



Population modelling of the spatial interactions between *Maculinea rebeli*, their initial foodplant *Gentiana cruciata* and *Myrmica* ants within a site

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A spatial computer simulation model has been developed to assist our understanding of the ways in which *Maculinea* butterflies depend upon the spatial distribution and abundance of their initial foodplant and their *Myrmica* host ant. It was initially derived for the *Maculinea rebeli*–*Myrmica schencki*–*Gentiana cruciata* system. It relates the population processes of the competing host and other ant species to an underlying gradient of habitat quality and incorporates the impact of adopted *Maculinea* caterpillars on the growth and survival of individual ant nests. The model was initially calibrated for a large site in the Spanish Pyrenees, but has since been successfully tested on 12 French sites and another in Spain. On such sites, with *M. rebeli* present, there is a close relationship between *Maculinea* population density and the density of the early larval foodplant *G. cruciata*. Optimum gentian density is estimated to be about 1500 plants ha⁻¹ on sites with the natural clumping of gentians found. However, any site management which added extra gentians, especially if filling the gaps, is predicted to reduce the *Maculinea* population. Meta-population studies of single species have shown that the size and spatial arrangement of patches of assumed uniformly 'suitable' habitat can influence their population dynamics and persistence. Our modelling suggests that the spatial pattern of 'suitable' habitat of varied quality within a single site can influence the local butterfly population size and perhaps also persistence. Despite being free-ranging over the whole area, the butterfly's dynamics may depend on the arrangement of habitat quality at a finer spatial scale, due to its interactions with ant species possessing narrower habitat niches and more localized dispersal.

Keywords: spatial modelling; habitat heterogeneity; *Maculinea*; *Myrmica*.

Introduction

The decline and local extinction of many populations of butterflies, including *Maculinea*, can be related to changes in the availability and quality of their habitat (Thomas and Morris, 1994; Ae *et al.*, 1996). Where populations still exist within a region, the size, shape and degree of isolation of sites or patches of 'suitable' habitat can have profound effects on the persistence of populations on individual patches and at the regional or metapopulation scale, due to the relatively poor dispersal shown by many butterflies (Thomas *et al.*, 1992). Recent research has led to the development of metapopulation models whereby the probability of local extinction on a patch is often assumed to be propor-

tional to its area, whilst the probability of colonization of an empty patch is determined by its distance from occupied patches and their area (Hanski and Thomas, 1994; Hanski *et al.*, 1995).

Such spatial multi-site (metapopulation) studies have usually assumed, for simplicity, that the landscape is composed of patches of 'suitable' habitat, assumed to be of the same uniform quality, surrounded by areas of 'unsuitable' habitat. However, a species' local population size and chances of persistence on a single patch or site can also depend on the quality of the habitat within the site (Singer, 1972). The loss of 'suitable' habitat within a landscape is often accompanied by a change in habitat quality of many of the remaining patches of 'suitable' habitat due to changes

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in land management practices, such as cessation of grazing or scrub clearance (Thomas, 1991).

The habitat niches occupied by the immature stages of many insects, and especially butterflies, have proved to be narrower than was once thought, and superficially trivial changes in vegetation structure, often associated with altered management, may change the quality of a species' habitat within a site, greatly affecting its intrinsic rate of increase and the carrying capacity of the site (Thomas, 1991).

This paper describes the development and use of a spatial simulation model to help increase understanding of how habitat quality and pattern within a single isolated site may influence the local population dynamics of large blue *Maculinea* butterflies through their interactions with the *Myrmica* ant species on which they depend.

Methods

Hochberg *et al.* (1994) developed a mechanistic spatial model for *Maculinea rebeli*, but this model could, in principle, be adapted for other *Maculinea* species. The biology of *Maculinea rebeli* and its associated species is described extensively elsewhere (e.g. Thomas, 1995; Elmes *et al.*, 1996). The following details are related to the spatial interactions and model. The butterfly oviposits on the flowers of *Gentiana cruciata*, regardless of whether these grow near nests of its host ant species, *Myrmica schencki*, or any other *Myrmica* (Thomas *et al.*, 1989; Elmes *et al.*, 1991a). Thus the distribution of the plant determines the boundaries of a site. After feeding on *G. cruciata* buds for two weeks and reaching their fourth and final instar, caterpillars drop to the ground and await discovery by *Myrmica* workers. Although workers of all the *Myrmica* species present on a site forage beneath gentians within 1.5–2 m of their nest and carry caterpillars back to their nests with equal probability, it is almost exclusively in *M. schencki* (termed the host species) that caterpillars survive to emerge as adults the next summer (Elmes *et al.*, 1991a, b). Inside a nest, *M. rebeli* caterpillars mimic the behaviour of ant grubs and are fed preferentially by the worker ants, experiencing contest competition (1 caterpillar survives per 50 workers) when a colony adopts more caterpillars than it can support (Thomas *et al.*, 1993). *Myrmica* colonies are highly dynamic, with small or disturbed colonies frequently going extinct and vacant nest sites being colonized by buds or offshoots from large neighbouring colonies (Elmes, 1991). *M. rebeli* caterpillars reduce the size of all *Myrmica* colonies which adopt them; increasing colony extinction rates.

However they have less impact on non-host *Myrmica* (*M. rubra*, *M. scabrinodis* and *M. sabuleti*, lumped together and referred to as 'Other' *Myrmica* in the modelling), in whose nests they seldom survive beyond winter. Because the caterpillars from any particular foodplant are likely to be adopted by, and impact on, the same nearby nest each year, the spatial distribution of the foodplant and the relative spatial distribution of the host and 'Other' *Myrmica* species within a site is likely to be important. This is the rationale for the spatially-explicit model of Hochberg *et al.* (1994), hereafter referred to as the HCET model.

The HCET model 'site' consists of a grid of 30×30 cells equal to a total area of 1 ha, with each cell corresponding to the foraging area (ca. 1 m²) of a large *Myrmica* colony and containing at most one ant nest (Fig. 1a). The sloping grassland site at Panticosa in the Spanish Pyrenees, for which the original model was calibrated, contained a physical gradient of habitat types in which gentians grew and over which the butterflies flew, ranging from cool moist (type 1) to hot dry grassland (type 30) (Fig. 1a). Each species of *Myrmica* has a narrower habitat niche than either the gentian or adult butterfly. This was represented by colonies of each ant 'species' (host and 'other') having different intrinsic growth rates and nest capacities according to their position (1–30) along this habitat gradient (Fig. 1b). The model was calibrated for these parameters to give best agreement between the predicted and observed percentages of baits under gentians attracting *M. schencki* and other *Myrmica* in each of the three major habitat types (Table 1). These field observations on baiting were independent of the field estimate of adult population size used to assess the model (see results). The probabilities of a colony adopting nearby caterpillars, going extinct or budding into a vacant neighbouring nest are all dependent on its current size (see Hochberg *et al.* (1994) for further details; see Appendix for corrections to typographical errors in the model specification in Hochberg *et al.*, (1994)).

In each model simulation a constant population of gentians is non-randomly distributed according to plant parameters estimated in the field. All model equations and parameter values were as in Hochberg *et al.* (1994), except the probability of budding which was as in Clarke *et al.* (1997). All results are based on the mean values over the last 10 years of 30 simulation runs, each of 120 years duration with one butterfly introduced in year 50.

The HCET model was tested by applying it to 13 other sites (12 from the French Alps and a second from the Spanish Pyrenees) where *M. rebeli* was present. The

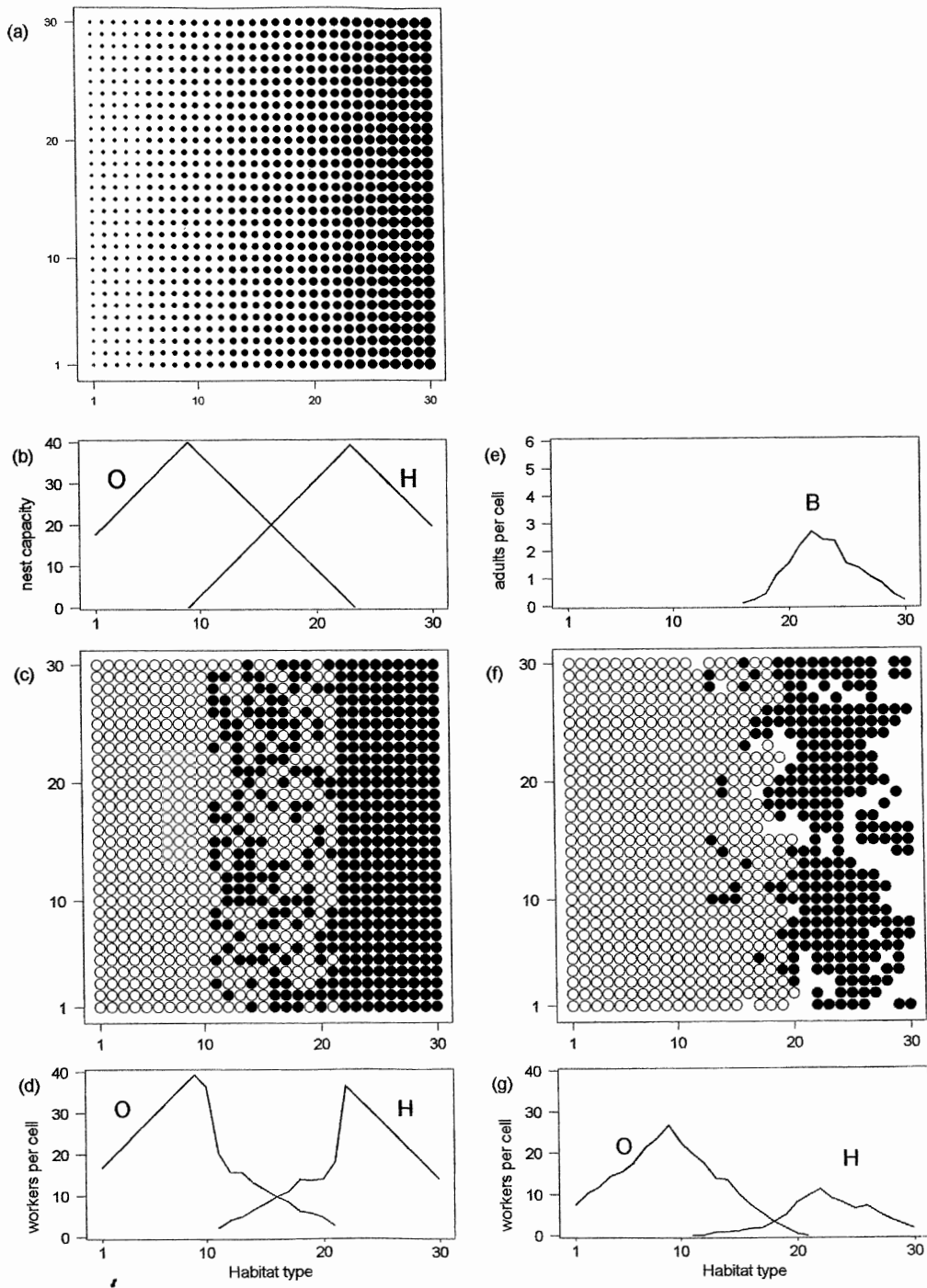


Figure 1. (a) Model I ha site comprising a grid of 30×30 cells with cell habitat-type arranged as a linear gradient ranging from cool and wet (smallest circles, type 1) to hot and dry (largest circles, type 30). (b) The size of host ant *Myrmica schencki* (H) and other non-host *Myrmica* (O) colony supported per cell (expressed in butterfly equivalents (1 butterfly = 50 workers)) in the absence of interspecific competition at each habitat type. (c) Typical distribution of host (solid circles) and 'Other' (open circles) *Myrmica* colonies; and (d) average size of colonies per cell in each habitat type when the butterfly is absent. (f), (g) are the equivalent colony distribution and colony size when the butterfly is present; (e) average number of butterflies (B) produced per cell. (d), (e) and (g) show the means of the last 10 years of 50 simulation runs, each of 120 years duration with one butterfly introduced in year 50.



Table 1. The distribution of gentians and *Myrmica* ant species in the three major habitat types occurring on the Panticosa site; the HCET model was fitted to give best agreement with the observed percentages of baits under gentians attracting *M. schencki* and other *Myrmica*

Major habitat type	Habitat gradient range	Total gentians baited (n)	% gentians attracting <i>M. schencki</i>		% gentians attracting other <i>Myrmica</i>	
			Observed	Model fit	Observed	Model fit
Cool-damp	1-8	26	0	0	85	90
Intermediate	9-22	52	15	16	62	59
Hot-dry	23-30	22	27	26	0	0

test site areas varied from 0.06 to 0.85 ha. At each site the following seven site-specific parameters were estimated: the density, degree of clumping and growth form (tillers per gentian and flower buds per tiller), together with the degree of clumping of eggs on the gentians and the relative density of gentians in the three major habitat types. See Elmes *et al.* (1996) for further details.

Results and discussion

In the absence of the butterfly on a site, the *Myrmica* species have habitat types where each is dominant and other areas where their niches overlap resulting in competition and a dynamic co-existence between the species (Fig. 1c, d). In all situations, the impact of the butterfly is to reduce the number and size of *M. schencki* nests. 'Other' *Myrmica* colonies are also reduced in size, but they may become more widespread by taking over nest sites vacated by *M. schencki* in the intermediate types of habitat where the two 'species' compete (Fig. 1f, g). Thus the presence of the butterfly modifies the spatial distribution of the competing *Myrmica* species. The range of habitat types within which the *Maculinea* caterpillars survive to maturity within nests is even narrower (Fig. 1e), highlighting that the whole site, as delimited by the distribution of the foodplant, is of very variable habitat quality for the butterfly population. The realized niche of the host ant decreases with the impact of the butterfly, especially in the intermediate types of habitat where it is now at a competitive disadvantage to less impacted non-host *Myrmica*.

The HCET model predicted an average butterfly population of 449 (with between simulation standard deviation of 41) for the Panticosa site, for which the best available field estimate was 598 ha⁻¹ (Hochberg *et al.*, 1994). This is a good agreement for a mechanistic population model.

How well does the HCET model apply to other *M. rebeli* sites?

When applied to the 13 test sites using the site-specific parameter values, the HCET model gave a very good general prediction of the egg density on the sites: the proportion of total variation (F_{mod}) in observed log egg densities explained by the model was 86% (Fig. 2a). Surprisingly, the model predictions were even better ($F_{mod} = 91%$) using only the site-specific gentian density together with the average values of the other parameters (Elmes *et al.*, 1996). This may be because little between-site variation exists in egg clumping and gentian characteristics (e.g. flower and tiller number) when averaged over the timespan simulated by the model; such that any increase in accuracy of predictions obtained by using site-specific parameter values is outweighed by errors introduced through estimating each parameter from a sample in just one year of that site.

Influence of gentian density and distribution

This suggests that if *M. rebeli* are known to be present at a site, the typical density (E) of their eggs can be estimated by measuring the average density (G) of *Gentiana cruciata* over the site and using the following log-log regression relationship:

$$\log_{10} E = 1.59 + 0.965 \log_{10} G \tag{1}$$

based on the 13 test sites (correlation $r = 0.955$, $p < 0.001$; Fig. 2b).

This close relationship between gentian and butterfly densities was unexpected because *M. rebeli* lives just 4% of its life on *G. cruciata* and gains < 2% of its biomass from eating it. Moreover, its caterpillars suffer relatively small mortalities on gentians (< 20% of total K), with the heaviest, density-dependent mortalities occurring in ant nests. For gentian densities of less than about 1000 gentians ha⁻¹, equation 1 can be approximated by the equation $egg\ density = 33 \times gentian\ density$,

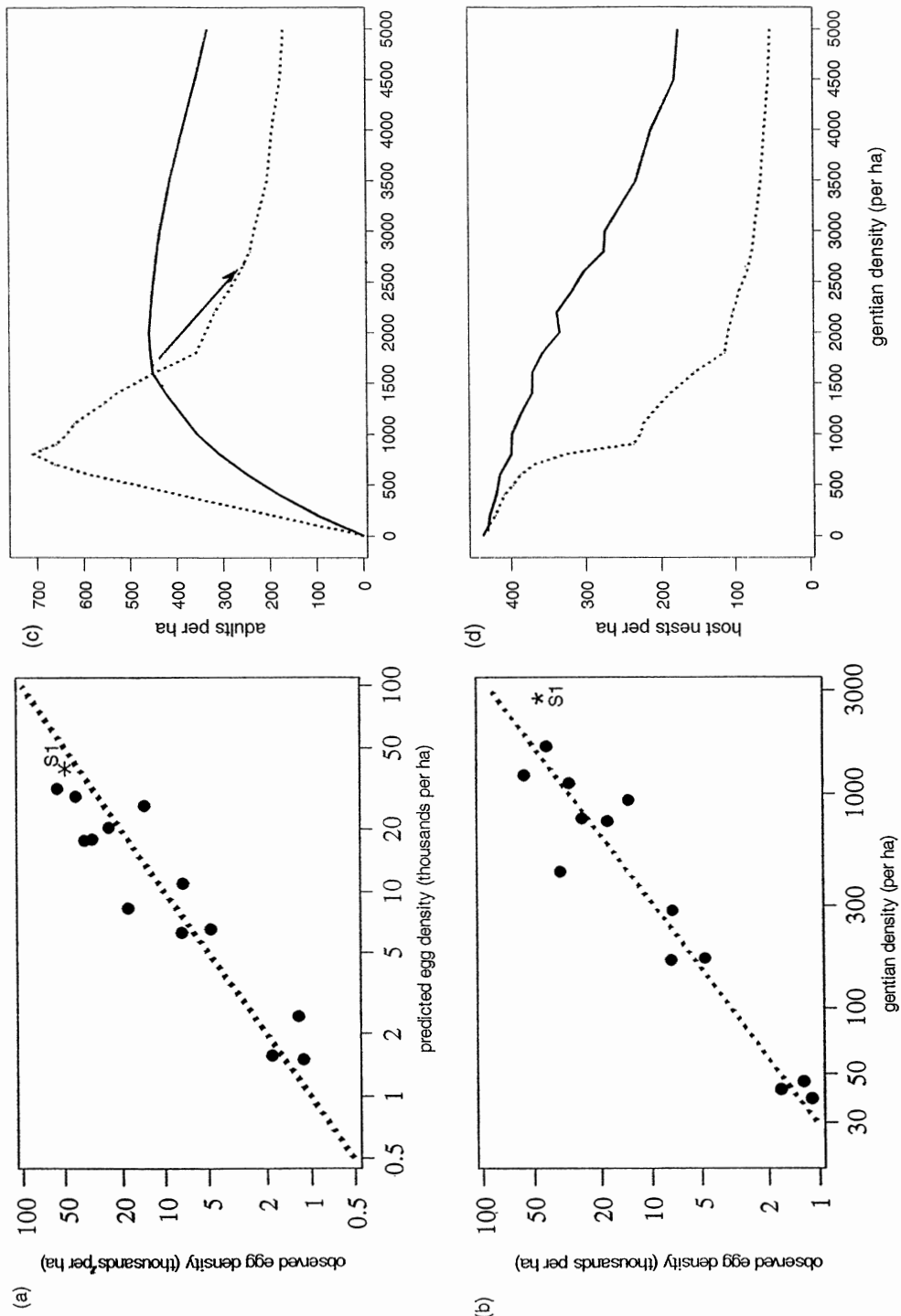


Figure 2. (a) The observed *Maculinea rebeli* egg densities (thousands ha^{-1}) at the Panticoso site (S1) and the 13 test sites plotted against the prediction from the HCET model using seven site-specific parameters; the dotted line indicates the expected (1 : 1) relationship if the model was a perfect predictor of egg density. (b) Observed egg density plotted against *Gentiana cruciata* density for the same 14 sites; the dotted line denotes their observed linear regression relationship (Equation 1). Effects of *G. cruciata* density on (c) *M. rebeli* butterfly density (solid line) and (d) density of host ant *Myrmica schencki* nests predicted from the standard HCET model but assuming either gentian clumping Equation 2 holds (solid line), or that the gentians are uniformly distributed across the site (dotted line). Arrow in (c) denotes model prediction of effect of adding 1000 more gentians to fill in the gaps on a naturally clumped 1 ha site with 1700 gentians.



which indicates, as a rule of thumb, that one adult *M. rebeli* can be supported by every 2–3 gentian plants ha^{-1} , on sites with the butterfly.

In the HCET model, the natural degree of clumping of gentians at each site was measured from the negative binomial parameter ($1/K_G$) estimated from the frequency distribution of gentians in a sample of 3×3 m quadrats (i.e. model cell size). There was a strong correlation ($r = 0.92$, $n = 8$ sites, $p < 0.001$) between K_G and gentian density (D), described by the regression relationship:

$$K_G = 0.000701 \times D \quad (2)$$

and indicating that gentians tend to be more aggregated on sites with lower gentian densities.

Although the HCET model appears to be a good predictor of *M. rebeli* population sizes on other sites (Fig. 2a), if equally good predictions of butterfly egg numbers can be made by using a simple regression relationship with just the foodplant density (Fig. 2b), is it worthwhile to develop this complex model? We believe that it is. The Panticosa site for which the HCET model was originally developed and calibrated had a very high gentian density (2672 ha^{-1}) compared to all the subsequent test sites (range 38–1645 gentians ha^{-1}) (Fig. 2b). Repeated runs of the HCET model varying only the gentian density and its related degree of clumping (equation 2) suggest that butterfly population size only increases linearly with gentian density on sites with < 1000 gentian ha^{-1} (Fig. 2c, solid line). Moreover, it predicts that maximum population size occurs with ca 1500 gentians ha^{-1} . Beyond this, the HCET model predicts that higher gentian densities lead to a decline in the overall capacity of *M. schencki* to rear the butterfly, because most of its nests are now near gentians and repeatedly adopt caterpillars, making them prone to being supplanted by other *Myrmica* species.

The above relationships (Equation 1 and solid line in Fig. 2c) are both based on the 'natural' degrees of gentian clumping found on our test sites. The HCET model predicts that the degree of clumping of gentians is also important; if gentians were evenly distributed across a site then the impact on *M. schencki* is greater (Fig. 2d, dotted line) and the optimum gentian density for the butterfly is far less, at ca 800 gentians ha^{-1} (Fig. 2c, dotted line). All increases in gentian density tend to lead to a reduction in both the density and average size of *M. schencki* nests, irrespective of the degree of gentian clumping (Fig. 2d). However, when gentians are evenly distributed throughout the site, all nests tend to be impacted to roughly the same extent (any remaining variability being due to stochastic variation in gentian

growth form and egg distribution); at gentian densities $> 900 \text{ ha}^{-1}$ no nest escapes parasitism. Thus the total sustainable capacity of *M. schencki* to support *M. rebeli* on a site is used up most 'efficiently' (i.e. with less gentians) by the butterfly when the foodplants are evenly distributed. The maximum achievable butterfly population (ca 700 ha^{-1}) is also predicted to be greater (Fig. 2c). However, because few, if any, host nests are safe from impact to act as 'refuge' areas for the host ant species, further increases in gentian density (evenly across the site) are predicted to result in over-exploitation of the butterfly's ant resource, leading to dramatic falls in the density of host-ant nests and corresponding falls in the butterfly population.

What are the implications for conservation management? It is quite understandable for a site manager to think that adding extra foodplants for the early larval instars would be beneficial or, at least, could not be detrimental. However, our model predicts otherwise. As an example, a conservation manager with a 1 ha site with 1700 gentians and around 400–500 butterflies would interpret, from the simple regression Equation 1, that adding, say, 1000 new plants to fill in the gaps between existing plants would be expected to increase and roughly double a *M. rebeli* population. The HCET model predicts that it would have the opposite effect (see arrow in Fig. 2c).

Effects of spatial pattern of habitat types within a site

The HCET model (Hochberg *et al.*, 1994) was based on a real smoothly sloping grassland site containing heterogeneous habitat, ranging from cool-moist to hot-dry ground, that was arranged as a simple linear habitat gradient. The effect of different spatial patterns of the same variation in habitat types within a site was investigated by re-arranging the 30 cells of each of the 30 types (Fig. 1a) to form 1 ha model sites composed of 1, 2, 4, 8, 16, 32 and 64 hot/dry 'hills' using the algorithm developed by Clarke *et al.* (1997); greatest habitat spatial heterogeneity or 'ruggedness' was obtained by distributing the cells randomly (Fig. 3a–c). This generates a wide range of realistic patterns of habitat quality within a site, including the reverse patterns of 'damp hollows' (e.g. small bogs) (Fig. 3d). Standard HCET model simulations for each type of site suggest that *M. rebeli* population size will be up to 35% lower on very 'rugged' sites, even though the area of each habitat type is unchanged (Fig. 3e). Adding annual density-independent nest mortality (e.g. by cattle trampling), a factor previously ignored, increases the effects of habitat ruggedness, such that small sites (< 0.25 ha)

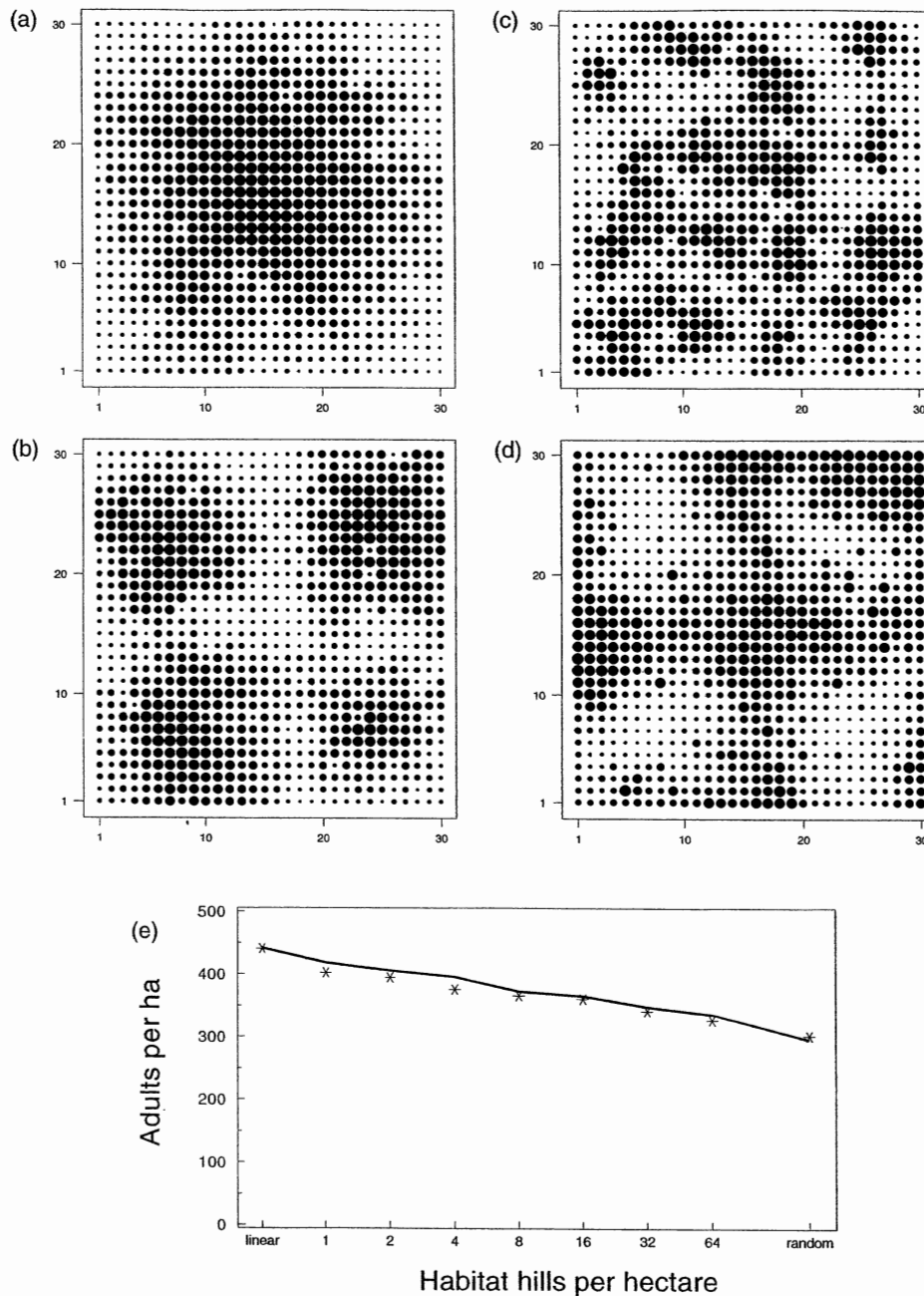


Figure 3. Examples of spatial ruggedness of habitat quality within sites. Notional 1 ha sites each comprising a grid of 30×30 cells, with 30 cells of each habitat type ranging from cool and wet (smallest circles, type 1) to hot and dry (largest circles, type 30), exactly as for the linear gradient site of Fig. 1a, but now arranged as (a) one dry 'hill', (b) four dry 'hills', (c) 16 dry 'hills' and (d) four damp 'hollows'. (e) Effects of habitat spatial ruggedness on the average butterfly abundance predicted by the standard HCET model on 1 ha sites. The ruggedness of sites varied from the simple linear gradient base-line (linear), through an increasing number of hot/dry hilltops (1, 2, 4, 8, 16, 32, 64 ha^{-1}); greatest ruggedness was obtained by distributing the cells of habitat randomly. Results show the means of the last 10 years of 50 simulation runs, each of 120 years duration with one butterfly introduced in year 50. Stars denote the results for sites with habitat arranged to give the equivalent density of 'damp hollows' ha^{-1} .



may be far more prone to local extinction if the habitat is spatially heterogeneous (Clarke *et al.*, 1997). Despite being free-ranging over the whole gentian site, the butterfly's dynamics may depend on the arrangement of habitat quality at a finer spatial scale, due to its interactions with ant species possessing narrower niches and more localized dispersal.

These predictions have yet to be confirmed in the field, but observations around our main study sites (near Panticosa in the Pyrenees and Gap in the Alps) suggest the simulated microhabitat patterns are representative of real sites, at least to the level of 64 'hills' ha⁻¹. Unfortunately, these are unsuitable places to test these spatial predictions as they are the European strongholds of *M. rebeli*; several sites exist in close proximity in each region, and all experience frequent immigrations of adults, negating the reduced population levels and possible local extinctions we predict for isolated sites with rugged habitat. We stress that we are not suggesting that *Maculinea* species persist better on sites with habitat that is uniform in quality, rather than for a given range of habitat types within sites, their chances of persisting may be greater on sites where the spatial distribution of the habitat is least rugged, especially if the sites are small and isolated. This is the opposite to what most conservationists would intuitively have guessed when choosing between the otherwise identical sites represented by Figs 1a and 3c. The prediction is a feature of the very localized (successful) dispersal of the ant colonies within an isolated site combined with the competition between the host and other ant species. If confirmed, this prediction may become increasingly important when sites are selected for conservation because, as more sites are destroyed, the remaining populations are likely to become increasingly restricted to solitary fragments, even in current strongholds.

Other applications of the spatial-explicit model

By using a cruder classification (e.g. 5–6 classes) of habitat type, or perhaps replacing it by a temperature gradient and using 'field recorders' of (near) surface temperature throughout a site, it would be feasible to produce a habitat map for a particular field site to use within the model. The effect of losing particular parts of the site could then be assessed; the implications would be expected to depend on the quality of the lost habitat and not just its area.

The development of the spatial HCET model has enabled us to integrate and synthesize our current knowledge of how the *Maculinea*–*Myrmica* communi-

ties interact and co-exist. It also highlights those aspects where the population processes and parameter values are not well known, such as the dynamics of whole ant colonies in the processes of abandoning nest sites when under stress or subdividing and spreading into vacant nearby nest sites. Following unexpected predictions made from the HCET model, Thomas *et al.* (in press) have confirmed that there is apparent competition between the host-ant species and the early larval foodplant in the field, which indicates that the adoption of caterpillars has a considerable impact on ant colony size, and probably survival, the following year. Thus understanding the ant colony dynamics is important.

It is remarkable that the HCET model, developed at one very large site with a gentian density higher than that found on any other site, and higher than the optimum for the butterfly predicted by the model, should still predict the *M. rebeli* population density so well for a range of other sites. One reason is that *M. rebeli* populations appear to be remarkably stable in the short/medium term, probably due to the way they compete by contest within the ants' nests (Thomas *et al.*, 1993). Other *Maculinea* species, such as *M. arion*, which predate upon the ant-brood and are hence subject to scramble-type competition, are expected to have more volatile population densities, to be more prone to over-exploitation, and consequently more susceptible to local extinction. Our next stage is to generalize the model to other *Maculinea* species.

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Appendix

Corrections to the model specification given in Hochberg *et al.* (1994): Table 2: (i) maximum size of nest for disbandment to occur (Z_T) should be 4 not 8; (ii) intercept in maximum yearly reproductive rate of other *Myrmica* (b_x) should be 1.35 not 2.61.

Equation 8 should be:

$$\hat{P}_{ij}[t] = \text{minimum of } \{P_{ij}[t] \text{ and trunc } ((1 - \alpha) \hat{Z}_{ij}[t + 1])\}$$

Equation 9a should be:

$$Z_{ij}[t + 1] = \hat{Z}_{ij}[t + 1] - \text{minimum of } \{P_{ij}[t] \text{ and } (1 - \alpha)\hat{Z}_{ij}[t + 1]\}$$

Equation 9b should be:

$$Z_{ij}[t + 1] = \hat{Z}_{ij}[t + 1] - \mu \times \text{minimum of } \{P_{ij}[t] \text{ and } (1 - \alpha)\hat{Z}_{ij}[t + 1]\}$$

The correct parameter values and equations were used in both Hochberg *et al.* (1994) and this paper.