CONSERVING COMMUNITY MODULES: A CASE STUDY OF THE ENDANGERED LYCAENID BUTTERFLY *MACULINEA ALCON*

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Abstract. We develop a ''case model'' approach to investigate how conservation measures may affect the ecology of a community module, defined as a small number of tightly interacting species. The community module consists of a parasitic butterfly and its two hosts, a plant and an ant. The butterfly *Maculinea alcon* and its host plant *Gentiana pneumonanthe* have long been used as indicators of high-quality Palearctic heath and moist grassland ecosystems, and both species have been targeted for ecological research and specific conservation management. We constructed a mechanistic model of this community module, including dynamics for the three species, and conducted simulation studies of different conservation strategies (burning, sod cutting, mowing, and grazing). We identified several key parameters for the conservation of *Maculinea alcon* and its host plant as well as the most efficient conservation strategies for their dual long-term persistence. Our results show that the conditions that optimize the size of the butterfly and the plant populations differ, suggesting that choices must be made in adopting conservation measures. Despite the potential for apparent competition between the ant, *Myrmica scabrinodis*, and the plant via the butterfly, realized apparent competition is asymmetric (ants are more affected than plants) and occurs only at intermediate successional stages. Our study provides an example whereby an endangered species (the plant) and its endangered specialist natural enemy (the butterfly) are adversely affected by successional dynamics via direct (for the plant) and indirect (for the butterfly) effects. We argue that different field situations will necessitate particular conservation solutions.

Key words: butterflies; case model; community module; conservation; Gentiana pneumonanthe; Maculinea alcon; *management;* Myrmica; *population dynamics; social parasite.*

INTRODUCTION

Community modules consist of small numbers of interacting species (typically three or four closely coupled species) whose dynamics and interactions can be understood in isolation from the surrounding community (Hochberg et al. 1996, Holt 1997). Apparent competition (Holt 1977) and keystone predation (Paine 1969) are good examples of the insights that community modules have provided toward understanding the mechanisms that generate patterns in more complex communities. In applied ecology, Holt and Hochberg (2001) have shown how this concept could help in understanding the consequences of indirect interactions in biological control. Here, we use a ''case model'' approach to investigate how conservation measures may affect the ecology of a community module. Our approach (Hochberg et al. 1996) is to construct a mechanistic model of intermediate complexity that should

apply more generally to other biological systems. For example, if two species are involved in negative reciprocal interactions, then any measure favoring one species would have a negative impact on the second. When more than two species are involved, conservation predictions become more complicated, since direct interactions may be modified or supplanted by indirect effects. In such circumstances it may be impossible to optimize conservation for any single species, and some kind of priority weighting will be necessary. Our case model will treat one aspect of this larger problem: how conservation alternatives affect a three-species module.

We focus on *Maculinea* butterflies, each of whose five species exploit two sequential larval hosts. All *Maculinea* species are listed as ''Endangered'' or ''Vulnerable'' by the IUCN (1990) and have already experienced extinctions at regional and national levels (Thomas 1980, Munguira and Martin 1999, Thomas and Settele 2004). Urgent conservation measures are necessary for both the persistence of the *Maculinea* and for the hundreds of endangered plant and animal species that are characteristic of their habitats in Europe (Thomas 1995). All *Maculinea* butterflies have spe-

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cialized larvae that exploit a specific initial food plant followed by a single species of *Myrmica* red ant. This system forms the basis of a community module, since the butterfly requires its two resources to coexist, and may significantly impact the population ecology of one or both of them, generating ''apparent competition'' (Holt 1977) between the plant and ant via the link with their common enemy (Hochberg et al. 1994). The subject of our study, the alcon blue, *Maculinea alcon*, lays its eggs on *Gentiana pneumonanthe*, where the caterpillars develop as herbivores. Final-instar caterpillars fall to the ground and spend the rest of the larval period in *Myrmica scabrinodis* colonies as parasites.

Another species of *Maculinea* (*Maculinea rebeli*) has already been studied employing case models (e.g., Hochberg et al. 1994, Clarke et al. 1997, 1998); the studies show that the population dynamics of *Maculinea rebeli* is more influenced by interactions within ant nests than on plants, and that butterfly population numbers were maximized at intermediate food plant densities. However, the model developed for *Maculinea rebeli* did not consider plant dynamics because the populations of its food plant (*Gentiana cruciata*) are generally extremely stable (Hochberg et al. 1992). In contrast, *Gentiana pneumonanthe* population dynamics are highly variable, and it is itself an endangered species (Oostermeijer et al. 1992). Thus, for *M. alcon*, more than for any other species of *Maculinea*, conservation strategies must take both plant and butterfly dynamics into consideration.

We develop a mechanistic model for *M. alcon*, including dynamics for the host ant, the host plant, and the butterfly. Each component of this system was studied for >20 years, and parameters were taken from a mix of previously published and unpublished results. Using the formalism proposed by Hochberg et al. (1992) for *M. rebeli*, we simulate the effects of four different conservation strategies: burning, sod cutting, mowing, and grazing (after Oostermeijer et al. 1994, 1998, Maes et al. 2004). We identify the key parameters for the conservation of *M. alcon* and its host plant *G. pneumonanthe* as well as the most efficient conservation strategies for their long-term persistence. Our results show that the conditions that optimize the size of the butterfly and the plant populations differ, suggesting that choices must be made in adopting conservation measures. We argue that different field situations will necessitate particular conservation solutions and that conservation may have to be done on a case-by-case basis.

BIOLOGY OF THE SPECIES INVOLVED

Gentiana pneumonanthe

The marsh gentian (*Gentiana pneumonanthe*, L.) is a perennial herbaceous plant found in boggy meadows, fens, and moist heaths. This species was locally common in Europe as recently as the 1950s, and has become increasingly rare due to the reductions in its natural habitat and to the absence of appropriate conservation policies (Oostermeijer et al. 1992). It is now a species of high conservation value in all regions where it survives (Rose et al. 1998), and is used as a key plant indicator for the selection of wetlands of international importance under the RAMSAR treaty (*available online*).[5] Plants can reproduce at and beyond their third year of growth, producing several flowering shoots, and spend the winter as a rosette or as a dormant rooting system. Reproduction takes places only via seeds that are produced in large quantities (~400 per pod) and are dispersed by wind over relatively short distances. Six different stages can be distinguished based on demographic criteria: seeds, seedlings, juveniles, vegetative adults, reproductive adults, and dormant adults (Oostermeijer et al. 1996). Juvenile recruitment is related to the proportion of bare soil and has been shown to be the key stage of the life cycle of this plant (Oostermeijer et al. 1996, Rose et al. 1998). More details on the biology of *G. pneumonanthe* are described by Simmonds (1946).

Populations of *G. pneumonanthe* can be divided into two types (after Oostermeijer et al. 1992, 1994): ''dynamic'' populations with high numbers of seedlings and juveniles abundant each year, and ''senile'' populations where practically no germination and seedling recruitment takes place. Dynamic populations are characteristic of open habitats (for example after fire), and senile populations are characteristic of more closed habitat dominated by mature heath or grasslands (Simmonds 1946, Oostermeijer et al. 1992). Closed populations may persist for almost 50 years before going extinct (Chapman et al. 1989).

Maculinea alcon

Maculinea alcon (see Plate 1) is a globally threatened species (IUCN 1990). Its adults emerge in late summer and typically live in small closed populations from which they seldom emigrate (Maes et al. 2004, WallisDeVries 2004). Females oviposit on the young flower buds of *G. pneumonanthe*, selecting prominent plants (Thomas and Elmes 2001). *G. pneumonanthe* is the only known food plant on the majority of known sites in Europe. An alternative host, *Gentiana asclepiadea*, is present at certain alpine sites at frequencies on the order of <10%, but it has been shown for these sites that *G. pneumonanthe* is used preferentially (M. Bräu, *personal communication*). For this reason we will consider a model where *M. alcon* are treated as true specialists of *G. pneumonanthe*. The first three larval instars feed and live inside the *Gentiana* seedpods where they experience density-dependent mortalities. After the third and final molt the 1–2 mg caterpillar drops to the ground to await discovery by a *Myrmica* worker. Once found, the ant carries it into the brood

chambers of its underground nest (Elmes and Thomas 1987, Als et al. 2001).

Like its sibling species *Maculinea rebeli* (Elmes et al. 1991, 2004, Schönrogge et al. 2004), *M. alcon* uses chemical mimicry to achieve a high level of social integration inside host *Myrmica* nests (Als et al. 2001). Caterpillars are treated as ''super larvae'' by the worker ants, and are fed in preference to the ant's own brood on eggs, foraged food, and by trophallaxis (Elmes and Thomas 1987). The caterpillars have an apparently fixed growth polymorphism, with most individuals taking two years to grow to form the 100–120 mg pupae; some individuals take one year (Schönrogge et al. 2000). Individual *Myrmica* nests frequently adopt more caterpillars than they can support, resulting in density-dependent contest competition between caterpillars. A typical *Myrmica scabrinodis* colony occupied by *M. alcon* rears six butterflies, with a maximum of 20 butterflies recorded per nest (Thomas and Elmes 1998).

Despite strong host specificity in *M. alcon* (Thomas et al. 1989, Als et al. 2001) there are clear-cut host switches across *M. alcon's* European range, each representing a distinctive, and different, conservation unit (Als et al. 2004): central-southern and eastern populations exclusively exploit *Myrmica scabrinodis*, populations in the Netherlands and parts of Denmark exploit *Myrmica ruginodis*, while those in Sweden and north Denmark generally exploit *Myrmica rubra* (Elmes et al. 1994). Here we model the population responses to management of the *scabrinodis*-exploiting populations of *M. alcon*, which are considered to be the most common form of this endangered species.

Some *M. alcon* populations that exploit *Myrmica scabrinodis* are parasitized by a large (possibly race-specific) ichneumonid parasitoid, provisionally identified as a sibling species of *Ichneumon eumerus* Wesmael (Thomas and Elmes 1993, Hochberg et al. 1996). Known infestation rates range from ∼20% to 65% of *M. alcon* caterpillars (M. Sielezniew and A. Stankiewiz, *personal communication*).

Myrmica *ants*

Ants of the genus *Myrmica* form small polygynous, polydomous societies, each typically of 150–400 workers. In optimal habitat, densities may approach 1 nest/m², although 1 nest/5–10 m² is more usual (Elmes et al. 1998). Up to five *Myrmica* species are common in the moist grass and heathland inhabited by *G. pneumonanthe* and *Maculinea alcon* in Europe. Each occupies a narrow, partially overlapping niche (Hochberg et al. 1994, Elmes et al. 1998, Thomas et al. 1998b). Presence, absence, and quality of a species' habitat vary greatly with the management of the site, which may result in the top 5 cm of soil temporarily becoming 20°C warmer, and correspondingly drier, following a perturbation (mowing, grazing, fire, turf cutting) to mature vegetation (Thomas 1995). *Myrmica* populations react quickly to these changes, abandoning nests within

one season if conditions deteriorate, and budding from existing colonies into vacant nest sites in new suitable habitat during spring and summer.

Model Development

Current recommendations for the design and management of conservation areas to promote *Maculinea alcon* (Maes et al. 2004, WallisDeVries 2004) apply only to populations in northwest Europe that exploit *Myrmica ruginodis*. Here we present a basic model describing interactions between *G. pneumonanthe*, *M. alcon*, and *Myrmica scabrinodis* that applies to the majority of *M. alcon* populations, including all those known from Spain and Brittany (France) to Poland, Hungary, and perhaps farther east (Elmes et al. 1994). The model parameters are defined in Table 1.

A model for G. pneumonanthe

Basic model.—Our model of *G. pneumonanthe* is based on the work of Oostermeijer and colleagues (1996), using information on individual plant survival and reproduction to infer population dynamics. We consider a matrix population model (Caswell 2001) with five stages: seedlings (S), juveniles (J), vegetative adults (V), reproductive adults (R), and dormants (D). The life cycle is represented in Fig. 1. Since we do not explicitly consider the seed stage, each year t begins just before the birth pulse.

The equations are

$$
\begin{pmatrix} S \\ J \\ V \\ R \\ D \end{pmatrix}(t+1)
$$

$$
= \begin{bmatrix} 0 & 0 & 0 & S_{0c}F_{g1} & 0 \\ S_{0a}(G_t) & 0 & 0 & S_{0c}F_{g2} & 0 \\ S_{0b}(G_t) & S_{1a}(G_t) & S_2 & 0 & g_2 \\ 0 & S_{1b}(G_t) & S_3 & S_4 & g_3 \\ 0 & d_1 & d_2 & d_3 & S_5 \end{bmatrix} \times \begin{pmatrix} S \\ J \\ V \\ R \\ D \end{pmatrix}(t) \quad (1)
$$

with

$$
G_t = J_t + V_t + R_t. \quad (2)
$$

Population dynamics are obtained by multiplying the transition matrix by the initial population vector (Eq. 1) and by iterating this process through time. The parameters F_g correspond to seedling recruitment, and encapsulate adult fecundity, dispersal, seed survival, and germination success. The parameters S correspond to subsequent survival. These seedlings and juveniles suffer competition with older stages, resulting in lower survival parameters

$$
S_{ij}(G_t) = S_{ij}(1 - G_t/G_{max}) \qquad i = 0, 1
$$
$$
j = a, b, c \quad (3)
$$

where G_{max} is the population density above which no

TABLE 1. Parameter definitions and values used.

Community member	Parameter	Definitions and values
Gentiana pneumonanthe	S, J, V, R, D	seedlings S, juveniles J, vegetative V and reproductive adults R, dormants D
	$F_{g1,2}$	adult realized fecundity $F_{g1} = 4.5$ and $F_{g2} = 3.5$
	$S_{0a,b,c}$, $S_{1a,b}$, S_2, S_3, S_4, S_5	interstage survival; $S_{0a} = 0.1$, $S_{0b} = 0.15$, $S_{0c} = 0.5$ ($S_{0c} = 0.8$ when $t_s = 0$), $S_{1a} = 0.74$, $S_{1b} = 0.05$, $S_2 = 0.65$, $S_3 = 0.2$, $S_4 = 0.6$, $S_5 = 0.6$
	$d_{1,2,3}$	entry into dormancy; $d_1 = 0.4$, $d_2 = 0.2$, $d_3 = 0.2$
	$g_{1,2}$	exit from dormancy; $g_1 = 0.5$, $g_2 = 0.3$
	G_{max}	threshold density; $G_{max} = 300\,000$ plants/ha
	ε_G	average number of seedpods per plant; $\varepsilon_G = 25$
	k	rate of decrease of each plant parameter during the succession; $k = 0.06$
Maculinea alcon	N	adult butterfly population size
	M	number of caterpillars surviving on plants
	x_G	average number of competing caterpillars per flowering bud
	x_A	number of competing caterpillars among ant nests
	F	total number of female eggs laid per female butterfly; $F = 80$
	$\rho(A)$	proportion of caterpillars recruited into nests
	ϕ_1	proportion of eggs surviving on plants from density-independent mortality; $\phi_1 = 0.79$
	ϕ_2	proportion of young caterpillars (after first instar) surviving on the plant from density-independent mortality; $\phi_2 = 0.8$
	ϕ_3	proportion of caterpillars surviving the first few weeks following recruitment into ant nests; $\phi_3 = 0.88$
	ϕ_4	proportion of caterpillars surviving parasitism by *Ichneumon fulvicornis*; $\phi_4 = 0.6$
Myrmica scabrinodis	A	number of ant nests
	η	ant searching area; $\eta = 0.00126$ ha
	ε_a	mean number of caterpillars adopted per nest; $\varepsilon_A = 6$
	λ_A	basic growth rate of ant colonies; $\lambda_A = 1.4$ or $\lambda_A = 2.5$ (when $t_s = 0$)
	K_A	threshold density of ant nests; $K_A = 2000$ ant nests/ha
	α	scaling parameter determining the strength of parasitism by *Maculinea alcon*; $\alpha = 0.1$
	h	rate of decrease of *Myrmica scabrinodis* parameters with successional stage; $h = 0.2$

seedlings or juveniles are assumed to survive and develop. The parameters d and g, respectively, correspond to entry into and exit from dormancy.

Successional dynamics.—To account for successional patterns, we assume that some plant parameters are functions of the time, t_s, since the last perturbation (fire, mowing, winter flooding, etc.), where t_s is referred to as the "succession age." For instance, Oostermeijer et al. (1994, 1996) have shown that flowering increases in the years following fire and then diminishes as heathland ages. More generally, we assume that the proportion of open vegetation declines exponentially with time t_s after a perturbation, and hence that some parameters decrease exponentially as succession proceeds (Chapman et al. 1989). The survival parameters are given by

$$S_{ij}(G_t, t_s) = S_{ij}(1 - G_t/G_{max})e^{-kt_s} \qquad i = 0, 1$$
$$j = a, b, c. \quad (4)$$

Interspecific competition becomes more intense as succession proceeds. The scaling constant k determines

the annual proportional rate of decrease of each survival parameter (and is related to the rate of succession and increase in vegetative competition). We assume also that flowering declines with t_s at a similar proportional rate, such that

$$F_{gt}(t_s) = F_{gi}e^{-kt_s} \qquad i = 1, 2. \quad (5)$$

It is also likely that dormancy is induced by environmental conditions, and we assume that entry into dormancy increases with t_s while exit from dormancy declines with t_s, such that

$$g_i(t_s) = g_i e^{-kt_s} \qquad i = 1, 2$$
$$d_i(t_s) = d_i(1 - e^{-kt_s}) \qquad i = 1, 2, 3. \quad (6)$$

In the absence of better individual estimates, we adopt the same parameter values k for all of Eqs. 4, 5, and 6, representing succession-age dependent population parameters.

Effect of M. alcon *on* G. pneumonanthe.—We allow *G. pneumonanthe* fecundity to decline with the density
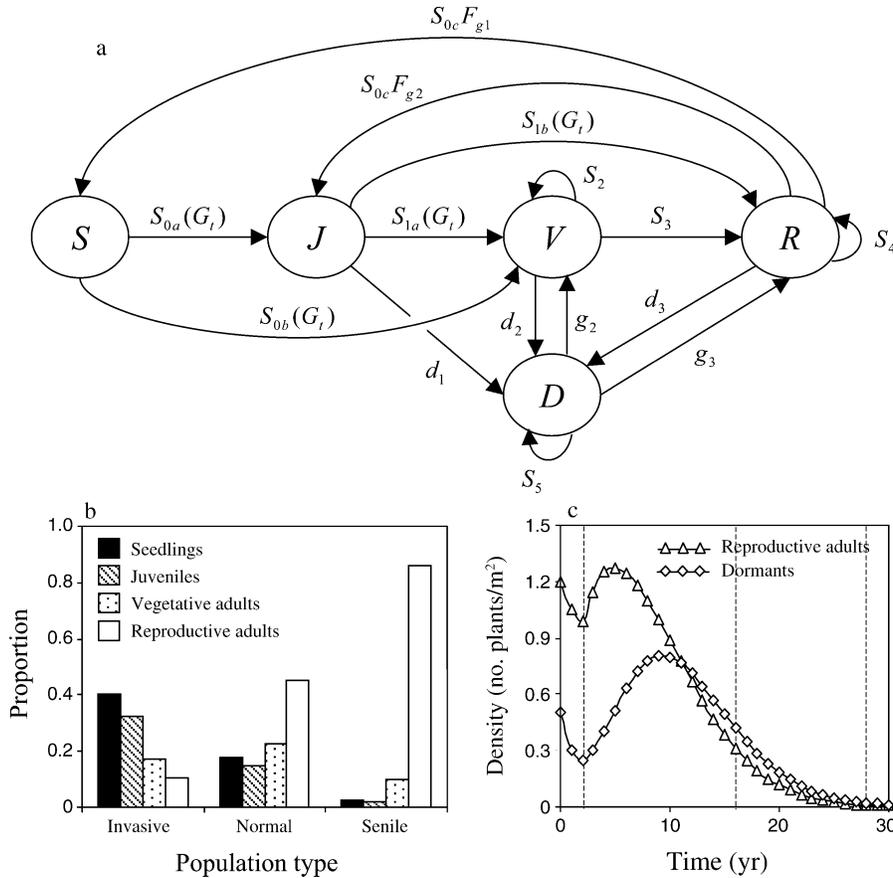
Fig. 1. (a) Life cycle of *Gentiana pneumonanthe*. Parameters are given in Table 1. (b) Age structure at three different time points in the succession (corresponding to the three dashed vertical lines in panel c). (c) Population dynamics for reproductive and dormant adults. Initial values are $S_0 = 20\,000$, $J_0 = 20\,000$, $V_0 = 20\,000$, $R_0 = 20\,000$, and $D_0 = 10\,000$.

of *M. alcon* due to damage to *G. pneumonanthe* seed-pods:

$$F_{gi}(t_s, N_t) = F_{gi}(1 - x_R)e^{-kt_s} \qquad i = 1, 2 \qquad (7)$$

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

$$x_R = N_t F_{gi} \phi_1 / \varepsilon_G R_t \qquad (8)$$

with the constraint that $F_{gi}(t_s, N_t) = 0$ if $N_t \phi_1 F_{gi} \geq \varepsilon_G R_t$ (a plant's fecundity is zero if it supports an average of more than one caterpillar per seedpod).

A model for Maculinea alcon

In any year t, adult butterfly population size N_t is the product of recruitment and competition on the R_t reproductive plants (function g_1) and in the A_t ant nests (g_2) such that

$$N_{t+1} = g_1(N_t, R_t)g_2(g_1(N_t, R_t), A_t) \qquad (9)$$

Recruitment and competition on the plant.—In generation t, the population of N_t adult butterflies lays FN_t eggs over the plant population. The eggs and the first-instar caterpillars suffer density-independent mortality

ϕ_1; older caterpillars suffer contest competition and density-independent mortality ϕ_2. The number of caterpillars M_t surviving on the plants is defined by the survival function g_1, where

$$M_t = g_1(N_t, R_t) = N_t F \phi_1 (1 + x_R)^{-1} \phi_2. \qquad (10)$$

The density-dependent mortality function $(1 + x_R)^{-1}$ is characteristic of contest competition models (e.g., Bellows 1981), such that M_t approaches the total number of buds when there are more caterpillars than buds.

Recruitment and competition within ant nest.—The events occur sequentially as follows. Caterpillars are adopted into *Myrmica scabrinodis* colonies with probability $\rho(A)$. Caterpillars then suffer density-independent mortalities (ϕ_3) within the first weeks of adoption, density-dependent mortality (contest competition) during the next eight months prior to pupation, and finally parasitism by *Ichneumon fulvicornis* (ϕ_4). The model is

$$g_2(M_t, A_t) = \rho(A_t)\phi_3\phi_4(1 + x_A)^{-1} \qquad (11)$$

with x_A the average number of competing caterpillars per ant nest, or

$$x_A = M_t \rho(A_t) \phi_3 / \varepsilon_a A_t \qquad (12)$$

and $\rho(A)$ is the probability of a caterpillar being found and retrieved by an ant colony. The parameter $\rho(A)$ is assumed to obey a Poisson distribution of ant searching area η and ant nest numbers A_t, such that

$$\rho(A) = 1 - e^{-\eta A_t}. \qquad (13)$$

The general model (Eq. 9) reads

$$N_{t+1} = N_t F \phi_1 (1 + x_R)^{-1} \phi_2 \rho(A_t) \phi_3 \phi_4 (1 + x_A)^{-1}. \qquad (14)$$

A model for Myrmica scabrinodis

We propose a simple model that resembles classical models of host–parasitoid interactions in which the host is limited by intraspecific competition in the absence of the parasitoid (e.g., May et al. 1981, Hochberg and Lawton 1990). Ant nest growth rate is directly linked to the population dynamics of the butterfly and to intraspecific competition (we assume that the two forms of density dependence act independently). The equation describing the changes in the number of ant nest numbers A_t is

$$A_{t+1} = \lambda_A A_t \left(1 - \frac{A_t}{K_A}\right)(1 - \alpha x_A)^{-1}. \qquad (15)$$

The basic growth rate of the number of ant nests is λ_A. The first term in brackets is intraspecific competition. In the absence of caterpillar parasitism, the equilibrium density (stable or otherwise) is $K_A(\lambda_A - 1)/\lambda_A$, with K_A being the number of ant nests above which the effect of intraspecific competition becomes marked. The second term in brackets describes mortality due to caterpillar parasitism, where α is a scaling parameter determining the strength of parasitism by *M. alcon*.

Myrmica scabrinodis is also influenced by the stage of succession; its population builds to a peak about two years after a major perturbation and then declines (in unmanaged grassland) as this gets to 3–4 years growth (J. A. Thomas, *personal observation*). At this stage it is progressively replaced by *Myrmica ruginodis* or *Myrmica rubra* (depending on site and soil chemistry, etc.), which emerge in later successional stages. Like the model for *G. pneumonanthe*, we assume that the growth rate λ_A of *Myrmica scabrinodis* declines exponentially with time since the last perturbation, namely,

$$\lambda_A(t_s) = \lambda_A e^{-h t_s}. \qquad (16)$$

The parameter h determines the rate of decrease of λ_A as succession proceeds. Note that $h < k$, because the decline of *Myrmica scabrinodis* occurs over a shorter successional time scale than for *G. pneumonanthe*.

Conservation strategies

As is the case for the majority of early- to midsuccessional plants, and the insects that depend upon them, in subalpine heaths or grasslands across the Palearctic,

the persistence of this community module has been associated with human activities (perturbations) for the past 5000 years. All the conservation strategies used in our simulations (based on Oostermeijer et al. 1994, 1998, Maes et al. 2004; G. Oostermeijer, *personal communication*) were thus once traditional forms of land-use patterns on these sites, used either for agriculture (burning, grazing, mowing) or to provide fuel (cutting sods of peat). *Burning* is important for the long-term local persistence of *G. pneumonanthe* (Chapman et al. 1989). Flowering increases in the years following fire and then declines as the heathland develops through later successional stages. *Sod cutting* consists of removing the top layers of the soil, enabling colonization by *G. pneumonanthe* seeds (Oostermeijer et al. 1994). It takes about one year before a sod-cut area is suitable for colonization by gentians, because a mildly toxic ammonia-peak occurs in the soil during the first year after cutting, which kills seedlings and juveniles. *Mowing* is frequently used to promote grassland *G. pneumonanthe* populations (Oostermeijer et al. 1994). It must be done in late September when *M. alcon* larvae have already left *G. pneumonanthe*. *Grazing* by cattle, sheep, horses, and occasionally deer creates short turf, and their hoofprints expose bare soil that is also advantageous to *G. pneumonanthe* (Oostermeijer et al. 1994). Table 2 explains how each strategy was simulated with the model, and more detailed descriptions are given in Appendix A.

Parameter estimation

Details of parameter estimation are given in Appendix B, and their values, together with the symbols used in all equations, are summarized in Table 1. In brief, knowledge of the parameters describing the dynamics and interactions of the four components of our model (ants, butterfly, plant and ecosystem/conservation management) is more or less equally complete, and resulted from >20 years of detailed field and laboratory experiments. Parameters for gentians and management were obtained largely from the published literature, and those for ants and the butterfly from our own published and unpublished studies, including an intensive analysis of an *M. alcon* site in Sarthe, France.

RESULTS

Gentiana alone

The results obtained with the model for *G. pneumonanthe* alone correspond to what is found in the literature. Fig. 1b shows the age state structure at three different successional times (corresponding to the three vertical dashed lines in Fig. 1c). Fig. 1c illustrates the time series obtained for reproductive and dormant adults. Extinction occurs after 30 years. Since entry into dormancy increases with successional time, there is a delay in the decline of dormant plants compared to reproductive adults.

TABLE 2. Conservation strategies used in our simulations.

Strategy and species affected	Effects
Burning (t_s is set to 0 the year after burning.)	
Gentiana pneumonanthe	*Seedling survival* is set to zero the year of the fire. *Juvenile survival* is reduced by 50% the year of the fire.
Myrmica scabrinodis	In peat bogs, 75% of nests are destroyed.
Maculinea alcon	In peat bogs, *caterpillar survival* within ant nests ϕ_3 is reduced by 75%.
Grazing (With periodic grazing, t_s is reduced by 75% if grazing is intense, by 50% if intermediate, and by 25% if grazing is weak. With year-round grazing, t_s is relatively stable; $t_s = 2$ if grazing is strong; $t_s = 4$ if intermediate, and $t_s = 6$ if weak.)	
Gentiana pneumonanthe	*Adult survival* is reduced by 10%. *Seedling and juvenile survival*, and *adult fecundity*, are reduced by 60% if grazing is intense, 30% if intermediate, and 10% if weak.
Maculinea alcon	*Survival on the plant* is reduced by 60% if grazing is intense, 30% if intermediate, and 10% if weak.
Mowing (t_s is reduced depending on height of mowing; $t_s = 2$ for mowing 5 cm aboveground; $t_s = 4$ for mowing at 10 cm.)	
Gentiana pneumonanthe	Mowing at 5 cm: *juvenile survival* reduced by 25% and *adult survival* by 5%. *Seedling and juvenile survival* are reduced by 10% by trampling.
Myrmica scabrinodis	If mowing is done at 5 cm, *ants growth rate* λ_A is reduced by 25%.
Maculinea alcon	If mowing is done at 5 cm, then *ant searching area* η and the *number of caterpillars adopted* per nest ε_a are reduced by 25%.
Sod cutting (t_s is reduced by 30% if $Sd = 5\%$, by 60% if $Sd = 15\%$, and by 80% if $Sd = 25\%$. Importantly, the reduction in t_s occurs 1 year after a sod cut.)	
Gentiana pneumonanthe	*Seedling, juvenile, vegetative adult*, and *dormant survival* are reduced by the percentage area removed, *Sd*.
Myrmica scabrinodis	*Number of ant nests* is reduced by the percentage area removed, *Sd*.
Maculinea alcon	*Caterpillar survival* within ant nests (ϕ_3) is reduced by the percentage area removed *Sd*.

Note: The "succession age," t_s, is the time since the last perturbation (fire, mowing, winter flooding, etc.).

Gentiana pneumonanthe *with* Maculinea alcon *and* Myrmica

Without successional dynamics.—It is helpful to first consider the general properties of our model without successional dynamics (with $t_s \rightarrow \infty$). This will help us to clearly understand the effect of each species within the community module without the complexity added by the successional dynamics. Fig. 2a illustrates the effect of *M. alcon* on *G. pneumonanthe* reproductive adults when the number of ant nests is assumed to be fixed for any one simulation. This effect is relatively weak, since the adult population of *G. pneumonanthe* is reduced by only 9% after the butterfly reaches its equilibrium population size of 957 individuals. The butterfly (and its effect on *G. pneumonanthe*) is limited by the number of ant nests, as illustrated in Fig. 2b. As simulations contain more ant nests (keeping a fixed number of ant nests in any given simulation), the number of *M. alcon* increases and the number *G. pneumonanthe* reproductive adults decreases. Above a threshold density of ant nests, there are not enough plants for the butterfly population size to increase in response to further increases in the number of ant nests, and this results in the local extinction of plant and butterfly. The butterfly is thus either limited by *G. pneumonanthe* or by *Myrmica scabrinodis* depending on the density of plants in the environment. When the number of ant nests is no longer fixed and we vary the number of plants by varying the plant survival (in this example we increase the survival from vegetative to

reproductive adult stages S_3), the number of butterflies first increases with plant numbers (Fig. 2c). In parallel to this, the number of ant nests decreases due to the impact of *M. alcon* caterpillars. After a threshold (indicated by the two black arrows in Fig. 2c), increasing the number of plants leads to a lower number of butterflies because *M. alcon* becomes limited by the number of ant nests (which is decreasing) rather than by the number of plants. These results illustrate the apparent competition between *G. pneumonanthe* and *Myrmica scabrinodis* via *M. alcon*.

With successional dynamics.—Fig. 3a illustrates the population dynamics obtained during succession for the three species. As expected from the successional rate, the ant *Myrmica scabrinodis* goes extinct rapidly (9 years), while *G. pneumonanthe* persists for more than 20 years. Since the presence of both ants and plants is necessary for the butterfly, *M. alcon* is also rapidly excluded (typically after 10 years). Butterfly population size peaks after the peak in ant nests because there is a one-year delay between the recruitment within ant nests and emergence of butterfly adults. Consequently it takes a few years before the negative impact of the butterfly starts to affect both ant and plant population sizes (Fig. 3b). The ants are affected earlier and more intensively by the presence of the butterfly than are the plants (Fig. 3b), because at the values used in our case model they are the limiting factor of *M. alcon*.

The magnitude of apparent competition between *G. pneumonanthe* plants and *Myrmica scabrinodis* medi-
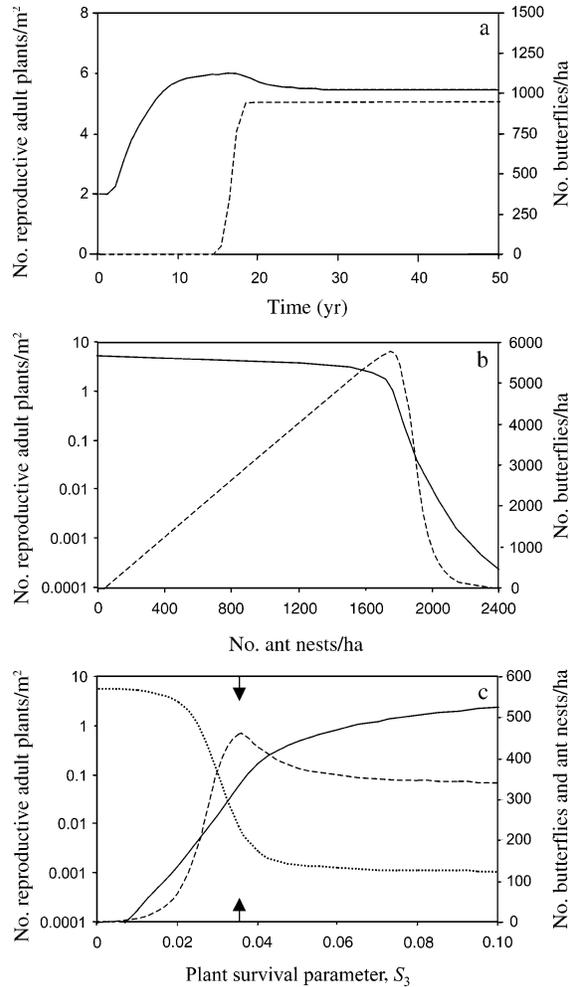
FIG. 2.   (a) Effect of introducing *Maculinea alcon* (dashed line) on the population size of reproductive *Gentiana pneumonanthe* (solid line). In each simulation, two butterflies were introduced at $t = 15$ years. Parameters are as in Table 1, and A_t was held constant at 300 nests. (b) Effect of increasing the number of ant nests on reproductive *G. pneumonanthe* (solid line) and *M. alcon* (dashed line) populations sizes at $t = 60$ years (the butterflies are introduced at $t = 15$). (c) Effect of increasing the survival parameter S_3 on reproductive *G. pneumonanthe* (solid line), *M. alcon* (dashed line), and *Myrmica scabrinodis* (dotted line) population sizes (taken at $t = 30$ years). The two arrows represent the threshold above which *M. alcon* becomes limited by the number of ant nests rather than by the number of plants. The three species were introduced at $t = 0$ ($N_0 = 50$, $A_0 = 100$, and initial values for *G. pneumonanthe* are as in Fig. 1). Other parameters are in Table 1. Note the log-scale y-axis.

ated via *M. alcon* varies during the course of succession. This is particularly true for ants (Fig. 3c). In this simulation we reduced the number of *G. pneumonanthe* reproductive adults (by decreasing their survival parameters) at three different time points during succession ($t = 2$, 5, and 9). Both the negative direct effect on the butterfly and the positive indirect effect on the ants were maximal at intermediate stages of succession

($t = 5$), i.e., when the realized population size of the butterfly was high (Fig. 3a). Thus, despite the potential for apparent competition between the ant and the plant via the butterfly, the realized apparent competition is asymmetric (ants are more affected than plants) and occurs only during a distinct time frame in the successional process.
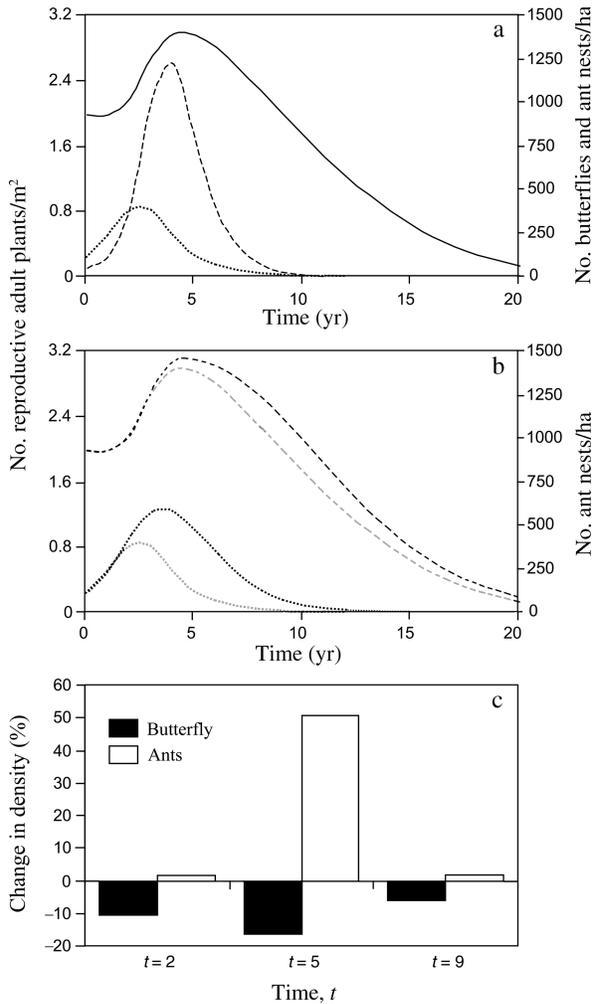

FIG. 3.   (a) Successional dynamics of *Gentiana pneumonanthe* (reproductive adults: solid line), *Maculinea alcon* (dashed line), and *Myrmica scabrinodis* (dotted line). (b) Successional dynamics of *M. alcon* (dashed line) and *Myrmica scabrinodis* (dotted line) with and without *M. alcon*. The curves corresponding to succession where *M. alcon* is present are gray. (c) Effect of reducing the number of reproductive adults of *G. pneumonanthe* (R) on *M. alcon* and *Myrmica scabrinodis* at different times during succession ($t = 2$, 5, and 9 years). The effect is measured in percentage change of population size compared to values obtained in (a). The reduction in R is obtained by setting S_{1b}, S_3, S_4, and g_3 to 0.01 when $t = 2$, 5, or 9. This results in reducing R from, respectively, 2, 2.8, and 2.1 individuals/m² to 0.11, 0.12, and 0.08 individuals/m². The three species were introduced at $t = 0$ ($N_0 = 50$, $A_0 = 100$, and initial values for *G. pneumonanthe* are as in Fig. 1). Parameter values and definitions are in Table 1.

Conservation strategies

The results of simulating different conservation strategies (described in Table 2 and Appendix A) are presented in Table 3. For each regime, we considered different frequencies of application ranging from 2 to 15 years, corresponding to traditional field practice. Fig. 4 shows one example: the time series obtained by sod cutting 25% of the available habitat every 15, 6, 3, and 2 years. Since the plants and ants have different successional rates, the plant persists in the long term with sod cutting every 6 years, while the ants do best with sod cut every 2 years. The butterfly requires the presence of both of the other species, and thus persists only when sod is cut every 3 years. Interestingly, more frequent sod cutting (2 years) leads to the extinction of the plant and the butterfly, while the ant becomes more abundant, with the decline of the plant being accelerated by the presence of the butterfly (Fig. 4d). With sod cutting, butterfly and ant population sizes do not markedly oscillate in time after management events, because small-scale sod cutting is relatively innocuous and does not ''reset'' successional time (t_s) to zero (Table 2). More destructive strategies, such as burning, that sets t_s to zero, lead to higher population size and high-amplitude oscillations, because the species attain their maximal growth rate when $t_s = 0$ (Fig. 5a).

Other regimes give similar results with different optimal frequencies of management for ants and plants (Table 3). This results in the butterfly being present at intermediate frequencies of management (between 3 and 6 years depending on the strategies). For the plants, burning and mowing are the best strategies. For the butterfly, burning, periodic grazing (strong and intermediate), mowing at 5 cm, and heavy sod cutting (15 and 25%) are productive regimes, while weak grazing, mowing at 10 cm and sod cutting at 5% are unsuitable. In terms of conserving the entire community module, the best conservation strategy is burning every 3 or 4 years, or periodic grazing (at intermediate levels every 2 years and intensely every 3 years), or mowing at 5 cm every 2 or 3 years. We also simulated continuous grazing, but did not obtain long-term persistence of the community module (Fig. 5b, c) due to the strong and continuous impact of grazing on plant fecundity.

Finally, we explored mixed management regimes. For instance, mixing sod cutting of 25% of the available habitat every 2 years with burning every 10 years leads to an average butterfly population size of 571 individuals (Fig. 5d; the mean was calculated between $t = 60$ and $t = 100$). Other good combinations of management regimes include sod cutting 5% of the available habitat every 4 years and burning every 10 years, and the combination of continuous grazing at intermediate intensity and burning every 10 years (not shown). Interestingly, none of these strategies on its own maintains our community module in the long term.

TABLE 3. Effect of different conservation strategies on the mean population sizes of the three species.

Strategies	Years					
	2	3	4	6	10	15
Burning						
M. alcon	0	952	755	448	0	0
M. scabrinodis	1100	302	242	160	30	0
G. pneumonanthe	0	2.5	3.6	3.65	2.84	0.018
Grazing (strong)						
M. alcon	0	664	480	0	0	0
M. scabrinodis	982	619	184	33	0	0
G. pneumonanthe	0	0.219	1.98	1.47	0.032	0
Grazing (inter)						
M. alcon	602	111	0	0	0	0
M. scabrinodis	214	67	0	0	0	0
G. pneumonanthe	1.71	1.74	0.86	0.022	0	0
Grazing (weak)						
M. alcon	0	0	0	0	0	0
M. scabrinodis	0	0	0	0	0	0
G. pneumonanthe	0.3	0.005	0	0	0	0
Mowing (5 cm)						
M. alcon	252	198	120	0	0	0
M. scabrinodis	114	92	66	3	0	0
G. pneumonanthe	3.46	3.58	3.48	2.9	1	0.015
Mowing (10 cm)†						
M. alcon	...	...	0	0	0	0
M. scabrinodis	...	...	0	0	0	0
G. pneumonanthe	...	...	1.97	1.01	0.048	0.0008
Sod cutting (5%)						
M. alcon	0	0	0	0	0	0
M. scabrinodis	0	0	0	0	0	0
G. pneumonanthe	1.15	0.049	0.0018	0	0	0
Sod cutting (15%)						
M. alcon	260	43	0	0	0	0
M. scabrinodis	102	40	0	0	0	0
G. pneumonanthe	1.81	1.59	0.908	0.05	0.0002	0
Sod cutting (25%)						
M. alcon	0	274	125	0	0	0
M. scabrinodis	616	108	64	0	0	0
G. pneumonanthe	0	0.72	0.84	0.37	0.0037	0

Notes: Simulations ran for 100 time steps, and the mean is taken between $t = 60$ and $t = 100$. We present only the mean population size, but similar trends were found for minimal population size. The gray gradient highlights the most efficient conservation strategies for each species and each management frequency (2–15 years). The three species were introduced at $t = 0$ ($N_0 = 50$, $A_0 = 100$, and initial values for *G. pneumonanthe* as in Fig. 1). Parameters are given in Tables 1 and 2. Densities are butterflies/ha, nests/ha, and plants/m².

† Ellipses indicate that there is no effect of the strategies on the species.
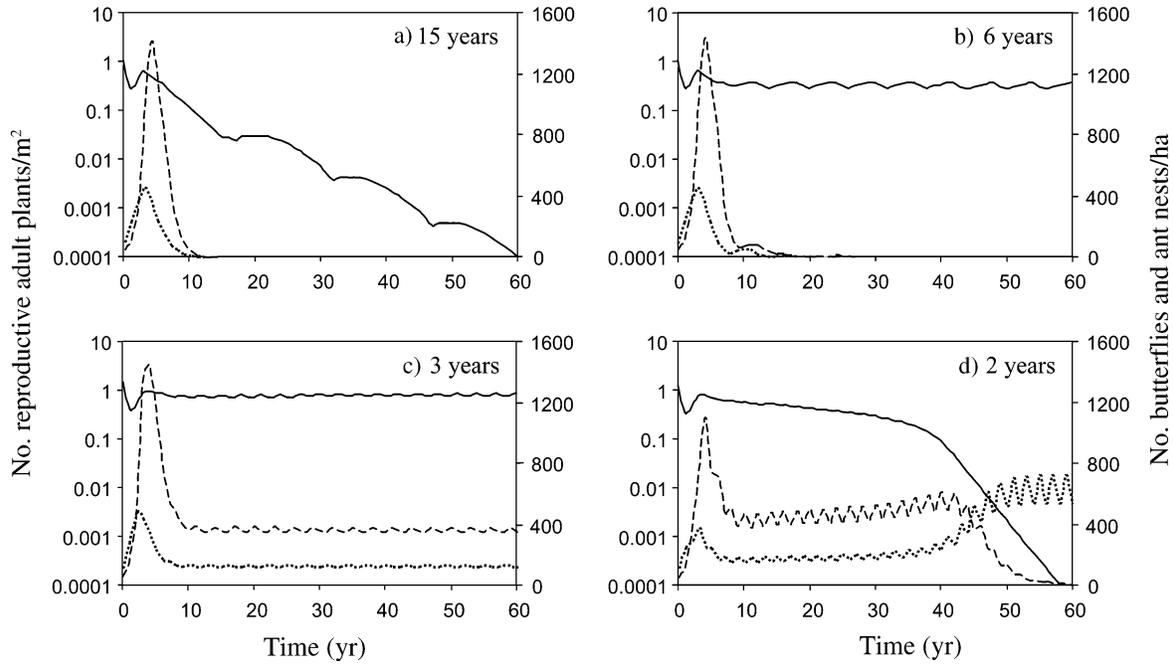
FIG. 4. Population dynamics of reproductive *Gentiana pneumonanthe* (solid line), *Maculinea alcon* (dashed line), and *Myrmica scabrinodis* (dotted line) obtained for four different sod cutting frequencies when 25% of the available habitat is sod-cut (a) every 15 years, (b) every six years, (c) every three years and, (d) every two years. The three species were introduced at $t = 0$ ($N_0 = 50$, $A_0 = 100$, and initial values for *G. pneumonanthe* are as in Fig. 1). Parameters are defined in Tables 1 and 2. Note logarithmic divisions on ordinate scales.
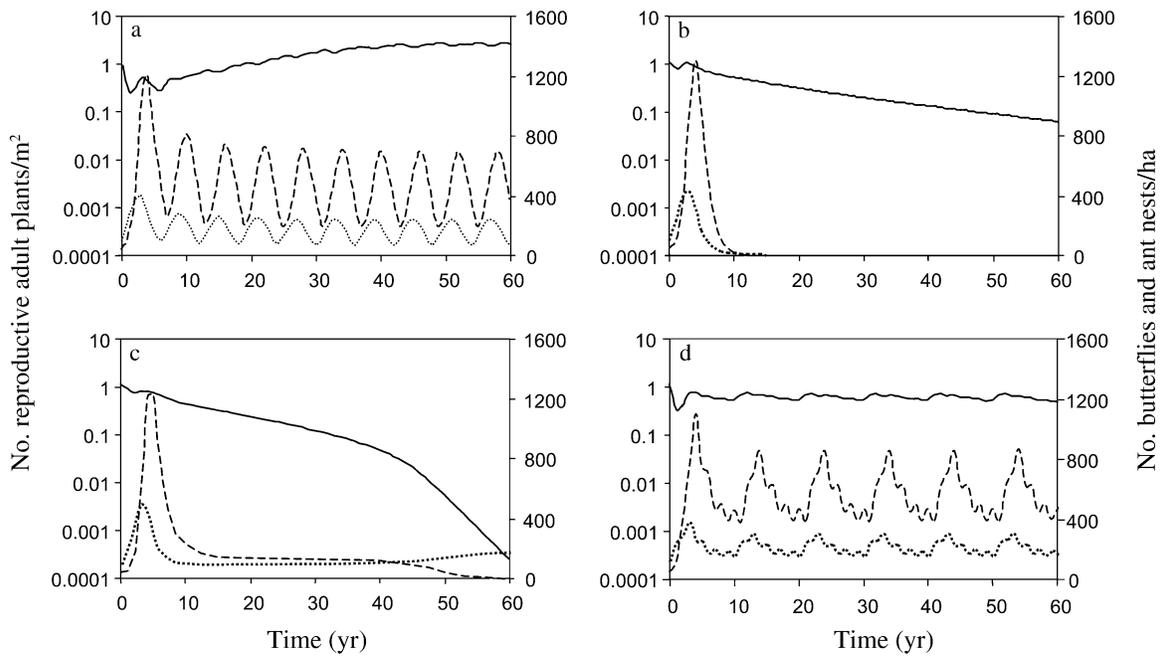

FIG. 5. Population dynamics of reproductive *G. pneumonanthe* (solid line), *M. alcon* (dashed line), and *Myrmica scabrinodis* (dotted line) obtained with (a) burning every six years; with continuous grazing at (b) weak and (c) intermediate intensities; and (d) with mixing sod cutting at 25% every two years and burning every 10 years. The three species were introduced at $t = 0$ ($N_0 = 50$, $A_0 = 100$, and initial values for *G. pneumonanthe* are as in Fig. 1). Parameters are defined in Tables 1 and 2. Note logarithmic divisions on ordinate scales.

SPECIAL FEATURE

PLATE 1. The alcon large blue, *Maculinea alcon*, is an endangered inhabitant of moist Palaearctic heath and grasslands. As well as requiring the rare marsh gentian, its larvae live 1–2 years inside *Myrmica scabrinodis* ant nests. A model of these interactions suggests how all three species can be conserved. Photo credit: J. A. Thomas.

DISCUSSION

Our model generates predictions about the persistence and population sizes of *M. alcon*, *G. pneumonanthe* and *Myrmica scabrinodis*. Despite the likelihood of some site-to-site variation in realized population sizes due to local environmental conditions, the simulations generated such major differences in species' persistence and abundance that comparisons between management regimes are possible. A similar range of densities is recorded from the field: for *G. pneumonanthe* observed population sizes vary between 0.2 and 10 reproductive adults/m², for *Myrmica scabrinodis* between 50 and 1000 nests/ha, and for *M. alcon* between 10 and 1000 individuals/ha (Oostermeijer et al. 1994, Rose et al. 1998, Maes et al. 2004, WallisDeVries 2004; J. A. Thomas, *personal observation*; J. Mercier, *personal communication*).

Extensive survey of 39 wet heathland sites in Belgium by Maes et al. (2004) has shown that *M. alcon* could potentially survive in small habitats with low host plant density as long as the ants were present. It is likely, however, that the populations present in areas with few plants would decline and not persist in the long term without conservation measures. The apparent competition between the plant and the ants should make extinction of the plant even more rapid at sites where the plant is sparse. Unfortunately, data are insufficient to test our predictions about apparent competition. We found that the negative effect of ants on plants occurred only at very high nest densities, suggesting that it is

not likely that this phenomenon will be significant in the field. However, it is important to note that the results presented in Fig. 2b concern systems with relatively high plant population sizes. In other simulations (not shown), we employed lower figures for *G. pneumonanthe* fecundity ($F_{g1} = 2.5$ and $F_{g2} = 1.5$) and found a strong negative effect of the ants on plants starting at 50 ant nests/ha, with extinction of the plants at 400 nests/ha. This suggests that, at sites with low numbers of plants, the intensity of apparent competition between ants and plants will be stronger and can jeopardize the persistence of this community module in the long term.

One of the practical problems posed by the *M. alcon–G. pneumonanthe–Myrmica scabrinodis* module is that the realized niches of the ant and gentian are well separated and overlap only in suboptimal habitat for each species, with the former preferring earlier successional stages, and hence requiring more frequent conservation measures than the latter. *M. alcon* requires certain threshold densities of host ant and gentian to coexist, and occupies a narrow niche midway between the optima for the ants and the plant. The model simulations define a range of conservation options under which *M. alcon* is predicted to persist, including suitable, but suboptimal, regimes for the butterfly that simultaneously generate high populations of flowering gentians: for example, burning patches of heath or grassland every 4–6 years. These options are summarized in Tables 2 and 3. Of the four traditional management techniques that we considered, regular burning produced the high-

est densities of all three species, with *Myrmica sca-brinodis* predominating under a regime of biennial burns and *G. pneumonanthe* flourishing typically under intervals of 3–10 years (on the very nutrient-poor sites, such as United Kingdom heathlands, gentians peak at 10–13 years between burns [Chapman et al. 1989]). Periodic strong grazing produced the second highest densities of ant and butterfly, and acceptable populations of gentians. Historically, both techniques were part of the same process: farmers created a mosaic of small-scale annual burns, with individual patches of heath being burned every 3–10 years (depending on the vigor of dwarf-shrub regrowth) to create a brief flush of ''sweet grass'' for grazing animals. Today, this form of pastoral farming is seldom used, and conservation managers are reluctant to use fire in many regions. We recommend that the inexpensive and controllable technique of regular winter burning be gradually reestablished on Palearctic heathlands.

Sod cutting is an easily controlled technique for sites that are impractical to graze. It is perhaps more suitable for the quick, small-scale restoration of abandoned sites that have lost their populations of *Maculinea alcon*. Like grazing, sod cutting has also been successfully employed on sites containing *Myrmica ruginodis*, using *M. alcon* populations in The Netherlands, although there a combination of grazing and sod cutting on the same site is detrimental (WallisDeVries 2004). Finally, our model predicts that regular mowing can produce spectacular displays of flowering gentians, but results in low, if any, *Myrmica scabrinodis* or *M. alcon* numbers. We have indeed observed mown heath and grassland nature reserves in Europe where the meadow was blue with gentian flowers but which had lost their colonies of *Myrmica* and *M. alcon* (J. A. Thomas and G. W. Elmes, *unpublished data*). Finally, we showed that mixing different strategies leads to the persistence of the entire community module for less conservation effort, in some cases where single conservation actions are insufficient.

It has been shown for the sister species of *M. alcon* (*M. rebeli*) that caterpillars have two growth strategies while parasitizing ant colonies: ~25% of the caterpillars live 10 months before pupating, while ~75% live 22 months (Thomas et al. 1998*a*). It has been suggested that this polymorphism has evolved as a bet-hedging strategy to face environmental uncertainty and competition between caterpillars for resources within ant nests (Thomas et al. 1998*a*; D. Tesar and M. E. Hochberg, *unpublished data*). More recently the same polymorphism has been demonstrated for other species of *Maculinea* including *M. alcon* (Schönrogge et al. 2000). For simplicity we did not include this polymorphism in our model, but we suggest that it would introduce a delay in the density-dependence regulation loop of the butterfly. In some cases, delayed density dependence creates strong overcompensation and unstable dynamics (May et al. 1974). However, in our

case we predict that the polymorphism will homogenize caterpillar densities through time and space, and given the type of competition *M. alcon* caterpillars experience within ant nests (contest competition) it is not likely that the population dynamics will be destabilized. At the same time, it is not clear how this polymorphism will affect the realized population size of the three species of the community module. Preliminary data obtained with the HCET model for *Maculinea rebeli* (Hochberg et al. 1994) have shown that the butterfly population size is smaller when polymorphism is included and that the realized ants population size is higher (D. Tesar and M. E. Hochberg, *unpublished data*). Similar results are expected for *M. alcon*, whose life cycle is very close to that of *M. rebeli*.

We did not include metapopulation dynamics in our model even though it is often considered important for this butterfly's conservation (Wynhoff et al. 1996). WallisDeVries (2004) and Maes et al. (2004) surveyed extinct and occupied *M. alcon* sites in The Netherlands and Flanders, respectively, to analyze the metapopulation structure and habitat quality of sites in which the species persisted. Maes et al. (2004) found that adult dispersal was low and WallisDeVries (2004) found little evidence for metapopulation dynamics. While both these authors (and we ourselves) emphasize the need to reestablish connectivity between populations, appropriate management of remaining and potential sites is a high priority. We therefore focused only on this aspect of within-site habitat quality and management in our model of the *Myrmica scabrinodis* form of *Maculinea alcon*.

Finally, our quantitative analysis has general lessons for the conservation of community modules. Conservation usually implies different sites, based for example on the number of threatened species present in a given area (e.g., see, most recently, Wilson et al. 2005). We suggest that within-area priorities are also important. When more than one species in a target community is endangered, measures for one species may lessen the efficacy of measures for other species (Simberloff 1998). This aspect of conservation science requires further attention. In addition to community-level compromises, in cases where conservation is based on individual species in isolation from one another, our study suggests that conservation measures need to be modified when endangered species interact (see also Ives and Cardinale 2004). For any single species, some kind of priority weighting will be necessary rather than any optimal conservation strategies. Ives and Cardinale (2004) found that strong trophic interactions could mask explicit hierarchies in species sensitivities to environmental perturbations. Our study provides an example of this effect, whereby an endangered plant and its endangered specialist natural enemy are adversely affected by successional dynamics via direct (for the plant) and indirect (for the butterfly) effects. More generally, endangered species may interact via interference

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or exploitative competitive interactions, or may be linked via indirect trophic links (e.g., apparent competition). Some attention should also be given to the community-wide implications of the conservation management of one particular community module, since it is likely that a strategy that promotes one module might be disadvantageous or even disastrous for other endangered species. A variety of factors may be responsible for population endangerment (e.g., Shaw and Hochberg 2001), and we argue that conservation measures, particularly for communities with more than one endangered species, must therefore be formulated on a case by case basis.

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APPENDIX A

A detailed description of the conservation strategies studied is available in ESA's Electronic Data Archive: *Ecological Archives* E086-173-A1.

APPENDIX B

A detailed description of the parameter estimations is available in ESA's Electronic Data Archive: *Ecological Archives* E086-173-A2.

SPECIAL FEATURE