillatory damping to cycles, and finally chaos (Fig. 3a–d, respectively). From Eq. 15 we see that the finite rate of increase of caterpillars among ant nests varies with adult butterfly population size. This introduces another level of complexity into the model, resulting in all parameters potentially influencing the dynamical properties. In Figs. 4–6 we show bifurcation diagrams obtained for different model parameters. These graphs are fully described later in the study.

Conditions for simple dynamics

The stability of the equilibrium depends on the slope of the relationship between N_{t+1} and N_t at the intersection $N_t = N_{t+1}$ (May and Oster 1976). Rodriguez (1988) has shown that in models with nested density dependence, the shape of the N_{t+1} vs. N_t curve depends on key parameters derived from the equations describing each episode of density dependence independently (Appendix B). When, as for *Maculinea arion*, the first episode is contest competition (N_{t+1} vs. N_t approaches an asymptote; Fig. 1, left) and the second is scramble competition (N_{t+1} vs. N_t is unimodal; Fig. 1, right), an equilibrium can be reached monotonically if the former is strong enough to keep the species at such low densities so as not to be affected by the second episode of density dependence (that can be destabilizing). In our model, this condition is given by

$$\varepsilon_P P \phi_2 - A\varepsilon_A[b/(b-1)]^{-b} < 0 \tag{16}$$

(see Appendix B for details). Inequality 16, combined with $R_0 > 1$, guarantees population persistence and a locally stable equilibrium point reached monotonically. From Inequality 16 we see that $A\varepsilon_A[b/(b-1)]^{-b}$ is an increasing function of b, and asymptotes at $A\varepsilon_A/e^1$ for high values of b. This may seem surprising, because high values of the strength of density dependence (b) are known to destabilize equilibria in the case of scramble competition acting alone (Hassell 1975, Hassell and May 1985; Fig. 3c,d). However, the parameter b also increases the maximal density beyond which the density effect becomes negative for caterpillars within ant nests. Similar counterintuitive effects were identified by Hochberg and Lawton (1990).

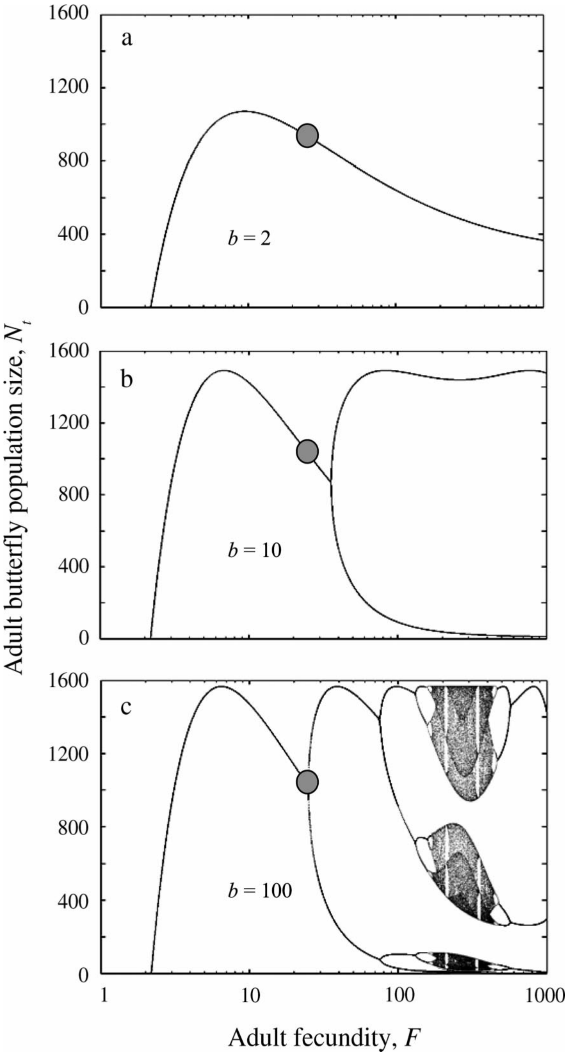

FIG. 4. Bifurcation diagrams of the adult butterfly population size with varying species adult fecundity F for three values of the density-dependence parameter: (a) $b = 2$, (b) $b = 10$, and (c) $b = 100$. Other parameters are as for Scenario 1 (Table 2). The gray circle represents the values of species fecundity measured in the field (Table 2, Scenario 1).

Stable monotonic dynamics are also favored by low plant resources (P and ε_P) and density-independent larval survival on the plant (ϕ_2), because fewer caterpillars enter the second phase of the life cycle. Moreover, high ant resources (A and ε_A) reduce the importance of the second episode of density dependence and make it more likely for the equilibrium to be monotonic. Interestingly, fecundity F which we have shown to destabilize the equilibrium at high values (Fig. 3c,d), does not affect the threshold defined in Inequality 16. This is because it comes into play both positively in the basic growth rate and negatively in the first episode of density dependence (see Eqs. 2 and 3). We cannot solve Inequality 16 for b. Rather, letting A/P be represented by μ, we find that the equilibrium point is locally stable and reached monotonically if $\mu \geq \mu_{\text{Max}}$ with

$$\mu_{\text{Max}} = \frac{\varepsilon_P \phi_2 [b/(b-1)]^b}{\varepsilon_a} \tag{17}$$

where μ_{Max} is bounded by

$$\lim_{b\to1}(\mu) = +\infty \qquad \lim_{b\to+\infty}(\mu) = \frac{e^1 \varepsilon_P \phi_2}{\varepsilon_a} \tag{18}$$

meaning that at low values of b, the number of plants

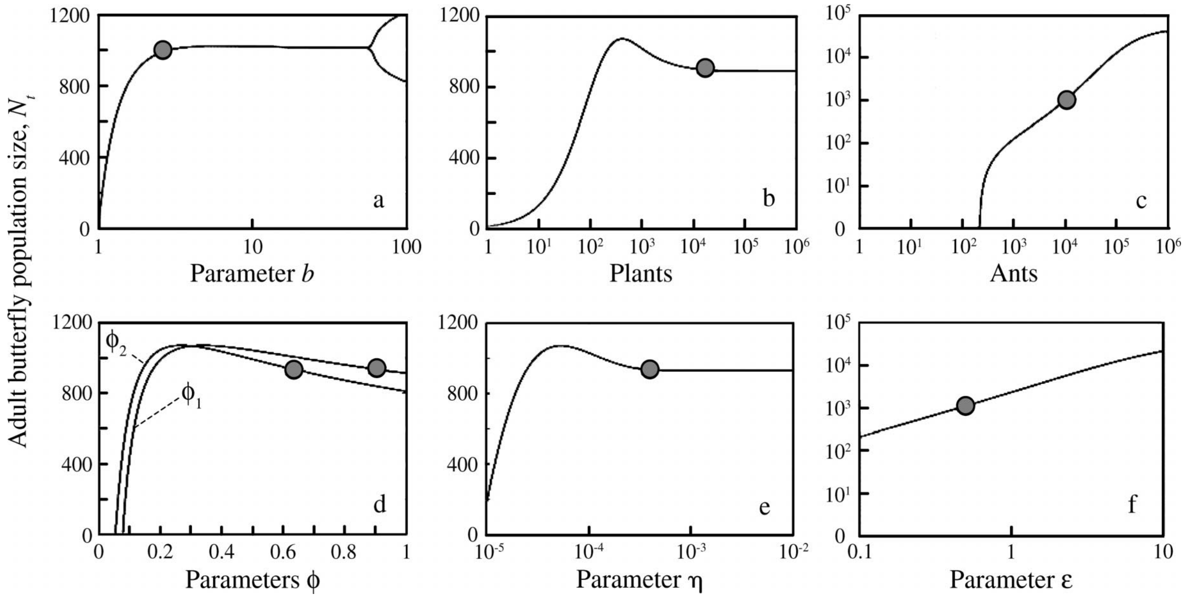

FIG. 5. Effect of the principal parameters of the model on adult butterfly equilibrium values with fixed adult fecundity, $F = 25.5$. We varied (a) the density-dependence parameter b, (b) the number of plants P, (c) the number ant nests A, (d) the density-independent survival parameters ϕ_1 and ϕ_2, (e) the ant search area η, and (f) the carrying capacity of the average nest ε_A. When they do not vary, the parameters are as for Scenario 1 (Table 2). In (d) the curve for ϕ_3 is not shown because it is very similar to the curve obtained for ϕ_1. We do not show variation in the number of flower heads per plant ε_P because it has qualitatively the same effect on the equilibrium values as the number of plants. A gray circle indicates the value of each parameter observed in the field (Table 2, Scenario 1).

must be very small relative to the number of ant nests for the dynamics to be locally stable and monotonic. As b increases, stable butterfly populations can occur for increased plant resources, because higher caterpillar densities are tolerated before the negative density-dependence effect begins within ant nests. Given the parameter estimates in Table 2, we find $\mu_{\mathrm{Max}} = 184.2$ (Scenario 1) or $\mu_{\mathrm{Max}} = 215.2$ (Scenario 2), meaning that in the field, population stability and monotony are ensured if the number of ant nests is ~200 times greater than the number of plants. However, additional field observations where both plant and ant nest densities were estimated indicate lower figures for μ in the range of 0.1–5 (N. Mouquet, *unpublished data*), meaning that natural butterfly populations might exhibit the complex dynamics illustrated in Fig. 3b–d.

More complex dynamics and equilibrium properties

As described, the equilibrium and dynamic properties of the model are difficult to resolve analytically. Here we present the results of numerical studies to help understand the effects of several key parameters on *Maculinea arion* dynamics. We first focus on two quantities known to influence dynamics: adult fecundity F and density dependence within ant nests b. We then present the effects of other parameters for the two ecological scenarios we have chosen. For each scenario we explore the equilibrium values and sensitivities to parameter values.

Adult fecundity F.—Fig. 4 shows the bifurcation diagrams obtained with varying adult fecundity for three values of b ($b = 2$, $b = 10$, and $b = 100$). This suggests that intermediate fecundity leads to locally stable dynamics and maximizes the butterfly population density. There is a threshold minimal fecundity, below which the butterfly cannot persist as defined by Eq. 11. When fecundity is high, the negative density dependence within ant nests due to caterpillar competition reduces adult population size. At even higher fecundities, the equilibrium is destabilized, with cycles and even chaotic behavior emerging as within-nest competition becomes increasingly overcompensatory (i.e., high b).

Density dependence within ant nests b.—This variable can also have complex effects. When the number of caterpillars entering nests is low, b has a positive effect on adult population size due to an interaction with parameter a (Eq. 7). Larger values of b generate more random caterpillar distributions among ant nests, and less nest destruction than if the caterpillars were aggregated. This, in turn, maintains high adult butterfly densities (Fig. 5a), and cycling only at very high b when population level density dependence is highly overcompensating. As the butterfly's finite rate of increase takes on higher values (i.e., higher F and ϕ_2 as in Scenario 2), the number of caterpillars that enter ant nests increases, and there is more latitude for complex dynamics through increases in overcompensation (Fig. 6a). In the example in Fig. 6a, values of b increasing

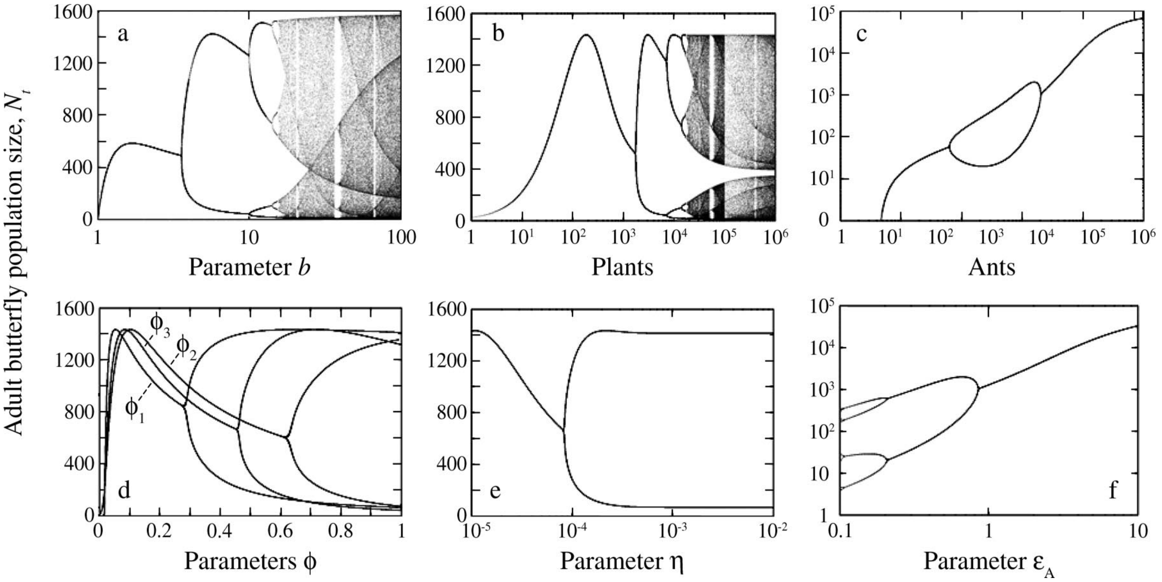

FIG. 6. The effect of the principal parameters (as in Fig. 5) on adult butterfly equilibrium values for Scenario 2. When they do not vary, parameters are as for Scenario 2 (Table 2).

from 1 to roughly 2.5 first result in an equilibrium increase and then a slight equilibrium decrease. Higher values of *b* lead to more complex population behavior.

Number of plants P.—The number of host plants has an interesting impact on butterfly levels (Figs. 5b and 6b). As *P* increases from low levels, the butterfly population increases, but beyond an intermediate value, it decreases. As for high values of fecundity, too many plants mean more caterpillars within ant nests and thus a potential for overcrowding and complex dynamics (Fig. 6b).

Number of ant nests A.—In contrast to plants, increasing the number of ants always increases adult population size (Figs. 5c and 6c). A minimum density of host ant nests (defined in Eq. 12) is required for the butterfly population to persist (Figs. 5c and 6c). Given sufficiently strong density regulation on plants and low adult fecundity, increasing the number of ant nests has no effect on stability (Fig. 5c), whereas if the finite growth rate is high and caterpillars are more randomly distributed, then high nest numbers can destabilize the system (Fig. 6c). Interestingly, in this case, further increases in nest number can result in the reestablishment of a stable equilibrium point (Fig. 6c). This is due to a dilution effect, where increasing *A* results in the decline of the mean number of caterpillars per nest, and hence competition. The number of adult butterflies then approaches the asymptote for very high numbers of ant nests (Figs. 5c and 6c).

Density-independent survival parameters ϕ.—The survival parameters have qualitatively similar effects on adult butterfly population size (Figs. 5d and 6d). According to Eq. 10, minimal values exist for each ϕ, below which $R_0 < 1$ and the butterfly population goes extinct. Similar to the effect of fecundity and the number of plants, intermediate values exist that maximize adult population size. And as follows from our main results, high overall density-independent survival can destabilize the equilibrium and lead to limit cycles (Fig. 6d).

Ant mean potential search area η.—Like the other parameters that cause increased caterpillar densities within ant nests, increasing the ant search area η first has a positive effect on adult population size, then beyond a threshold, a negative one (Fig. 5e). In particular, in Scenario 2 the positive effect is not observed over the range of variation we have chosen (but is found for very low values of η), and complex dynamics are readily obtained for η in the region of our best estimate (Fig. 6e).

Ant nest carrying capacity $\varepsilon_{\mathbf{A}}$.—Increasing ε_A tends to increase adult population size (Fig. 5f) because it shifts the density at which negative density dependence acts within ant nests to higher values. At high fecundity, low values of ε_A lead to instability (Fig. 6f) because the number of caterpillars that enter each ant nest is high compared to the host's carrying capacity. Increasing ε_A stabilizes the dynamics and leads to higher population sizes.

Composite λ *and density-dependence parameter b*.—Following Hassell (1975), we provide a general graph that summaries the properties of our model along two major axes: variation in the density-dependence parameter *b* (that is inversely correlated to the degree of spatial heterogeneity in the distribution of individuals) and variation in the caterpillar population growth rate among nests (composite λ in Eq. 15). In our model, λ

is an increasing function of R_0 (Eq. 10), the number of plants P, and buds ε_P. For $N_t = 1$ we have

$$\lambda = \frac{\varepsilon_P PF\phi_1\phi_2\phi_3\rho(A)}{\varepsilon_P P + F\phi_1} \tag{19}$$

which is the maximum growth rate of caterpillars among ant nests (the number of caterpillars produced by one butterfly adult, that will enter into competition among ant nests). Fig. 7a presents how this composite λ and the density-dependence parameter b affect dynamics. The greater the number of competing caterpillars produced per adult and the less caterpillars are spatially aggregated, the less likely the equilibrium point will be locally stable. Fig. 7b shows the population size obtained for each combination of λ and b. As an indication of potential local extinction, we present only the minimal value of population density obtained in cases where dynamics were cyclic or chaotic. This figure shows that populations are most viable for intermediate values of both λ and b.

Our results also illustrate that the sensitivity of the model to any given parameter will be dependent on the values of other parameters. For example, reducing the plant population from 3000 to 1000 plants has almost no effect on the butterfly population in Scenario 1 ($N_{P=3000} = 939$ while $N_{P=1000} = 1017$; Fig. 5b), whereas the effect is dramatic in Scenario 2; when $P = 3000$ the butterfly population size oscillates between 1433 and 86 individuals, whereas it is constant and equals 657 adults when $P = 1000$ (Fig. 6b).

ENVIRONMENTAL VARIATION

Environmental variation can be frequent and dramatic, resulting from natural or anthropogenic perturbations, or it can show slower, more regular changes resulting from deterministic ecological succession or meteorological cycles. We explore only a few of the wide range of scenarios that can be envisaged, focusing first on the combined effect of varying the number of plants and ant nests before considering the consequences of climatic variation on the dynamics of *Maculinea arion*.

Variation in the number of plants vs. ant nests

The number of plants P and host ant nests A can vary between or within different sites during ecological succession or after perturbations. For instance, *Myrmica sabuleti* can be largely replaced by its competitor *M. scabrinodis* in just one season after grazing has ceased (Thomas 1984). To illustrate the consequences of varying P and A (see also Figs. 5 and 6), we present in Fig. 8 the dynamical equilibrium properties as a function of the number of plants and ant nests. We reconsider the two scenarios presented previously (Fig. 8a, c) and an intermediate situation (Fig. 8b). As already shown, simple dynamics are more likely when $A > P$ (Inequality 16 and Eq. 17), but intermediate values of A can lead to cycles or chaos. Echoing this

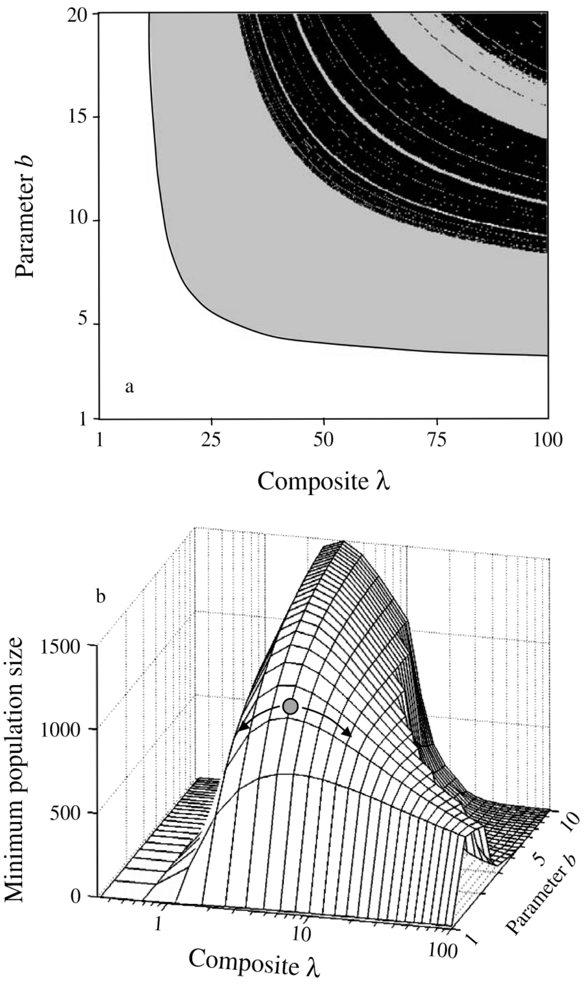

FIG. 7. (a) The stability boundaries between the density-dependence parameter b and the potential basic growth rate of the caterpillar population among ant nests λ (Eq. 19). The parameter λ is composed of ε_P, ϕ_1, ϕ_2, ϕ_3, η, ε_A, P, F, and A. To vary this parameter, we fixed low values ($\phi_1 = 0.5$, $\phi_2 = 0.2$, $\phi_3 = 0.4$, $\eta = 0.0001$, $P = 25$, $F = 5 \rightarrow \lambda = 0.126$) and high values ($\phi_1 = 1$, $\phi_2 = 1$, $\phi_3 = 1$, $\eta = 0.001$, $P = 25\,000$, $F = 100 \rightarrow \lambda = 99.98$) and progressively increased all the parameters together from their low to their high values. We did not change ε_P because it has the same effect as P; nor did we change A because it contributes more to the magnitude of the equilibrium through the parameter a (Eq. 7) than via $\rho(A)$ (we obtained qualitatively the same result when we added variation in A). Other parameters are as for Scenario 1 (Table 2). In the white region, the equilibrium is reached monotonically or with damped oscillations, the gray region corresponds to cycles, and the black regions correspond to chaotic behavior. The limits to chaotic dynamics were obtained by computing the Lyapunov exponent as explained in Appendix C. (b) The adult butterfly population size obtained at equilibrium. When the population dynamics were oscillatory, we used the smallest population size observed over one period of the cycle. When the population dynamics were chaotic, we employed the smallest population size obtained over 2000 iterations after having let the simulation run for 50 time steps. The gray circle and the two arrows illustrate a case where the cause of butterfly decline can be either a decrease or an increase in the composite λ.

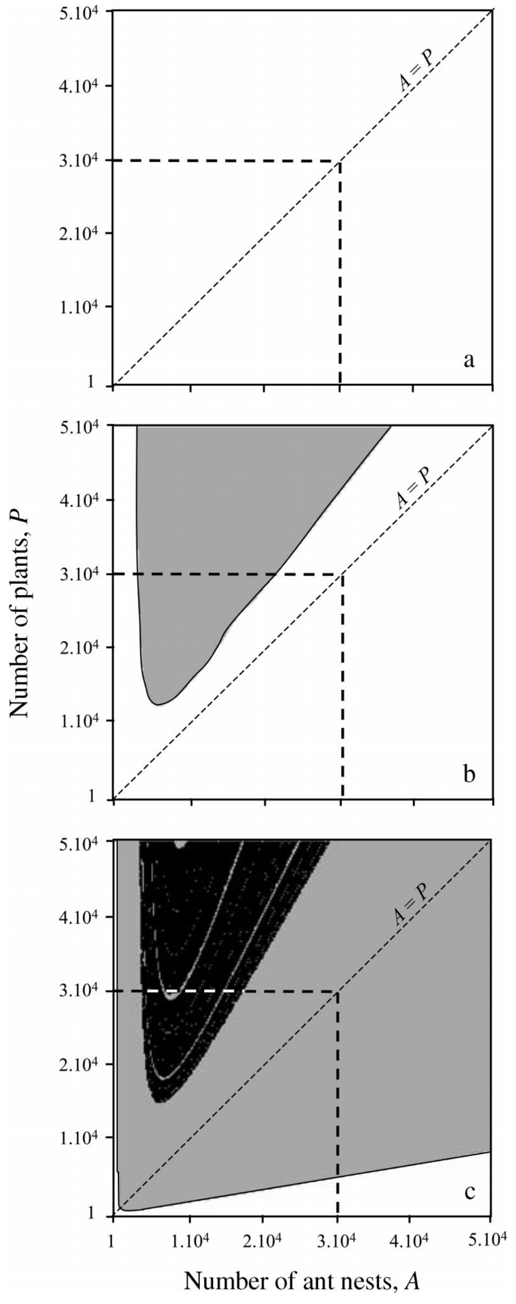

FIG. 8. Stability boundaries obtained with varying the number of plants and the number of ant nests. In the white region, the equilibrium is reached monotonically or with damped oscillations, the gray region corresponds to cycles, and the black regions correspond to chaotic behavior. The limits to the chaotic dynamics were obtained by computing the Lyapunov exponent (Appendix C). We represented the line $A = P$ for reference. In (a) the parameters are as for Scenario 1 (Table 2). In (b), $F = 60$, $b = 3$, and $\phi_2 = 0.8$. In (c), parameters are as for Scenario 2 (Table 2).

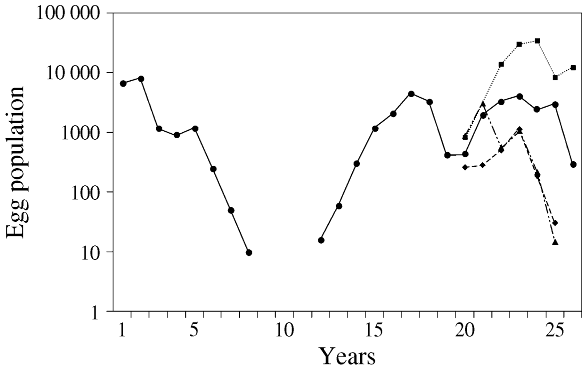

FIG. 9. Fluctuation of *Maculinea arion* egg populations among four different U.K. sites recorded by J. A. Thomas between 1970 and 1996. More details are given in Thomas et al. (1998).

theme, the size of the zone yielding unstable dynamics is a function of the density-dependence parameter b, adult fecundity, and density-independent parameters. Variation in the number of ant nests in either direction can shift the dynamics into unstable regions (Fig. 8b, c), whereas only an increase in the number of plants can lead to instabilities. Even if the population of adult butterflies declines with the number of plants (Figs. 5b and 6b), having fewer plants is less important to the persistence of the butterfly than decreasing the number of ant nests. Note that Scenario 1, which corresponds to field estimates, does not lead to instabilities (Fig. 8a). When parameters approach Scenario 2 (Figs. 6 and 8c), stable dynamics can only be obtained with low plant numbers and high ant numbers. Any perturbation that increases the number of plants or decreases the number of ant nests leads to instabilities and high probabilities of local butterfly extinction, given the low minimal densities generated when the system oscillates (Fig. 6).

Climatic variation

Thomas et al. (1998) have shown that some populations of *Maculinea arion* oscillate in time by two orders of magnitude over a period of 20 years (Fig. 9). In our model, oscillations can exhibit similar amplitudes (see Figs. 3 and 5), but act over shorter periods. The pattern observed by Thomas et al. (1998) might thus also be driven by exogenous causes, such as climatic variation (Roy et al. 2001), especially extreme drought, which can catastrophically reduce the capacity of ant nests to support *M. arion* (Thomas 1980). Here we use our model to predict which environmental scenario is most likely to generate the field-observed patterns, as well as how much variation is required. We focused on four parameters that are the most likely to vary from year to year in the field: the number of ant nests and plants, adult fecundity, and density-independent survival on the plant ϕ_2 (we have not varied ϕ_1 because it has roughly the same effect as ϕ_2). We as-

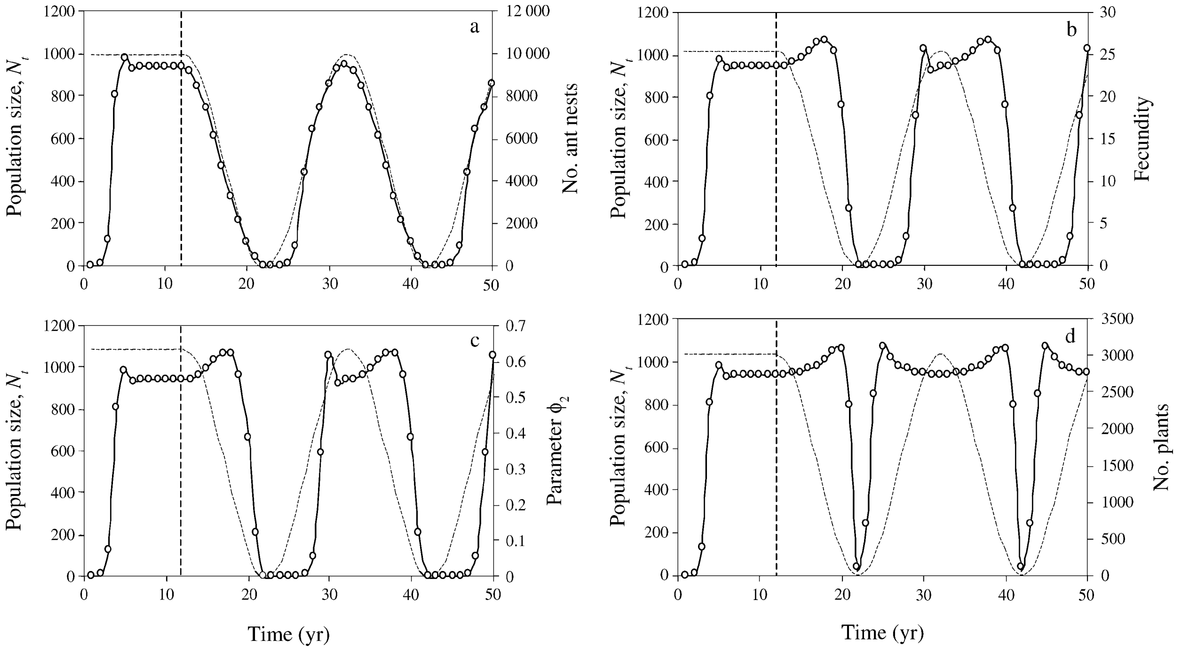

FIG. 10. Examples of time series obtained for *Maculinea arion* for Scenario 1 (Table 2) with temporal variation in (a) the number of ant nests *A*, (b) the adult fecundity *F*, (c) the survival parameter ϕ_2, and (d) the number of plants *P*. The dashed curve describes the variation of model parameters in time (right axis), and the plain curve (with circles) indicates the adult population size (left axis). In each example, the simulation was run with constant environmental conditions until an equilibrium was reached, after which the parameters varied. The dashed vertical line separates these two different environmental regimes.

sume that each parameter varies between an initial value (corresponding to that measured in the field) and very low levels. (Other parameters are as for Scenario 1). Environmental variation is described by a simple cosine function (between 1 and 0):

$$X(t) = X_{\text{basic}}\left[\cos\left(\frac{2\pi t}{P}\right) + 1\right]\Big/ 2 \qquad (20)$$

with X the response parameter and X_{basic} its initial (and maximal) value. P is the period of the oscillation ($P = 20$ years in our simulation). Encouragingly, variation in each of the four parameters generates patterns similar to those observed in the field (Figs. 9 and 10). Variation in the number of ant nests shows a regular pattern that closely tracks the environmental fluctuation (Fig. 10a). Variations in adult fecundity, the survival on the plant, and the number of plants show less simple patterns: as they decline, the number of adult butterflies first increases and then decreases (Fig. 10a, b, and c, respectively). This latter result is due to the hump-shaped relationship between these parameters and adult butterfly population size (Fig. 4a and Fig. 5b,d). Note that in Fig. 10b and 10c, the adult butterfly takes 4–5 years to begin recovering from very low (near zero) numbers, despite adult fecundity and survival parameters rapidly attaining higher values. This suggests that *M. arion* is more likely to recover from a given amount of variation in the number of plants than is the case with realized adult fecundity (including adult survival) and larval survival on the plant.

In Fig. 11 we present the equivalent simulation with parameters from Scenario 2 (which generates instabilities when the parameters are constant over time). This figure illustrates how endogenous (high growth rate) and exogenous (environmental forcing on ϕ_2) factors can both contribute to population fluctuations (Murdoch 1994, Den Boer and Reddingius 1996). Interestingly, as the parameter ϕ_2 decreases, the dynamics stabilize but the population declines. We suggest that this mixed pattern corresponds to the population dynamics observed in the field.

CONSERVATION BIOLOGY IN THE FIELD

How to manage a stable population

Given the dynamics attributable to nested density dependence, conservation ecologists need to maximize some combination of both the size of the *Maculinea arion* population and its long-term stability. As illustrated in Fig. 7, maximum population size is obtained at intermediate values of caterpillar population growth rates (composite parameter λ). Large populations are also obtained for high values of the density-dependence parameter b, but only when λ is intermediate; at high λ, increasing b generates more variable trajectories. Thus if the objective is to maximize population size *and* stability, a sensible strategy is to have a population

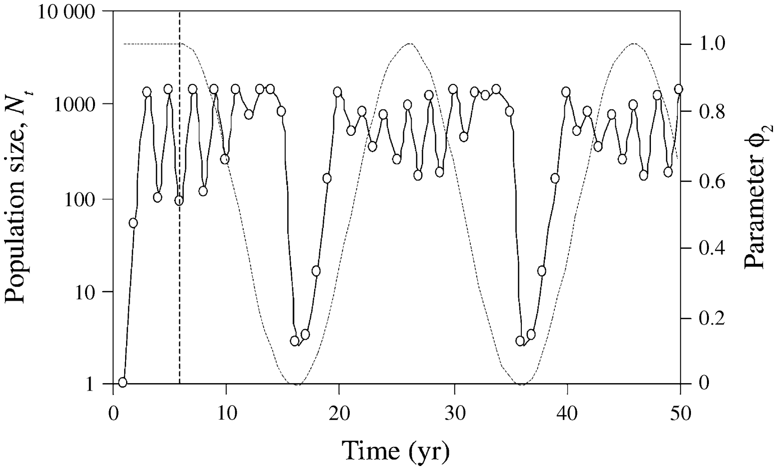

FIG. 11. Examples of time series obtained for *Maculinea arion* for Scenario 2 (Table 2) with variation in time of the survival parameter ϕ_2. Line descriptions are as in Fig. 10.

with intermediate values of λ and a random distribution of caterpillars among ant nests (high *b*). In contrast, if the population has a high λ, then the caterpillar distribution should be aggregated (low *b*). Managing the distribution of caterpillars among ant nests could be obtained in the field indirectly by manipulating the spatial distribution of plants (e.g., mowing *Origanum*, grazing *Thymus*). Changing caterpillar population growth rate λ is more problematic, particularly because the ability of each parameter to determine the population size depends on the values of other parameters (Figs. 5 and 6). It might be achieved by creating zones with plants, but without *Myrmica sabuleti* (host) ant nests within the butterfly habitat, i.e., absolute or partial sinks. Under this regime the number of caterpillars per ant nest should decrease, and *Maculinea arion* population dynamics would stabilize. It is likely that the spatial distribution of sinks will determine the efficiency of this strategy, but explicit spatial models are needed to verify this prediction (R. Clarke et al., *unpublished manuscript*).

How to manage an unstable population

Chaos or cycles can jeopardize population persistence in the long term. For instance Fig. 6b illustrates that even simple cycles of period two lead to very low population sizes (<50 butterflies per ha when $P > 3500$) and an ostensibly elevated risk of extinction. How can conservation ecologists manage unstable populations? As illustrated by the arrows in Fig. 7b, in certain cases, it is difficult to identify the causes of decline because they can, paradoxically, result from either a decrease or an increase in the growth rate λ. The life cycle of *Maculinea arion* potentially generates complex population dynamics, and this means that nonintuitive management decisions will sometimes alleviate population declines.

We have shown for a model based on field-estimated parameters (Table 2, Scenario 1) that *M. arion* is not likely to experience cycles or chaotic dynamics. However, strong instabilities could be generated if, for example, the number of ant nests is suddenly, drastically reduced, or after a substantial increase in survival parameters. These situations are predicted to lead to oscillations or chaos and even local extinction if population excursions are sufficiently pronounced (Fig. 7b). If confronted with a fluctuating population, could a conservation ecologist modify the environment to stabilize the butterfly population? Our model shows that reducing the finite growth rate of caterpillars among ant nests, as well as maintaining a sufficiently aggregated distribution of caterpillars among ant nests, leads to stability. Again, this can be achieved by reducing the number of plants to make them more aggregated than the ant colonies (e.g., through mowing, grazing) or by reducing the caterpillar population growth rate.

Although counterintuitive, theory suggests that another way to regulate unstable populations might be through immigration (McCallum 1992, Stone 1993). Succinctly, immigration can modify the period-doubling route to chaos and create period-doubling reversals, and it reduces the impact of overcompensation obtained through strong local density dependence. As a consequence, the amplitude and the shape of the N_{t+1} vs. N_t curve is modified, and this leads to simpler dynamics (but see Stone and Hart 1999). To study whether immigration could stabilize the dynamics of *M. arion*, we considered the case where a constant number I of butterflies immigrate (or are released) each generation. Eq. 1 becomes

$$N_{t+1} = g_1(N_t,P)g_2[g_1(N_tP), A] + I. \qquad (21)$$

In Fig. 12 we present the bifurcation diagrams obtained after varying the density-dependent parameter *b*

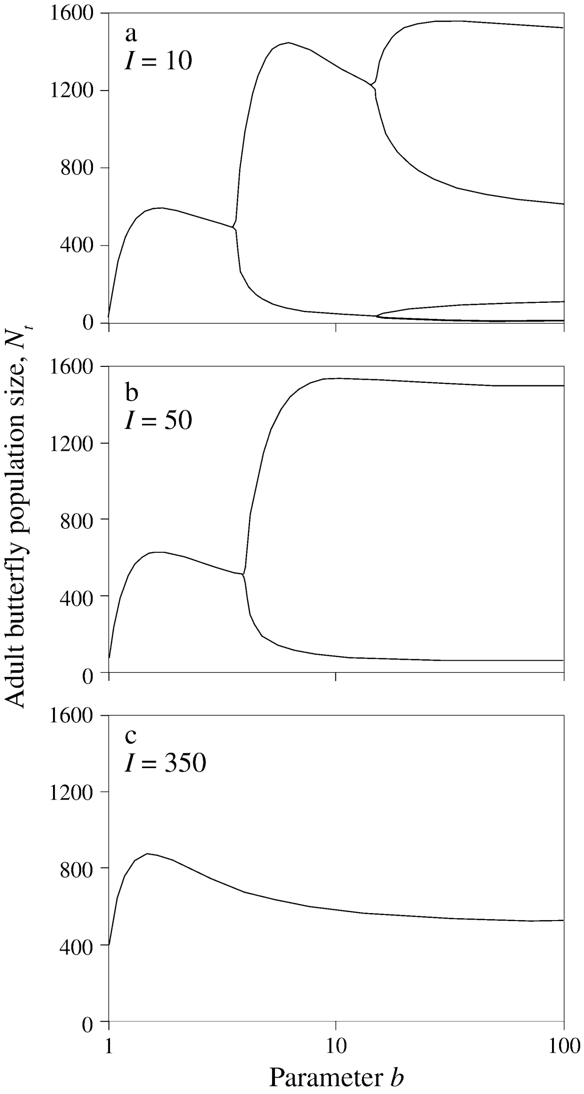

FIG. 12. Bifurcation diagrams obtained for Scenario 2 (Table 2) when b (the density-dependence parameter within ant nests) varies (corresponding to Fig. 6a). We have added different levels of immigration (Eq. 21): (a) $I = 10$, (b) $I = 50$, and (c) $I = 350$.

(under Scenario 2). As in Fig. 6a, in the absence of immigration (not shown in Fig. 12) the equilibrium follows a route to chaos with a cascade of period-doubling bifurcations. As expected, immigration results in a period-doubling reversal with increasingly simpler dynamics as immigration increases (Fig. 12a–c). Note that with low values of immigration, the risk of extinction is *not* reduced since the system still oscillates strongly (Fig. 12a,b), but extinction becomes unlikely when immigration is of the same order as the population size (Fig. 12c). The extent to which such phenomena may actually occur is not clear (Stone and Hart 1999), but our predictions open the way for straightforward conservation strategies, such as increasing connectivity within metapopulations (Hastings 1991) and creating patches of optimum habitat that are close together. In the same vein, it is likely that populations showing simple dynamics when connected might switch to more complex dynamics, and even go extinct, when dispersal fluxes are interrupted due to human perturbations, as can occur in metapopulations.

How to manage a reintroduction

Our model (Eq. 12) supports Thomas's (1995) conclusion that reintroducing *Maculinea arion* requires, above all, sufficient numbers of host ant nests and a sufficient distribution of larval food plants in the habitat. It does not make realistic predictions regarding minimal plant numbers, but it does show that their numbers should not be too high, thus avoiding complex dynamics once the size of the butterfly population is large enough to saturate the rearing capacity of the ant population. A similar result was found by Hochberg et al. (1994) for *M. rebeli* (see also Elmes et al. 1998), but with the important difference that excessive plant numbers did not provoke complex dynamics. Our model suggests that the basic growth rate of caterpillars among ant nests λ (Eq. 19) should be maximized in the first stages of the reintroduction, and thereafter be maintained at intermediate values. Sensitivity analyses of Eq. 19 lead to two different scenarios. First, when the total number of flower heads ($P\varepsilon_P$) greatly exceeds the number of larvae produced per adult butterfly that enter into competition on the plant ($F\phi_1$), then the basic growth rate of the caterpillar equals the basic reproductive rate R_0. This corresponds to a scenario where the number of plants at a site prior to the reintroduction is very high. In this case, maximizing λ will require high values of adult fecundity F and density-independent parameters ϕ (we do not consider $\rho(A)$, which is apt to be very difficult to control in the field). However, if the number of plants at the reintroduction site is low ($P\varepsilon_P \approx F\phi_1$), then only increasing the survival of the larvae on the plant and in the ant nest (ϕ_2 and ϕ_3) are likely to increase λ. In the field only ϕ_2 can be sensibly manipulated through the presence or absence of butterfly larval predators and/or plant herbivores. In general, it is more likely that $P\varepsilon_P \gg F\phi_1$, and thus ecologists should focus on maximizing both F and ϕ_2 in the first stages of any reintroduction.

DISCUSSION

Our study shows that *Maculinea arion* can potentially exhibit complex dynamics due to the nature of its life cycle. In particular, the episode of scramble competition between caterpillars within ant nests can lead to cycles or chaos. Any modification of the parameters that increases the number of caterpillars that enter into competition per ant nest has complex effects on the equilibrium. Each (adult fecundity, total number of flower heads, probability of being adopted by an ant, and survival parameters) maximizes the population size of adult butterflies at intermediate values (see also

Hochberg et al. 1994, Clarke et al. 1998, Griebeler and Seitz 2002), but at very high values can lead to complex dynamics, through cycles to chaos and sometimes extinction.

Field data show that *M. arion* populations usually range from 100 to 1500 individuals per ha, depending on the habitat quality of different sites (J. A. Thomas, *personal observation*). This corresponds to the range of equilibrium values predicted by our independently parameterized model. The two ecological scenarios generate very different dynamics, and only Scenario 2 leads to true instability. Since Scenario 1 is derived from field measures, whereas Scenario 2 corresponds to hypothetical deviation from Scenario 1, it is likely that in most source habitats, *M. arion* will not show highly complex dynamics. However, this result must be interpreted carefully because we have shown that the conditions that guarantee simple dynamics (Inequality 16 and Eq. 17) are probably never found in the field, meaning that even if the equilibrium is stable the transitory dynamics will be complex. For instance, no cycles or chaos are found when varying the number of plants and ant nests in Scenario 1 (Fig. 8a), but rather damped oscillations toward a stable equilibrium (not shown). From a conservation point of view, damped oscillations can jeopardize species persistence as much as cycles, since it is more likely that in the field the population will always converge toward equilibrium between two perturbations, rather than simply being constant at equilibrium values. As discussed by Hastings (2004) transitory dynamics must be taken into account if one wants to fully understand ecological systems, and this seems particularly true in conservation biology, where population excursions can have dramatic effects.

It is interesting to note that *M. arion* is among the most variable in terms of population variance-to-mean ratios of U.K. univoltine phytophagous species (Thomas et al. 1998, Table 11.2). In contrast, its congener *M. rebeli* exhibits exceptionally stable dynamics (Thomas et al. 1998), a property attributed to the contest competition within ant nests of this ‘‘cuckoo-feeding’’ species (Hochberg et al. 1992). Thus although Scenario 1 does not cause instability in our model, the predacious life-style of *M. arion* has the potential of unstable dynamics that can jeopardize its long-term persistence. We expect that the other predacious *Maculinea* species have populations that behave like that of *M. arion*. These species could thus react strongly to habitat or environmental perturbations, which would shift their parameters into zones of potential instability (see Fig. 8 for an example) and thus to site-level extinction.

Our work illustrates how population dynamics can be driven by both endogenous and exogenous factors. Environmental (exogenous) constraints set the range of variation of potential population sizes, and endogenous mechanisms influence the realized population size within this range. For instance, Thomas et al. (1998) show that population changes in the egg stage of *M. arion* on four conservation sites in the United Kingdom are highly variable (Fig. 9). Over a period of 30 years, they identified 12 annual declines and 20 increases in population size, of which at least 9 declines occurred when the caterpillar population exceeded the capacity of ant nests. Some severe declines were due to environmental factors, especially drought and overgrazing that reduced the carrying capacity of the sites, whereas others were possibly due to endogenous factors. Unfortunately, data are inadequate to evaluate the relative importance of these two processes of limitation, but we strongly suspect that their effects interact, as illustrated in Fig. 11. Certainly, the life history traits of the predacious *Maculinea* make them more sensitive to exogenous drivers than for the cuckoo species, since environmental variation can bring their populations into zones of instability.

Our model shows that the episode of density dependence within ant nests is crucial in shaping *M. arion* population dynamics; however, one important limitation is that we assume a constant number of ant nests, whereas in reality it should vary, in particular with the size of the butterfly population (Hochberg et al. 1994). We have explored the consequences of explicit ant nest dynamics (Appendix D) and found that the same potential for complex dynamics exists with explicit changes in the ant population, but the limit to complex dynamics is shifted to higher values of species parameters. This is due to the coupling between the dynamics of *M. arion* and the ant nests, which acts as a buffer against overcompensation and thus stabilizes the butterfly’s population, compared to when ant nest numbers are set constant. However, more realistic models of ant dynamics (see Hochberg et al. 1994, Clarke et al. 1997 for *M. rebeli*) should be developed to verify the robustness of these findings. We did not consider the case of explicit plant dynamics because it is unlikely that the butterfly will have a sufficient impact on the plant population to create the negative feedback necessary to endanger the butterfly itself (Thomas et al. 1998).

Spatial distribution and population regulation

An interesting feature of our model is that it forges links between spatial aspects of the environment (the spatial distribution of caterpillars among ant nests), density dependence, and the kind of dynamics the butterfly will experience. We assumed that the intensity of density dependence within ant nests is directly related to the spatial distribution of caterpillars among ant nests (after Hassell and May 1985). We showed that a clumped distribution of caterpillars among ant nests, while leading to lower population size, guarantees stable dynamics and might thus be important in conservation planning. It is well known that spatial heterogeneity in the distribution of predators and their prey can be stabilizing (Hassell and May 1974, Chesson and Murdoch 1986). Here we assumed that the distribution of caterpillars among ant nests follows a negative binomial distribution (after May 1978, Hassell and May 1985), allowing the relationship between spatial heterogeneity and the nature of density dependence to be encapsulated in a simple parameter: the clumping index *k* of the negative binomial distribution. This is bound to be an oversimplification for the population ecology of other species, for example, when the distribution itself is a function of the population size of competitors (Taylor et al. 1979).

Unlike the general case, the predators (caterpillars) in our system do not actively pursue their prey (ant nests), but are adopted by ants from the host plants. Chesson and Murdoch (1986) have shown that even if predators do not actively aggregate into zones of high prey density, there is still potential for spatial heterogeneity and thus stabilization. Aggregation in our system can arise from several causes, such as the distribution of eggs among plants, the distribution of plants, the distribution of ant nests, and their spatial distributions relative to one another. We measured these on spatial parameters on two sites (Appendix A) and found that the distribution of caterpillars among ant nests, while difficult to predict, varies from clumped to random, depending on each site. Sites with low plant and ant nest numbers will probably have more clumped distributions than other sites. Elmes et al. (1996) showed that the distribution of *Gentiana cruciata*, the larval food plant of *Maculinea rebeli*, was less clumped, as measured by the negative binomial parameter *k,* on sites with higher plant densities.

Linking the density of plants and ant nests to the clumping parameter, and thus to the intensity of density dependence, is likely to change the dynamics of *M. arion*. If high numbers of food plants imply a more random distribution of caterpillars among ants (higher value of *b*), then this would destabilize further the dynamics of *M. arion*. We therefore argue that an interesting feedback loop might emerge from the interaction between *M. arion* and the ant *Myrmica sabuleti*. Indeed, as we have shown, the number of ant nests potentially oscillates with the butterfly at high values of *b* (Appendix D), because of the high impact of the butterfly on its host. However, if lower densities of ant nests imply a more clumped distribution of ant nests, this might lead to more stable dynamics. A similar feedback loop between aggregation and density was investigated by Atkinson and Shorrocks (1981), who showed that when the clumping index of the negative binomial *k* increases with density, it has a destabilizing effect on the equilibrium, such that low densities are related to higher clumping and thus more stable dynamics. Thus there is the potential for contrasted effects of the number of plants and ant nests via both their direct effects on population dynamics, as illustrated in our results, and their relationship with the spatial distribution of caterpillars among ant nests, as discussed here.

Nested density dependence

Our model of *Maculinea arion* differs from classical models of density dependence (Bellows 1981) by including two different kinds of competition during its life cycle (Fig. 1). It should apply to a broad range of species for which the form of competitive interactions changes predictably at distinct points in the life cycle. Species are often structured in different size classes and trophic groups or experience different growth stages that do not necessarily interact directly during their life cycle (Wilbur 1996). Introducing several levels of density dependence within the same life cycle loop drastically changes the dynamical properties of the equilibrium, compared with simpler models of only one source of density dependence (Bellows 1982, Kot and Schaffer 1984, Prout and McChesney 1985, Rodriguez 1988, Burkey and Stenseth 1994, Astrom et al. 1996, Hellriegel 2000, Kaitala et al. 2000).

Our model illustrates that nested density dependence can lead to negative feedbacks involving parameters that are usually thought to optimize population size. For instance, we found a hump-shaped relationship between butterfly population size and female fecundity, with high fecundity leading to an excess of caterpillars within ant nests and thus lower butterfly population sizes. Similar results were found with increasing numbers of plants (and flower heads) as well as the three survival parameters. These relate not only to nested feedback but also to the kind of density dependence that is acting in the two phases of *M. arion's* larval stages. For instance, *M. rebeli* experiences contest competition on both the flower heads and in ant nests, and shows no (Hochberg et al. 1992) or a weak (Hochberg et al. 1994, Clarke et al. 1998, Griebeler and Seitz 2002) negative feedback between these parameters and butterfly population size. In contrast, species that experience two episodes of scramble competition within the same life cycle may exhibit very complex dynamics with alternative stable states (Rodriguez 1988, Astrom et al. 1996).

Our results illustrate how predictions on population levels and dynamics require estimates of both the finite rate of increase and the shape of the density-dependence functions. They suggest that for specialist species with complex population dynamics, there is no ‘‘simple’’ conservation strategy; management should be determined only after applying site-specific parameter values to models. Thus for *M. arion*, maximizing the population growth rate might be an inappropriate strategy on sites where the distribution of plants and ant nests (and hence caterpillars among ant nests) is approximately random. Maximizing the size of the population and its stability may require contradictory conservation strategies, and thus no simple, overarching solution may be appropriate. It is also likely that species that experience several episodes of scramble competition (as in Rodriguez 1988) will necessitate different conservation measures than those combining both contest and scramble competition (as *M. arion* in our model), or only contest competition (as for *M. rebeli* in Hochberg et al. 1992).

ACKNOWLEDGMENTS

This research was funded by the European Community within the RTD project MacMan (EVK2-CT-2001-00126). We also thank Jonathan Chase, Marcel Holyoak, Martha Hoopes, Thomas Miller, David Tesar for discussions, Bertrand Gonard for help in the field, and Josef Settele for facilitating this project.

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APPENDIX A

Summaries of the main parameter estimations whose values are presented in Table 2 are available in ESA's Electronic Data Archive: *Ecological Archives* M075-021-A1.

APPENDIX B

A discussion of the condition for simple dynamics in the nested model of density dependence is available in ESA's Electronic Data Archive: *Ecological Archives* M075-021-A2.

APPENDIX C

A discussion of the Lyapunov exponent is available in ESA's Electronic Data Archive: *Ecological Archives* M075-021-A3.

APPENDIX D

A discussion of the population dynamics of ants is available in ESA's Electronic Data Archive: *Ecological Archives* M075-021-A4.